



## Lateral asymmetry of eye use in *Octopus vulgaris*

RUTH A. BYRNE, MICHAEL KUBA & ULRIKE GRIEBEL

Konrad Lorenz Institute for Evolution and Cognition Research

(Received 7 June 2001; Initial acceptance 24 July 2001;  
final acceptance 1 March 2002; MS. number: 6935R)

The lateralization of sensory and motor functions has been recently demonstrated in various groups of vertebrates. We examined lateral asymmetry of eye use in *Octopus vulgaris* by behavioural methods. *Octopus vulgaris* uses monocular vision almost exclusively and can move its eyes independently. The amount of binocular vision is small because the eyes are on the sides of the head. We tested eight octopuses in two conditions (one with and one without moving stimuli) where the use of the eye for frontal vision could be determined unequivocally. Data were recorded on videotape. All animals showed a preference for one eye (five left, three right). There was no correlation between eye use and the animal's direction of movement. Pigmentation of the ventral side of the arms tended to be most intense on the side of the preferred eye and the body was most pigmented on the side of the eye currently in use. We found no sex differences for visual lateralization. Pigmentation of the ventral side of the arms was lighter in females than in males.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

Hemispheric specialization of the brain and behavioural asymmetries were originally regarded as a unique, human trait associated with handedness, language and higher cognitive abilities. In the last three decades, however, studies have shown we share brain lateralization with many vertebrate species (reviewed in Hiscock & Kinsbourne 1995; Güntürkün 1997; Bisazza et al. 1998; Springer & Deutsch 1998; Vallortigara et al. 1999; Vallortigara 2000). Models, such as that of avian visual lateralization, are beginning to provide insights into the neuronal mechanisms of cerebral asymmetries (Güntürkün 1997). According to Bradshaw & Rogers (1993) the evolution of brain lateralization is likely to have predated birds and mammals. Evidence for this hypothesis has been reported in amphibians and fish (Bisazza et al. 1996a,b, 1998). Nevertheless, visual brain lateralization is thought to have evolved only in vertebrates. The presence of structural asymmetries is also well documented for other phyla, especially for invertebrates (reviewed in Neville 1976; Babcock & Robinson 1989; Bradshaw & Rogers 1993; Palmer 1996). To date, however, no one has studied behavioural asymmetries in invertebrates.

A brain is considered asymmetrical or lateralized if one side (hemisphere or other brain region) is structurally different from the other or performs a different set of functions (Bisazza et al. 1998). Several authors (Bradshaw & Rogers 1993; Güntürkün 1997; Bisazza et al. 1998;

Vallortigara et al. 1999) have suggested that the functional significance of lateralization may be to prevent conflicts of response to the visual input of two laterally placed, largely monocular, eyes.

In vertebrates, asymmetrical visual input processing has been extensively studied in birds (reviewed in Güntürkün 1997; Rogers 2000). The majority of birds have laterally placed eyes with only a small degree of binocular vision in the frontal field. Birds frequently use their two eyes independently to scan the environment. So each eye is able to examine different portions of the visual environment even in the binocular fields. Basically, each eye acts as an independent unit, with most information from each of the two visual fields being processed separately. In this condition, hemispheric specialization may have the important function of preventing conflicting responses elicited by stimuli perceived simultaneously in two monocular visual fields, each demanding a different response. If one hemisphere is dominant in the control of a certain behaviour, then conflicts of response would be avoided by having a lateralized brain. According to Rogers (2000), a lateralized animal has enhanced skill performance and faster reaction time than a non-lateralized animal, resulting in a fitness advantage to the individual.

Octopods live in heterogeneous shelf habitats. Like most cephalopods, they are voracious and mobile predators with highly developed sense organs that rival the complexity found in equivalent vertebrate sense organs. Fish, crustaceans and molluscs, including cephalopods and members of their own species, are the

Correspondence: R. A. Byrne, Adolf-Lorenz-Gasse 2, Altenberg a. d. Donau 3422, Austria (email: [ruth.byrne@kla.univie.ac.at](mailto:ruth.byrne@kla.univie.ac.at)).

preferred prey. The hunting mode of the cephalopod varies within and between species from ambushing and luring to stalking, pursuing and hunting in disguise. Such a predatory lifestyle requires highly effective sense organs and an elaborate nervous system (reviewed in Wells 1978; Abbott et al. 1995; Budelmann 1995; Hanlon & Messenger 1998).

Laboratory experiments have shown that octopods can learn quickly, even by vertebrate standards, and show flexible and adaptive behaviour in many situations (Hanlon & Messenger 1998). *Octopus vulgaris* is therefore an ideal outgroup model to compare with vertebrate behavioural asymmetry.

We present the first behavioural evidence for asymmetrical eye use in *O. vulgaris*. This species is able to make a variety of visual discriminations and its visual abilities seem to be comparable to those of many vertebrates (reviewed in Sanders 1975; Wells 1978; Messenger 1981, 1991). Octopuses can be trained to distinguish between shapes that differ in form, size, brightness, orientation and plane of polarization, but not in colour (Wells 1978; Messenger 1981, 1991; Shashar & Cronin 1996).

*Octopus vulgaris* uses monocular vision almost exclusively when looking at objects and during attack (Muntz 1963). We therefore sought a behaviour or situation where *O. vulgaris* would use monocular vision in such a way that an observer could easily determine which eye the octopus used to view the frontal visual field. *Octopus vulgaris* kept in a tank spend much time sitting at the front glass screen, viewing the scene in front of the tank almost exclusively with either the left or the right eye and only occasionally with both eyes. We filmed subjects as they were presented with moving stimuli to attract them to the front screen. As a control, we filmed the same animals without these visual stimuli. We predicted that the degree of lateralization of eye use would not differ between the experimental condition and the control but that the animals would spend more time attached to the front screen with a stimulus present.

Octopuses, like most cephalopods, possess a sophisticated chromatophore system in their skin. This is used to produce a variety of body patterns for cryptic and communication purposes (Boycott 1961; Chichery & Chanelet 1976; Dubas et al. 1986; Packard 1995). Octopods mirror their background in colour and texture using optical information (Kühn 1950; reviewed in Hanlon & Messenger 1998). We therefore also investigated the extent to which body pattern production is related to differential eye use or by the animal's direction of movement. Based on Ferguson et al.'s (1994) results on countershading in *Sepia officinalis*, we predicted that the pigmentation on the ventral side of the arms would be correlated with eye use in octopuses.

## METHODS

### Subjects

We used eight subadult *O. vulgaris* (four females, four males) collected in the Mediterranean Sea, two from

Corse, France (Stareso, Calvi) and six from Naples, Italy (Stazione Zoologica di Napoli). Mantle lengths were from 5 to 9 cm. All subjects were ca. 6 months old when they were brought to our laboratory, where they stayed for the rest of their lives, which ranged from a few months to over a year. Six of the eight animals died of old age and were fixed for further study. Two animals mated; as in the field, the male died after mating and the female died after guarding her eggs.

### Maintenance

The octopuses were held individually in glass tanks (1.0 × 0.6 m and 0.5 m high) that were part of two closed-circulation systems of 1700 and 2700 litres of artificial sea water with a turnover rate of 24 times/day. The tank water was filtered with protein skimmers, passive filters, UV-filters and denitrification tanks. Additional aeration in each tank produced a weak current. Water temperature was kept at ca. 16°C in winter and 22°C in summer. The backs and sides of the tanks were insulated by polystyrene sheets. Subjects were kept on a 12:12 h light:dark regime, with lights on at 0800 hours. We used artificial light (neon tubes with a daylight emission spectrum).

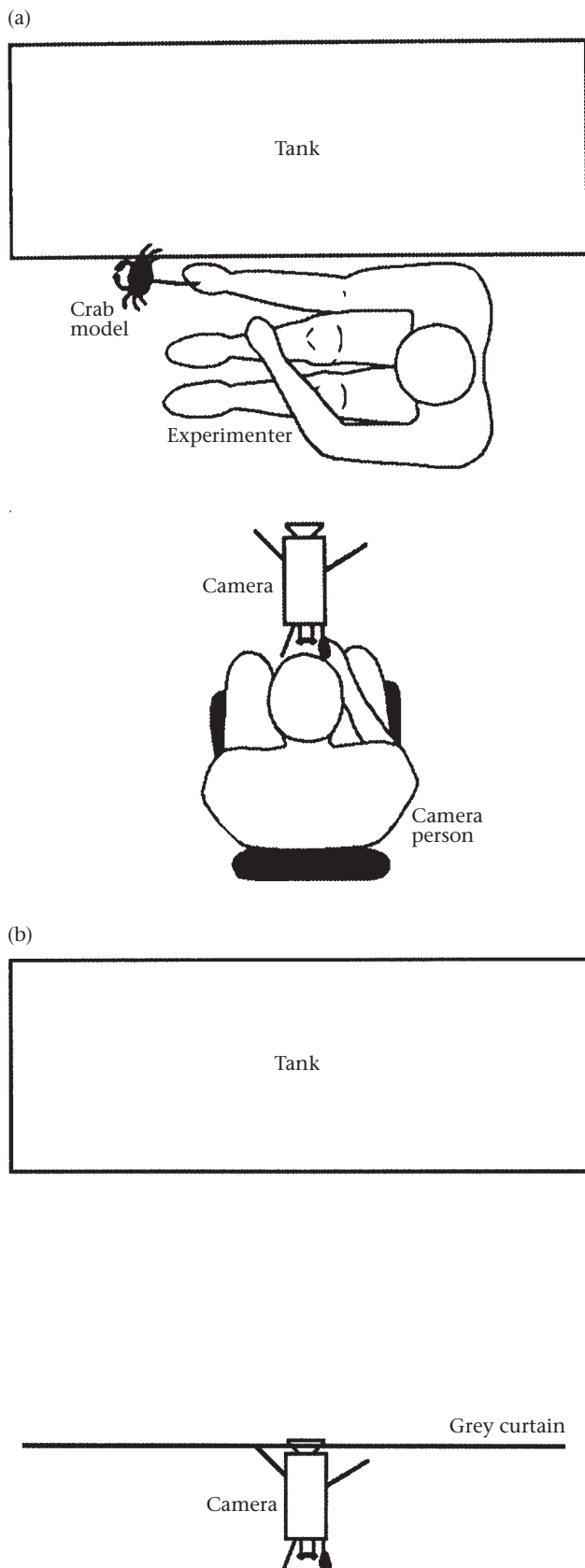
Since Dickel et al. (2000) have shown in cuttlefish that an enriched environment positively affects not only growth rate, but also the acquisition and retention of learning tasks, we provided the octopuses with a semi-natural environment. The tanks contained a sandy bottom, many small rocks and some large rocks with epigrowth, which provided building material for dens and shelters. An escape-proof Plexiglas lid was used to cover the tanks. The animals were fed ad libitum with live mussels, live and dead shrimp, and dead crabs and fish. It is important to feed the animals some live prey to provide all necessary nutrients. Subjects killed and ate prey as soon as they found it.

Pilot observations showed that the subjects were most active during the late afternoon. Therefore, all experimental sessions took place between 1600 and 2000 hours, after which we fed the subjects. All sessions were recorded with a digital video camera (Sony DVX 1000).

### Experimental Conditions

We observed that when a person entered the keeping facility, the octopuses immediately became active and approached the front glass screen, attaching themselves to it and looking out of the tank between two of their arms, most of the time using only one of their eyes. We used this behaviour to monitor the eye use of the octopuses.

We positioned the video camera in front of the tank a few minutes before the start of the experiment. One person filmed the movement of the animal (Fig. 1a). To attract the subject to the front of the tank, a second person sat on the floor between the camera and the tank, without being in the camera's line of sight, and moved a life-sized plastic crab model (resembling *Pilumnus* sp., ca. 7.5 cm) on a transparent Plexiglas stick along the front



of the tank. Five positions that were equidistant to each other were designated along the length of the tank. The crab was held at each position for 3 min. The sequence of the positions followed a restricted randomness pattern, so that the time at each of the five positions was the same over 1 h. Each octopus was filmed for 1 h per day. We filmed for a total of 5 h (sessions) for each subject, with an interval of at least 4 days between sessions.

As a control, we filmed additional sessions with the camera hidden behind a grey curtain with an opening for the camera lens (Fig. 1b). These sessions were randomly filmed before, between and after the experimental sessions. Since we found large individual differences in time of attachment to the front of the tank, we took the average time of 1.5 h for each octopus in the control session. Thus each octopus was filmed for 1 h each day until a minimum of 1.5 h of attachment to the front of the tank were available for analysis.

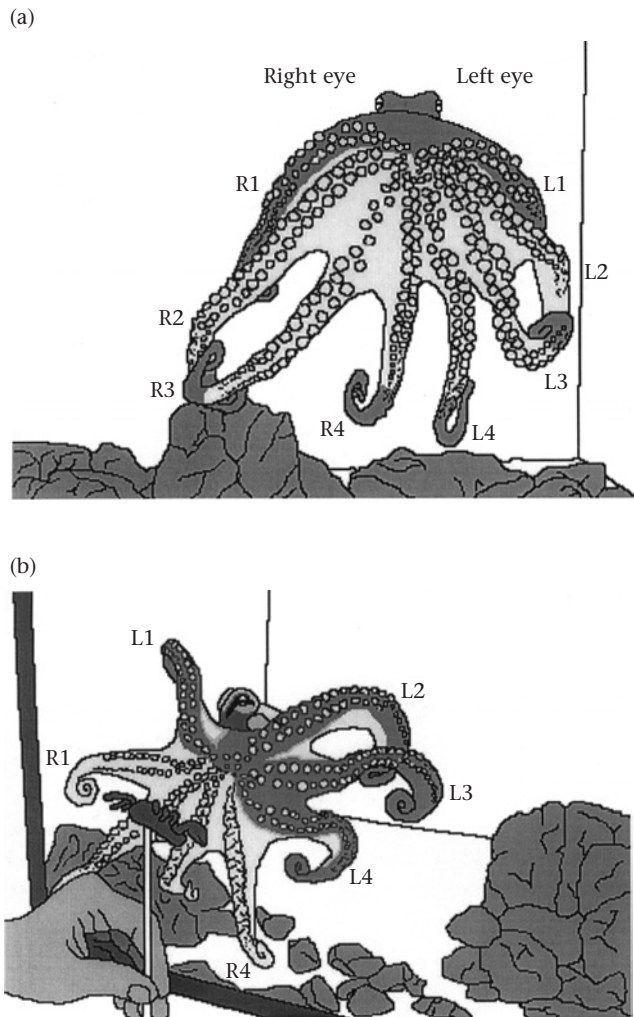
The total period of testing per octopus was 1–3.5 months. To avoid position effects of the keeping tanks, we switched the majority of the octopuses between tanks over the study period. Two animals were filmed successively in the same tank but showed opposite lateral eye use.

### Analysis

For the video analysis, we analysed single frames every 10 s. We used only those frames in which the octopus was attached to the front of the tank, since this was the only position where we could determine with which eye it was looking out of the tank. Of these we used only those where at least one eye was visible. We also omitted scenes in which the animals were resting or asleep. These phases were easily recognizable because the octopus rarely moved, the pigmentation was lighter than usual, the pupils were narrower, and the animal did not react to the crab model or to other movements. Lateral parameters were taken from the animal's point of view. We coded each subject's arms on each side, L1–L4 for the left side of the octopus from front to back, and R1–R4 for the right side.

Each video frame was viewed for the following parameters (Fig. 2): (1) eye(s) used to look out of the tank (right, left, both/binocular); (2) direction of movement of the octopus along the front of the tank (left, right, no movement); (3) arm spread: the arms between which the animal was looking (central arm spread: between L1 and R1; lateral arm spreads between either L1 and L2 or R1 and R2; other arm spreads did not occur for anatomical reasons); and (4) pigmentation of the ventral side of the arms: pigmentation was recorded for each arm, as either dark or light.

**Figure 1.** (a) The set-up for experimental sessions. The octopus was filmed with both the camera person and the experimenter visible to the octopus. The experimenter moved a plastic crab along the front of the tank to attract the subject's attention. (b) For the control, the octopus was filmed without moving stimuli. The camera was hidden behind a grey curtain.



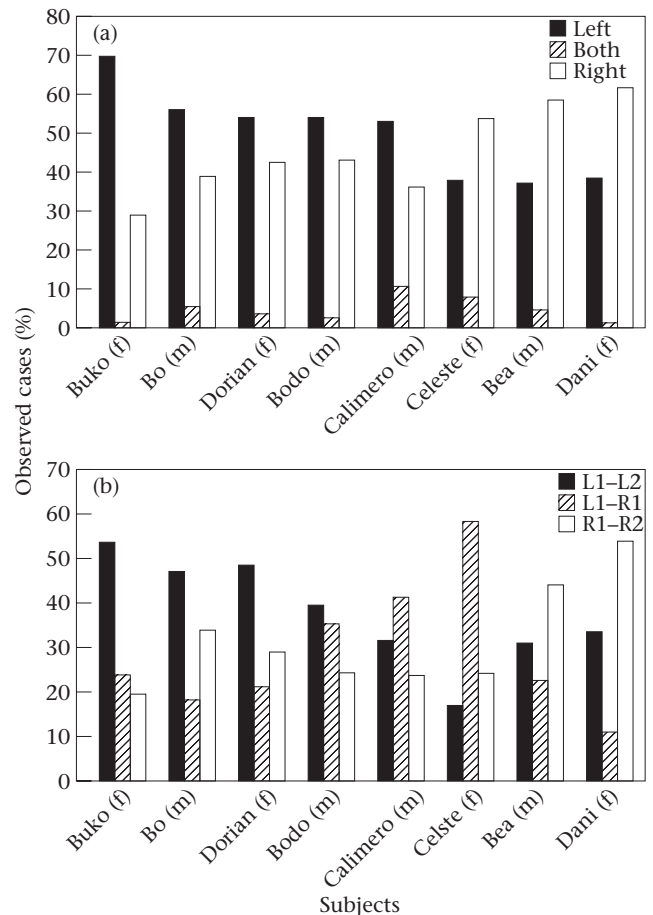
**Figure 2.** (a) Typical binocular eye use position with central arm spread (L1–R1); the pigmentation is darker on arms L1 and R1 than on the rest of the body. (b) Typical monocular eye use position (left eye) with left lateral arm spread (L1–L2) and dark pigmentation on the left side of the body (L1–L2–L3–L4).

Since we investigated the asymmetry of eye use at the individual level, we used chi-square tests against equal distribution for every subject individually. Sample sizes given in the results refer to data points for the two parameters compared in each calculation. Eye use in relation to pigmentation was calculated with a two-tailed Wilcoxon test. To calculate the difference in percentages of eye use between the experimental and control set-ups, we used a Spearman rank correlation.

For the inter-rater reliability 5% of each subject's film material was analysed by a second person. The mean inter-rater reliability was 99%. Agreement was 100% for the parameter eye use. Inter-rater reliability was at least 96% for all parameters.

## RESULTS

All eight animals had a significant preference for using one eye more often than the other for the frontal visual

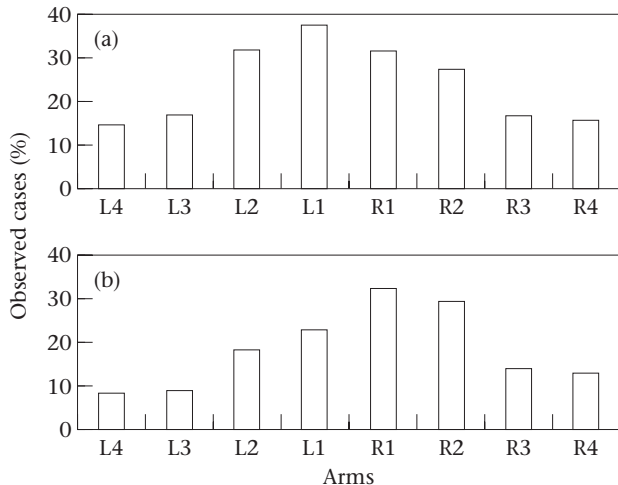


**Figure 3.** (a) Lateral asymmetry of eye use. (b) Choice of arm spread. m=male, f=female.

field (Fig. 3a). The left eye was dominant in five octopuses and the right in three. The highest value of lateral asymmetry was 70% and the lowest was 53% (mean 58%, for  $\chi^2$  values see Appendix 1,  $P < 0.001$ ). The percentage of binocular eye use differed between subjects (mean 5%, range 1–11%). The two subjects (Buko, Dani) that had the greatest difference in preferring one eye showed the least amount of binocular eye use.

Arm spread was consistent with the findings of eye use (Fig. 3b). Subjects using the left eye dominantly looked through arm spread L1–L2 more often than arm spreads L1–R1 and R1–R2 and vice versa (for  $\chi^2$  values see Appendix 1,  $P < 0.001$ ). The two octopuses (Calimero, Celeste) that had the highest percentage of binocular vision favoured the central arm spread L1–R1. When using binocular vision, all subjects looked exclusively through the central arm spread, whereas in monocular eye use they chose between the central spread (L1–R1) and the ipsilateral one, but hardly ever (range 0–3.8%) used the arm spread on the other side.

Seven of eight subjects showed no tendency to a particular direction of movement along the front of the tank (for  $\chi^2$  values see Appendix 1, NS). Only one left-eye-dominant female (Dorian) chose to move left rather than right ( $\chi^2 = 39.76$ ,  $P < 0.001$ ). Eye use was not associated with direction of movement (for all eight subjects: left



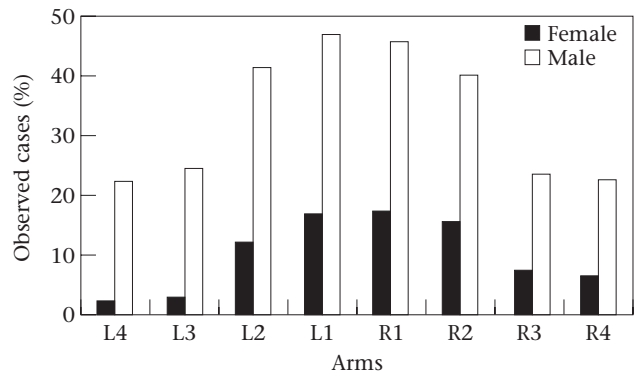
**Figure 4.** Average ventral arm pigmentation for *Octopus vulgaris* with either (a) the left ( $N=5$ ) or (b) the right ( $N=3$ ) eye dominant.

eye, moving left:  $\chi^2=0.7$ ,  $N=455$ , NS; right eye, moving right:  $\chi^2=1.16$ ,  $N=431$ , NS). The bouts of eye use were much longer than those for direction of movement. Calculated for one octopus (a right-eyed male, Bea), the mean length of bouts for eye use was 5 min for the right eye and 4.4 min for the left, while the corresponding value for the direction of movement (left and right had the same mean duration) was only 15 s. Direction of movement was not associated with preferred arm spread (for all eight subjects: L1–L2:  $\chi^2=0$ ,  $N=236$ , NS; R1–R2:  $\chi^2=2.35$ ,  $N=364$ , NS),

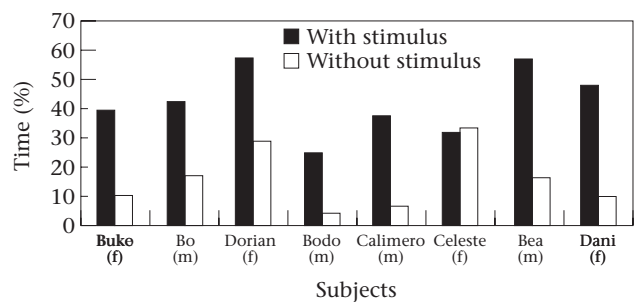
While moving along the front of the tank, the octopuses produced various patterns of pigmentation on the ventral side of their arms. The five most common pigmentation patterns were L1–R1, L1–L2, R1–R2, which are the same arm combinations as for the arm spread, and L1–L2–L3–L4 and R1–R2–R3–R4, which means that all the arms on one side of the body were pigmented (Fig. 2b). Figure 4 shows eye use in relation to pigmentation of the left-eyed and right-eyed individuals (Wilcoxon test:  $T=2$ ,  $N=8$ ,  $P=0.036$ ). Subjects with a dominant left eye showed, on average, darker pigmentation on L1–L2, and right-eyed animals had darker pigmentation on R1–R2.

Generally, the side of the body of the eye in use was darker than the other. Four out of five patterns (L1–L2, R1–R2, L1–L2–L3–L4, R1–R2–R3–R4) were associated with eye use (for all eight subjects: L1–L2:  $\chi^2=111.75$ ,  $N=218$ ; R1–R2:  $\chi^2=76.53$ ,  $N=234$ ; L1–L2–L3–L4:  $\chi^2=30.82$ ,  $N=102$ ; R1–R2–R3–R4:  $\chi^2=58.2$ ,  $N=122$ ;  $P_s < 0.001$ ). Only the pigmentation of L1–R1 could not be significantly linked to the eye in use. Two female octopuses rarely showed dark pigmentation and were omitted for this analysis.

The arms of the spreads in use were more darkly pigmented than the remaining arms (for all eight subjects: arm spread L1–L2 darkly pigmented:  $\chi^2=103.1$ ,  $N=178$ ; arm spread R1–R2 darkly pigmented:  $\chi^2=47.6$ ,  $N=183$ ;  $P_s < 0.001$ ). We found a weak association between the direction of movement and the pigmentation (for L1–L2 and R1–R2 and moving left and right: L1–L2:  $\chi^2=0.3$ ,  $N=195$ , NS; R1–R2:  $\chi^2=4.6$ ,  $N=208$ ,  $P < 0.05$ ).



**Figure 5.** Average ventral arm pigmentation for male and female *Octopus vulgaris*.



**Figure 6.** Curiosity behaviour in *Octopus vulgaris*. This is the time the octopuses spent actively attached to the front of the tank looking out.

There was a highly significant difference in pigmentation for males and females ( $\chi^2=99.5$ ,  $N=351$ ,  $P < 0.001$ ; Fig. 5). On average, females showed less pigmentation than males, but followed the same principal pattern of the front four arms being darker than the hind ones. This was the only intersexual difference that we found.

The main difference between the experimental and control sessions (with and without a stimulus) was in a behaviour we termed 'curiosity'. We measured this as the time that a subject was attached to the front of the tank and actively looked out of the tank. Subjects spent more time at the front when the stimulus was present, although large differences between individuals were apparent (Fig. 6). We found no significant difference overall in percentages of eye use between the experimental and control set-ups (Spearman rank correlation: right eye:  $r_s=0.86$ ,  $N=8$ ,  $P=0.007$ ; left eye:  $r_s=0.55$ ,  $N=8$ , NS; both eyes:  $r_s=0.17$ ,  $N=8$ , NS). Nevertheless, all eight animals showed the same dominant eye in both experimental and control sessions; only the percentages differed slightly. For two animals, the values remained exactly the same, for three they were higher in experimental sessions and for three they were higher in the control.

## DISCUSSION

All eight octopuses significantly preferred using one eye more frequently than the other, for the frontal visual

field. The sessions with and without the stimulus did not differ significantly in the percentages of eye use. In addition eye use was not associated with direction of movement. The subjects preferred turning and crossing their body axis towards their dominant eye instead of using the morphologically more logical eye for the direction of their movement. We take this observation as strong evidence for behavioural asymmetry at the individual level.

The lateralization of eye use at the individual level in octopuses could serve two functions. One possibility is that there is simply a spatial division of labour between the eyes, so that the animal is able to observe a visual field for an almost complete 360° circle. Alternatively, like vertebrates, they may process different features of the observed object with the left and the right eye. This lateralization of eye use is also potentially a result of a motor asymmetry, caused for example by arm preference. Further experimental work is needed to investigate these hypotheses.

In birds, lateral asymmetry of eye use in combination with hemispheric specialization has been documented extensively (Rogers 2000; reviewed in Bradshaw & Rogers 1993; Güntürkün 1997). According to these findings, the left hemisphere is mainly concerned with the detailed analyses of visual features, and the right with spatial processes and recognition of individuals in a social context. Since this is essentially also the pattern observed in human cerebral asymmetries (Davidson & Hugdahl 1995), at least a part of avian and mammalian lateralization may have a common root. Bisazza et al. (1996a) argued that pawedness and motor asymmetries found in natural populations of toads (*Bufo bufo*, *Bufo viridis*) could represent a precursor of handedness in higher vertebrates. Thus, they claimed, there must have been a common, lateralized vertebrate ancestor for birds and mammals (Bisazza et al. 1998).

Clearly, lateral asymmetry of eye use in an invertebrate, the octopus, must have evolved independently. Therefore, lateral asymmetry does not seem to be limited to vertebrates, but is a common principle that evolves when neuronal systems must cope with complex sensory inputs.

We found strong evidence for lateral asymmetry of eye use at the individual level in *O. vulgaris*. A population is said to be lateralized when more than 50% of the individuals are lateralized in the same direction (Lehman 1981). The number of animals we tested was therefore not large enough for us to make a statement about the population level.

In addition to these observations of eye use, we examined the arm position and the variation in patterns of arm spread in relation to the eye apparently in use. When attached to the front of the tank and using one eye (e.g. the left) the octopuses looked exclusively through the front two of eight possible arm spreads, L1–R1, L1–L2. The other six arm spreads are anatomically unlikely, because the head is usually not twisted that far. Although the choice of arm spread largely depended on the eye in use, there was still individual variation. The two octopuses (Calimero, Celeste) that had the highest

percentage of binocular vision favoured the use of the central arm spread, L1–R1. Since there are two choices of arm spread of an octopus using one eye, the lateralization is likely to be visual, although we cannot exclude the possibility of a motor lateralization of the head region and arms.

Octopuses, like most cephalopods, possess a sophisticated chromatophore system in their skin, which can produce a huge variety of body patterns for cryptic and communication purposes, and which is at least partly triggered by visual inputs (Messenger 1967; Packard & Hochberg 1977). Our results suggest that monocular eye use and the choice of arm spread influences body pattern production on the ventral side of the body. The two arms closer to the eye in use and, in general, all arms on the same body half tended to be more darkly pigmented than the others. There are two plausible explanations for this phenomenon. First, pigmentation might be triggered by optical lobe activity of the eye used for the frontal visual field. If, for example, the left eye is in use, the left optical lobe is stimulated, influencing adjacent brain areas on the same side. Packard (1995) described the neuronal pathways involved in body pattern production.

Another possible explanation is countershading. In squid, the eyes are involved in a dorsal light reflex (Preuss & Budelmann 1995), and in *S. officinalis* the chromatophore system creates a countershading reflex (Ferguson et al. 1994). In these cases, countershading provides camouflage in open water, with the dorsal side darker than the ventral. For benthic cephalopods, camouflage could also be involved because octopuses sit in their dens coiling their arms upwards around the mantle (Hanlon & Messenger 1998). In this position, the ventral side of the two arms surrounding the eyes is visible, and therefore must be concealed.

The main difference between the experiment and control set-ups was in 'curiosity' behaviour. As expected, subjects spent more time attached to the front of the tank when the stimulus was present, although we observed large individual differences. This observation could contribute to the notion of 'personalities' in octopuses described by Mather & Anderson (1993). No difference was found for percentages of eye use with and without the stimulus. Since subjects showed the same behaviour in both situations it is not surprising that they also showed the same asymmetry. In both cases, they used the same eye to view their surroundings. A shift to a different asymmetry might be expected in a completely different behaviour, such as spatial orientation.

Our finding of lateral asymmetry of eye use in octopuses has initiated an interesting line of investigation into octopus lateralization which might reveal other analogous asymmetries to vertebrates and contribute to the understanding of the possible functions of lateralization in general.

#### Acknowledgments

This work was carried out and financed by the Konrad Lorenz Institute for Evolution and Cognition Research. Animals were provided by the Stazione Zoologica di

Napoli with the help of Dr Flegra Bentivignia and Gianfranco Mazza. We thank Mag Daniela Meisel and Janja Ceh for their help and Dr Astrid Jütte and Dr Herbert Weilguni for assistance with statistical questions. We also thank Professors Werner Callebaut, Kurt Kotrschal, Jennifer Mather and Gerd B. Müller for their comments on the manuscript and Dr Michael Stachowitsch for proofreading.

## References

- Abbott, N. J., Williamson, R. & Maddock, L. 1995. *Cephalopod Neurobiology*. Oxford: Oxford University Press.
- Babcock, L. H. & Robinson, R. A. 1989. Preferences of paleozoic predators. *Nature*, **337**, 695–696.
- Bisazza, A. & Vallortigara, G. 1998. Rotational swimming preferences in mosquitofish: evidence for brain lateralization? *Physiology and Behavior*, **62**, 1405–1407.
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L. J. & Vallortigara, G. 1996a. Right-pawedness in toads. *Nature*, **379**, 408.
- Bisazza, A., Cantalupo, C. & Vallortigara, G. 1996b. Lateral asymmetries during escape behaviour in a species of teleost fish (*Jenynsia lineata*). *Physiology and Behavior*, **61**, 31–35.
- Bisazza, A., Rogers, L. J. & Vallortigara, G. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural brain lateralization in fishes, reptiles, and amphibians. *Neuroscience and Behavioral Reviews*, **22**, 411–426.
- Boycott, B. B. 1961. The functional organization of the brain of the cuttlefish *Sepia officinalis*. *Proceedings of the Royal Society of London, Series B*, **153**, 503–534.
- Bradshaw, J. & Rogers, L. 1993. *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect*. San Diego: Academic Press.
- Budelmann, B. U. 1995. The cephalopod nervous system: what evolution has made of the molluscan design. In: *The Nervous Systems of Invertebrates: An Evolutionary and Comparative Approach* (Ed. by O. Breidbach & W. Kutsch), pp. 115–138. Basel: Birkhauser Verlag.
- Chichery, R. & Chanelet, J. 1976. Motor and behavioural responses obtained by stimulation with chronic electrodes of the optic lobe of *Sepia officinalis*. *Brain Research*, **574**, 77–84.
- Davidson, R. J. & Hugdahl, K. 1995. *Brain Asymmetry*. Cambridge, Massachusetts: MIT Press.
- Dickel, L., Boal, J. G. & Budelman, B. U. 2000. The effect of early experience on learning and memory in cuttlefish. *Developmental Psychobiology*, **36**, 101–110.
- Dubas, F., Hanlon, R. T., Ferguson, G. P. & Pinsker, H. M. 1986. Localization and stimulation of chromatophore motoneurons in the brain of the squid, *Lolliguncula brevis*. *Journal of Experimental Biology*, **121**, 1–25.
- Ferguson, G. P., Messenger, J. B. & Budelman, B. U. 1994. Gravity and light influence the countershading reflexes of the cuttlefish *Sepia officinalis*. *Journal of Experimental Biology*, **191**, 247–256.
- Güntürkün, O. 1997. Avian visual lateralization. *Neuroreport*, **8**, iii–xi.
- Hanlon, R. T. & Messenger, J. B. 1998. *Cephalopod Behaviour*. New York: Cambridge University Press.
- Hiscock, M. & Kinsbourne, M. 1995. Phylogeny and ontogeny of cerebral lateralization. In: *Brain Asymmetry* (Ed. by R. J. Davidson & K. Hugdahl), pp. 535–578. Cambridge, Massachusetts: MIT Press.
- Kühn, A. 1950. Über Farbwechsel und Farbsinn von Cephalopoden. *Zeitschrift für Vergleichende Physiologie*, **32**, 572–598.
- Lehman, R. A. W. 1981. Lateralized asymmetry of behavior in animals at the population and individual level. *Behavioral and Brain Science*, **4**, 28.
- Mather, J. A. & Anderson, R. C. 1993. Personalities of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology*, **107**, 336–340.
- Messenger, J. B. 1967. The peduncle lobe: a visuo-motor center in octopus. *Proceedings of the Royal Society of London, Series B*, **167**, 225–251.
- Messenger, J. B. 1981. Comparative physiology of vision in molluscs. In: *Handbook of Sensory Physiology Vol VII/6C: Comparative Physiology and Evolution of Vision in Invertebrates* (Ed. by H. Autrum), pp. 92–200. Berlin: Springer-Verlag.
- Messenger, J. B. 1991. Photoreception and vision in molluscs. In: *Evolution of the Eye and Visual System* (Ed. by J. R. Cronly-Dillon & R. L. Gregory), pp. 364–397. Basingstoke: MacMillan.
- Muntz, W. R. A. 1963. Intraocular transfer and the function of the optic lobes in octopus. *Quarterly Journal of Experimental Psychology*, **15**, 116–124.
- Neville, A. C. 1976. *Animal Asymmetry*. London: Edward Arnold.
- Packard, A. 1995. Organization of cephalopod chromatophore systems: a neuromuscular image-generator. In: *Cephalopod Neurobiology*. (Ed. by N. J. Abbott, R. Williamson & L. Maddock), pp. 331–368. Oxford: Oxford University Press.
- Packard, A. & Hochberg, F. G. 1977. Skin patterning in octopus and other genera. *Symposia of the Zoological Society of London*, **38**, 191–231.
- Palmer, A. R. 1996. From symmetry to asymmetry: phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. *Proceedings of the National Academy of Science, U.S.A.*, **93**, 14279–14286.
- Preuss, T. & Budelman, B. U. 1995. A dorsal light reflex in a squid. *Journal of Experimental Biology*, **198**, 1157–1159.
- Rogers, L. J. 2000. Evolution of hemispheric specialization: advantages and disadvantages. *Brain and Language*, **73**, 236–253.
- Sanders, G. D. 1975. The cephalopods. In: *Invertebrate Learning, Vol. 3: Cephalopods and Echinoderms* (Ed. by W. C. Corning, J. A. Dyal & A. O. D. Willows), pp. 1–101. New York: Plenum.
- Shashar, N. & Cronin, T. W. 1996. Polarization contrast vision in octopus. *Journal of Experimental Biology*, **199**, 999–1004.
- Springer, S. P. & Deutsch, G. 1998. *Left Brain, Right Brain: Perspectives of Cognitive Neuroscience*. New York: W. H. Freeman.
- Vallortigara, G. 2000. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain and Language*, **73**, 189–219.
- Vallortigara, G., Rogers, L. J. & Bisazza, A. 1999. Possible evolutionary origins of cognitive brain lateralisation. *Brain Research Reviews*, **30**, 164–175.
- Wells, M. J. 1978. *Octopus. Physiology and Behaviour of an Advanced Invertebrate*. London: Chapman & Hall.

## Appendix

Table A1. Sample sizes and  $\chi^2$  values for all  $\chi^2$  tests for individual subjects,  $df=2$  for all calculations

	Bea	Bo	Bodo	Buko	Calime.	Celeste	Dani	Dorian
Eye use (l/r)	1572	1294	992	1258	1225	985	1411	1591
$\chi^2$ Eye use (l/r)	74.67	39.94	12.07	209.76	38.52	26.49	76.6	21.79
Arm spread with left eye (L1-L2/R1-R2)	584	719	537	875	639	376	528	849
$\chi^2$ Arm spread with left eye (L1-L2/R1-R2)	445.57	610	383.16	670.05	373.16	137.24	438.01	758.02
Arm spread with right eye (L1-L2/R1-R2)	919	500	429	365	420	528	845	670
$\chi^2$ Arm spread with right eye (L1-L2/R1-R2)	678.01	436.01	234.02	240	281.06	183.23	732.19	435.55
Movement (l/r)	1091	1048	689	768	707	770	1038	1262
$\chi^2$ Movement (l/r)	2.98	4.95	0.04	0.08	1.94	0.63	0	39.76
Movement with left eye (l/r)	424	576	375	509	372	257	422	708
$\chi^2$ Movement with left eye (l/r)	5.9	8.03	0.07	0.1	1.55	0.47	2.13	39.86
Movement with right eye (l/r)	617	410	290	244	261	440	605	578
$\chi^2$ Movement with right eye (l/r)	22.19	0.09	0	0.8	2.79	0.33	0.73	0.84
Movement with arm spread L1-L2 (l/r)	353	497	281	386	283	112	362	638
$\chi^2$ Movement with arm spread L1-L2 (l/r)	5.90	8.03	0.07	0.1	1.55	0.47	2.13	39.86
Movement with arm spread R1-R2 (l/r)	469	365	176	192	206	192	557	393
$\chi^2$ Movement with arm spread R1-R2 (l/r)	22.19	0.09	0	0.8	2.79	0.33	0.73	0.84
Pigmented L1-L2 with eye use (l/r)	328	540	341	202	156	155		
$\chi^2$ Pigmented L1-L2 with eye use (l/r)	139.62	221.70	181.82	146.46	128.61	76.65		
Pigmented R1-R2 with eye use (l/r)	483	499	264	156	153	299		
$\chi^2$ Pigmented R1-R2 with eye use (l/r)	255.07	34.39	145.52	0.23	77.65	231.33		
Pigmented L-half with eye use (l/r)	203	297	226	31	19	38		
$\chi^2$ Pigmented L-half with eye use (l/r)	72.98	67.26	153.35	5.88	7.35	12.9		
Pigmented R-half with eye use (l/r)	242	336	190	69	20	121		
$\chi^2$ Pigmented R-half with eye use (l/r)	123.02	122.79	106.58	11.56	12.25	95.22		
Pigmented L1-L2 with arm spread (L1-L2/R1-R2)	280	475	272	178	132	70		
$\chi^2$ Pigmented L1-L2 with arm spread (L1-L2/R1-R2)	126.23	216.93	184.47	136.72	112.76	84.06		
Pigmented R1-R2 with arm spread (L1-L2/R1-R2)	406	449	275	136	136	148		
$\chi^2$ Pigmented R1-R2 with arm spread (L1-L2/R1-R2)	212.9	35.92	86.45	1.06	72.46	73.08		
Pigmented L1-L2 with movement (l/r)	271	521	273	173	140	166		
$\chi^2$ Pigmented L1-L2 with movement (l/r)	4.52	0.09	0.09	0.69	1.83	0.02		
Pigmented R1-R2 with movement (l/r)	390	504	238	100	122	195		
$\chi^2$ Pigmented R1-R2 with movement (l/r)	25.64	0.96	5.44	4	6.42	5.69		

l=left; r=right. For arm designations (L1, R1, etc.) see Fig. 2.