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RESEARCH ARTICLE

Spatial learning in the cuttlefish *Sepia officinalis*: preference for vertical over horizontal information

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ABSTRACT

The world is three-dimensional; hence, even surface-bound animals need to learn vertical spatial information. Separate encoding of vertical and horizontal spatial information seems to be the common strategy regardless of the locomotory style of animals. However, a difference seems to exist in the way freely moving species, such as fish, learn and integrate spatial information as opposed to surface-bound species, which prioritize the horizontal dimension and encode it with a higher resolution. Thus, the locomotory style of an animal may shape how spatial information is learned and prioritized. An alternative hypothesis relates the preference for vertical information to the ability to sense hydrostatic pressure, a prominent cue unique to this dimension. Cuttlefish are mostly benthic animals, but they can move freely in a volume. Therefore, they present an optimal model to examine these hypotheses. We tested whether cuttlefish could separately recall the vertical and horizontal components of a learned two-dimensional target, and whether they have a preference for vertical or horizontal information. *Sepia officinalis* cuttlefish were trained to select one of two visual cues set along a 45 deg diagonal. The animals were then tested with the two visual cues arranged in a horizontal, vertical or opposite 45 deg configuration. We found that cuttlefish use vertical and horizontal spatial cues separately, and that they prefer vertical information to horizontal information. We propose that, as in fish, the availability of hydrostatic pressure, combined with the ecological value of vertical movements, determines the importance of vertical information.

KEY WORDS: Cephalopods, Spatial learning, Cognition, Spatial perception

INTRODUCTION

Navigating in a three-dimensional (3D) space represents a more complex task than moving in a flat environment, mostly because the space to be represented is larger (Jeffery et al., 2013). This is especially true for '3D-moving' species, which are able to move in a volumetric space by swimming or flying and which can exploit the vertical space to a greater extent than surface-bound species.

In order to deal with the increased amount of information, animals can acquire and store the vertical and horizontal components of space separately, rather than as a unique, integrated item of information (Holbrook and Burt de Perera, 2009). This has been demonstrated in fish. In a previous study, fish were trained to reach a goal at the end of one of the arms of a three-dimensional Y-maze (Holbrook and Burt de Perera, 2009). The maze arms were placed at a 45 deg angle to the vertical so that the goal to be learned had both a vertical and a horizontal coordinate. When the maze was rotated along its axis to position its arms either vertically or horizontally for the test trials, the fish selected the arm associated with the correct vertical or horizontal component of the previously learned location (Davis et al., 2014; Holbrook and Burt de Perera, 2009, 2011). Rats trained to reach a goal in a cubic lattice maze learned the vertical coordinate first (Grobéty and Schenk, 1992), and when both components were acquired, they went first to the horizontal coordinate and then climbed up to the correct height (Jovalekic et al., 2011). Therefore, both fish, 3D-moving species, and rats, surface-bound species, learn and use the horizontal and vertical components separately.

An animal's mode of locomotion is likely to influence how three-dimensional information is encoded in its brain (Flores-Abreu et al., 2014). Indeed, 3D-moving species acquire spatial information in the vertical plane with a similar or higher accuracy than information in the horizontal plane, whereas surface-bound species are less accurate in the vertical space (Dacke and Srinivasan, 2007; Eckles et al., 2012; Flores-Abreu et al., 2014; Holbrook and Burt de Perera, 2013; Hurly et al., 2010). However, locomotory style does not predict the relative importance of horizontal and vertical information to an animal: vertical information is preferred in fish (both benthic and non-benthic organisms) but not in hummingbirds, two equally 3D-moving species. For example, take fish that were trained in a Y-maze arranged at a 45 deg angle to the vertical. When they were tested with the opposite 45 deg orientation, in which the previous horizontal and vertical information were in conflict, the fish preferentially selected the vertically correct rather than the horizontally correct information (Davis et al., 2014; Holbrook and Burt de Perera, 2011). Hummingbirds tested in a similar way seem to prefer horizontal to vertical information (Flores-Abreu et al., 2013). Animals learn redundant spatial information to orient (Shettleworth, 2010); however, some spatial cues may be more salient and drive behavior more strongly than others (Cartron et al., 2012; Lebhardt et al., 2012). Davis et al. (2014) suggested that fish prefer vertical information because, unlike birds, they are exposed to hydrostatic pressure, a cue that is very salient and unique to the vertical dimension.

Studies on 3D spatial learning in invertebrates are limited. Learning vertical spatial information has been demonstrated in bees (Dacke and Srinivasan, 2007; Eckles et al., 2012), but the relative weight of vertical versus horizontal information has not yet been examined in any invertebrate species. Similarly, investigations on how vertical and horizontal information are stored in an internal representation of space (as integrated or separate information) are lacking in invertebrates. Cephalopod mollusks, which include octopuses, squid and cuttlefish, are often considered as the most advanced invertebrates. They possess extremely flexible behavior and highly developed attentional and memory capacities

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comparable in sophistication to that of some vertebrates (Borrelli and Fiorito, 2008; Darmaillacq et al., 2014). They also demonstrate good spatial learning abilities, including exploratory learning and spatial maze solution (Boal and Dunham, 2000; Jozet-Alves et al., 2008; Karson et al., 2003). Cuttlefish, for example, can locate a shelter in a maze by relying both on proprioceptive and exteroceptive cues (such as proximal and distal visual cues, and polarized light e-vectors) (Alves et al., 2007; Cartron et al., 2012). So far, a single study has addressed 3D spatial learning in cephalopods (Crook et al., 2009). In that study, *Nautilus* exposed to three different configurations of artificial coral reefs showed habituation to the same configuration over time, but increased exploratory behavior in response to topographical changes (Crook et al., 2009). This suggests that they are able to learn structural features of complex, 3D environments.

In the present study, we tested whether cuttlefish *Sepia officinalis* Linnaeus 1758 extract the vertical and horizontal components from a learned three-dimensional coordinate and use them independently of each other. Representing volumes as two separate components has been suggested to require lower memory capacity and allow more flexible use of spatial information (Holbrook and Burt de Perera, 2009; Jeffery et al., 2013). Therefore, we expected the cuttlefish to encode and recall horizontal and vertical components of a 3D location separately. We also tested whether cuttlefish prioritize vertical information over horizontal information in conflicting situations. Cuttlefish are mostly bottom-dwelling animals; nonetheless, they are very capable of moving freely in the water column. They are also likely to detect changes in hydrostatic pressure, as demonstrated in other cephalopod species (Jordan, 1988; Knight-Jones and Morgan, 1966). Therefore, we hypothesized that they will prefer vertical information to horizontal information.

MATERIALS AND METHODS
Subjects
Eight common European cuttlefish, *S. officinalis*, were tested. The animals were reared from wild-caught eggs until they were 2 months old. During this time they were housed in a group in a holding tank with running seawater at a temperature of ca. 18°C at the Centre de Recherche en Environnement Côtier (Luc-sur-Mer, France). At ca. 2 months of age, they were transferred into a larger 1000 liter tank at a temperature of ca. 15°C. Both tanks had shelters and rocks to provide an enriched environment, which promotes learning in cuttlefish (Dickel et al., 2000). Animals were fed live grass shrimp (*Palaemonetes* spp.) daily. Rearing conditions followed those described in Cartron et al., (2012). At the age of 2.5 months (and 2 days prior the start of training), the animals were separated and housed in individual tanks in which the experiments took place (80×40×17 cm, length×width×water depth). Rearing and training conditions were in compliance with European directive 2010/63/EU for the care and welfare of cephalopods in research. The experiments complied with the French animal testing laws. As no preliminary experiments were run, the minimum number of cuttlefish allowing us to run non-parametric statistical tests was chosen.

Behavioral procedure
Animals were individually trained to approach a visual cue to receive a shrimp. Training took place in the home tank, which was equipped with a shelter positioned at one of its ends. The trial was performed only if the animal was in the shelter or very close to it. In each trial, the visual cue was placed at the opposite side of the tank relative to the shelter so that the animal had to swim forward and move horizontally or vertically towards the correct cue. The order of behavioral tests was: (A) pre-training, i.e. learning to approach a single visual cue; (B) training to approach one visual cue of the two presented at a given height and side; (C) testing for side or height learning; and (D) conflict experiment testing for side (i.e. horizontal information) or height (i.e. vertical information) preference (Fig. 1). We measured latencies of approach to the visual cue during pre-training, training and probe tests (i.e. C and D). We also recorded choices made during each trial, and the number of trials needed to reach the learning criterion of nine out of 10 consecutive correct approaches during pre-training and during training. Only animals
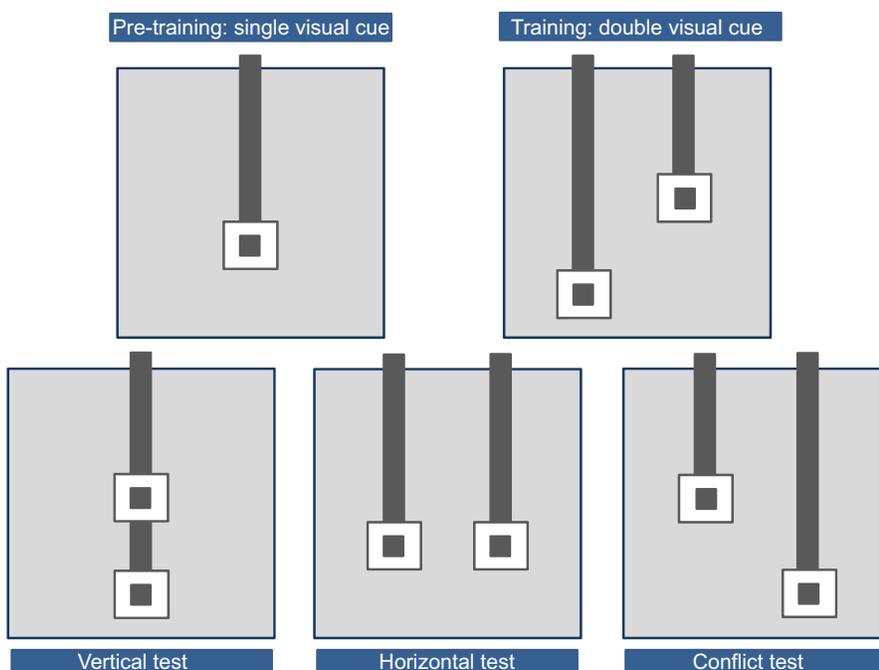
Fig. 1. Training and experimental procedure.
Top: training procedures. Pre-training: single visual cue; training: double visual cue in the '45 deg–up/right' configuration. Bottom: probe test setups. Horizontal and vertical tests (the order of these two first tests was randomly assigned for each animal), and conflict test (always the third probe test).

Pre-training: single visual cue

Training: double visual cue

Vertical test

Horizontal test

Conflict test

that reached the pre-training and training learning criterion were tested.

The visual cue consisted of a 3 cm white plastic square with a dark gray 1.5 cm square at its center. The visual cue was attached to a flat dark gray stick (the same color as the tank) that allowed its placement on the front wall of the tank.

During pre-training, to prevent the animals from focusing on a given presentation height, the visual cue was presented randomly 2.5 (down), 8.5 (medium) and 14.5 cm (up) from the bottom of the tank (coded D, M and U, respectively), and hence, 2.5 cm below the water surface for U.

During training, a double visual cue was used. The apparatus consisted of two of the visual cues described above joined together in a '45 deg–up/right' (45 deg–UR) configuration, in which one visual cue was positioned up and right and one visual cue down and left (with respect to the animal) (Fig. 1). An opposite 45 deg arrangement of the two visual cues was used for the conflict probe test ['45 deg–up/left' (45 deg–UL)].

For the horizontal probe test, two visual cues, at the same intermediate height (M), were used (with a spacing of 9 cm). For the vertical probe test, a 'vertical configuration' was used in which an up (U) and a down (D) visual cue were presented together on the same stick (spaced 9 cm apart).

Pre-training procedure

Two days prior to the start of pre-training, animals were placed in individual tanks to acclimatize. Pre-training followed Jozet-Alves et al. (2013) and consisted of three steps. Each cuttlefish became used to feeding in front of the experimenter with one of the three single visual cues (D, M or U, randomly chosen) which was constantly present in the tank for 2 days (step 1). During step 2, the single visual cue (D, M or U, randomly chosen) was placed on the front wall of the tank and after 1 min a shrimp was presented close to the visual cue on a small rod. The animal was given 4 min to approach the visual cue and catch the shrimp, after which both the shrimp and the visual cue were removed. This step was repeated several times with a random presentation of the three single visual cues. When the animal approached the visual cue before the shrimp was presented a few times in a row, step 3 was started. In this step, the visual cue was again placed in the tank, but the animal was given a shrimp only when it came to the front of the cue at the cue's height and closer than 5 cm to the visual cue. If the animal stopped swimming to the visual cue, step 2 was repeated a few times until the animal once again started approaching the visual cue within 1 min. When an animal performed this task (step 3) nine out of 10 times in a row, training was started.

Training procedure

During training, the cuttlefish was presented with the 45 deg–UR configuration of two visual cues (Fig. 1). Each individual was either trained to approach the UR visual cue or the DL visual cue (randomly pre-selected for each animal before the start of training with the use of the software Research Randomizer, version 4.0, available at http://www.randomizer.org/) to be rewarded with a shrimp. Training was achieved by rewarding the animal with a shrimp if it approached the correct visual cue. If the animal made the wrong choice, no food was provided and the double visual cue was removed. At the beginning of training, if an animal seemed undecided and remained in the middle of the two visual cues, a shrimp was presented in front of the correct visual cue to allow the animal to learn the correct choice. This strategy was only employed for the first few trials of training, after which the animal had to make

a clear choice between the two cues to be rewarded. Four randomly assigned animals were trained to approach the DL visual cue, and four were trained to approach the UR visual cue. When an animal reached the learning criterion (nine out of 10 correct choices in a row), the test phase began. To examine for innate side and/or height preference, the choice made by tested animals during the first exposure to the 45 deg–UR configuration was noted.

Probe test procedure

An animal was sequentially presented with three probe tests. Training sessions were performed in between tests to prevent any influence of the previous test on the subsequent choice made by the animal, and the next test was given only when the animal reached a learning criterion of four out of five correct choices. In the first and second tests, the animal was presented with a horizontal configuration ('horizontal test', two visual cues at the same height) and a vertical configuration ('vertical test', two visual cues presented one above the other). The order of presentation of these two tests was randomly assigned, and set to have an equal number of animals each. After this, the animal was presented with a third test in which the opposite 45 deg configuration of double visual cues (45 deg–UL) was used ('conflict test'; Fig. 1). The latency to attack or approach one of the two visual cues and which visual cue was chosen were recorded.

Each of the three tests was repeated only once per animal and the animal was always rewarded during tests regardless of the choice made. This constant reward prevented the animals from experiencing a negative signal by their activities and kept their motivation in experiments to come. The reward was a shrimp presented away from the visual cue approximately halfway across the tank to limit an association between the food and any post-choice activity.

Statistical analysis

Binomial tests with even (0.5) expectancy were used to compare the number of choices of the DL visual cue versus the UR visual cue during the first exposure to the 45 deg configuration, which examined innate preference. Binomial tests with even expectancy were also used to assess whether the animals' choices during the tests deviated from what was expected by chance, and whether the animals chose one visual cue over the other. Statistical analyses were performed using R version 0.98.501 (RStudio, Boston, MA, USA).

RESULTS

After pre-training, the animals were randomly assigned to two different training groups. Each group was trained to approach only one of two visual cues arranged in a 45 deg configuration, either the DL or the UR visual cue (Fig. 1).

Animals from the two training groups (DL: n=4; and UR: n=4) seem to need the same number of trials to reach the learning criterion of nine out of 10 consecutive correct choices [DL=98.0, 90–159 versus UR=92.5, 59–142 (median and range, respectively); Fig. 2]. To check whether cuttlefish had an innate preference for one of the two visual cues (DL and UR), we compared which visual cue was chosen by each of the eight animals at the first exposure to the 45 deg configuration (i.e. during the first training trial). We found no preference for either one of the two visual cues (DL or UR) among the animals (binomial test: P=0.72; data not shown).
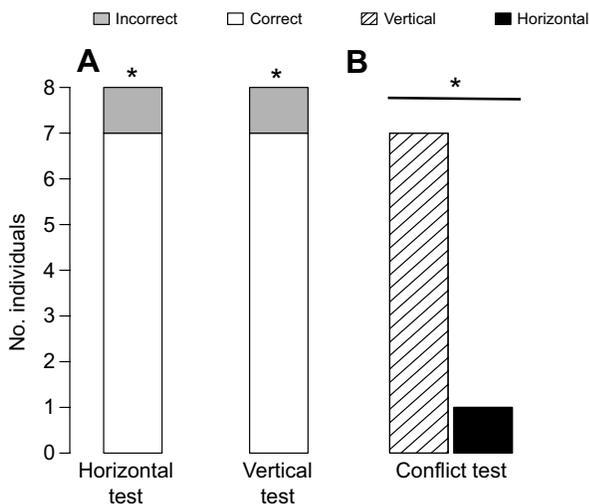
After reaching the acquisition criterion, cuttlefish were sequentially presented with three probe trials (Fig. 1). In the first two probe tests, when a uniquely horizontal or uniquely vertical
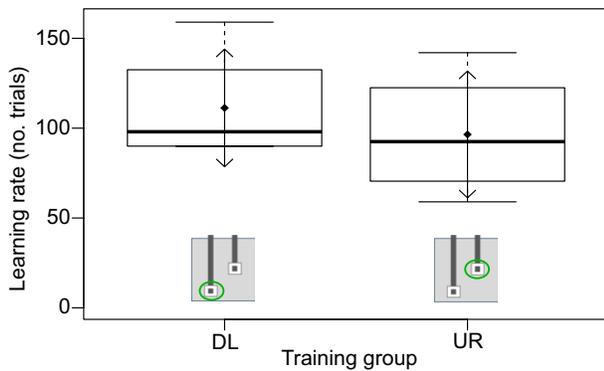
Fig. 2. Learning rates of the two training groups. The green circle indicates which of the two visual cues was rewarded in each training group [down/left (DL): n=4; up/right (UR): n=4]. Learning rate was assessed as the number of trials needed to reach the learning criterion of nine out of 10 consecutive correct choices. Thick horizontal line, median; whiskers, minimum and maximum values; points, means; and boxplot edges, first and third quartiles.

configuration of the two visual cues was presented (Fig. 1), the animals were able to extract the correct vertical or horizontal component from the learned 2D coordinates of the 45 deg training setup. For example, if the animal was trained to approach the UR visual cue, it should choose the right visual cue in the horizontal test, and the upper visual cue in the vertical test, as is consistent with its training. In both the horizontal and the vertical tests, seven out of eight animals made the correct choice (Fig. 3A). The animal that made the wrong choice in the vertical test (A1: trained to go UR, vertical test choice: down) is a different animal to the one that made a mistake in the horizontal test (A2: trained to go UR, horizontal test choice: left).

During the third probe test, the conflict test (Fig. 1), when animals were presented with a novel setup and were asked to make

Fig. 3. Results of the probe tests, obtained after cuttlefish reached the acquisition criterion of training (nine out of 10 choices of the correct visual cue in the 45 deg configuration). Visual cue chosen by the cuttlefish during (A) the horizontal and vertical tests, and (B) the conflict test, following training to either the DL or UR cue of the 45 deg configuration. The results of both training groups (DL and UR) were considered together (n=8). In both the horizontal and vertical tests, animals' choices were consistent with the position they were trained to choose during training. In the conflict test, the animals preferentially chose the previously correct vertical coordinate rather than the previously correct horizontal coordinate (binomial test: *P<0.05).

their choice based on one axis while contradicting the other, animals preferred the vertical component to the horizontal one (seven out of eight animals chose the correct vertical component over the correct horizontal component; binomial test, P=0.035; Fig. 3B). The animal that chose the horizontal component is the same one that made the wrong choice in the horizontal test (A2: trained to go up/right, conflict test choice: down/right).

DISCUSSION

In the present study, we aimed to test whether *S. officinalis* cuttlefish are able to separately recall either vertical or horizontal information, following training in which both kinds of information were simultaneously available. We also examined the preference of cuttlefish for vertical or horizontal spatial information. We showed that *S. officinalis* can extract the vertical and horizontal components of a learned 2D coordinate, and use them independently. Furthermore, we showed that cuttlefish prefer vertical to horizontal spatial information.

The ability to recall the vertical and horizontal components of a location independently from each other suggests that cuttlefish encode the two types of information separately, as do rats and fish (Davis et al., 2014; Grobéty and Schenk, 1992; Holbrook and Burt de Perera, 2009; Jovalekic et al., 2011). Hence, this may be the most convenient strategy for the brain to store 3D spatial information (Holbrook and Burt de Perera, 2009). In addition, this also allows for more flexible use of spatial information, such as calculating detours, as shown in studies on rats (e.g. Jovalekic et al., 2011).

During the conflict tests, seven out of eight animals preferred the visual cue at the correct height to the visual cue at the correct horizontal location. This choice was not biased by an innate preference for one of the two visual cues in the 45 deg configuration. Nor was it biased by a difference between the learning rate of animals needing to learn to approach the upper cue (up/right) or the lower cue (down/left). The similar preference for vertical information in phylogenetically distant species (i.e. cuttlefish and fish) might be driven by the shared environmental constraints of an aquatic medium. Among these, hydrostatic pressure could make navigation in the vertical plane more informative for cuttlefish, as suggested for fish, because it allows for accurate depth detection (Davis et al., 2014; Holbrook and Burt de Perera, 2011).

Hydrostatic pressure sensitivity among cephalopods has been demonstrated only in squid and nautilus (Rice, 1964). Cuttlefish lack swim bladders and their buoyancy mechanism is mostly independent of depth (Webber et al., 2000). Nonetheless, all cephalopods possess angular acceleration mechanoreceptors (statocysts) that may allow them to sense hydrostatic pressure as shown in crustaceans and dogfish (Fraser and Macdonald, 1994; Fraser and Shelmerdine, 2002; Fraser et al., 2008; Williamson and Chrachri, 2007).

The vertical dimension may be more informative also because it is characterized by several asymmetries, such as the light gradient and the presence of the tank floor on the bottom versus the water surface on the top of the tank.

The ecology of a species could also play a role in such a preference. Indeed, if a species mainly exploits its surroundings along the vertical or the horizontal axis, this might lead to a preference for either the vertical or the horizontal dimension, respectively. For example, in stingless bees, only species that forage along the vertical plane, but not species that forage over the ground, can communicate height to nestmates (Nieh et al., 2003). In addition, bumblebees that forage in meadows where species-specific floral patterns predict food resources mostly in the

horizontal plane learn to discriminate floral cues in the horizontal plane but disregard the same cues in the vertical plane (Wolf et al., 2015). Cuttlefish are known to be benthic sit-and-wait predators, and they have an area of high visual acuity in their eyes that allows for high detection of events occurring near the animal's horizon (Cronin et al., 2014). However, camouflaging cuttlefish attend to visual cues in the vertical plane as strongly as or even more strongly than those presented along the horizon (Barbosa et al., 2008; Ulmer et al., 2013). Furthermore, cuttlefish become neutrally buoyant and forage moving upwards in the water column at night (Denton and Gilpen-Brown, 1961; Wearmouth et al., 2013). Vertical displacement is also associated with a higher predation risk for both cuttlefish and the benthic fish *Corydoras aeneus*, which surfaces to breathe (Domenici et al., 2007, 2015; Kramer and McClure, 1980). This may contribute to assign a stronger ecological value to information in the vertical dimension. As careful as we were, we cannot completely rule out the possibility that the vertical preference shown in the present study is due to an experimental bias or to the animals learning an unrelated or unintended cue. For example, the visual cues used during the training with the 45 deg configuration (UR and DL) were somewhat closer to the tank borders in the vertical than in the horizontal plane. Thus, it is possible that the animals did not learn vertical information but rather estimated the distance to the edge. Other such potential unintentional cues are possible and as much as the experimental setup tries to avoid them, they are hard to fully eliminate. Comparative studies with aquatic and non-aquatic species will allow a better understanding of whether the preference for vertical information depends more on the ecological value of the vertical dimension or on the sensitivity to hydrostatic pressure.

References
Alves, C., Chichery, R., Boal, J. G. and Dickel, L. (2007). Orientation in the cuttlefish *Sepia officinalis*: response versus place learning. *Anim. Cogn.* **10**, 29-36.

Barbosa, A., Litman, L. and Hanlon, R. T. (2008). Changeable cuttlefish camouflage is influenced by horizontal and vertical aspects of the visual background. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **194**, 405-413.

Boal, J. G., Dunham, A. W., Williams, K. T. and Hanlon, R. T. (2000). Experimental evidence for spatial learning in octopuses (*Octopus bimaculoides*). *J. Comp. Psychol.* **114**, 246-252.

Borrelli, L. and Fiorito, G. (2008). Behavioral analysis of learning and memory in cephalopods. *Learn. Mem.* **1**, 605-627.

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.

Cronin, T. W., Johnsen, S., Marshall, N. J. and Warrant, E. J. (2014). *Visual Ecology*. Princton; Oxford: Princeton University Press.

Crook, R. J., Hanlon, R. T. and Basil, J. A. (2009). Memory of visual and topographical features suggests spatial learning in nautilus (*Nautilus pompilius* L.). *J. Comp. Psychol.* **123**, 264-274.

Dacke, M. and Srinivasan, M. V. (2007). Honeybee navigation: distance estimation in the third dimension. *J. Exp. Biol.* **210**, 845-853.

Darmaillacq, A.-S., Dickel, L. and Mather, J. ed. (2014). *Cephalopod Cognition*. Cambridge: Cambridge University Press.

Davis, V. A., Holbrook, R. I., Schumacher, S., Guilford, T. and de Perera, T. B. (2014). Three-dimensional spatial cognition in a benthic fish, *Corydoras aeneus*. *Behav. Processes* **109**, 151-156.

Denton, E. J. and Gilpen-Brown, J. B. (1961). The effect of light on the buoyancy of the cuttlefish. *J. Mar. Biol. Assoc. UK* **41**, 343-350.

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.

Domenici, P., Lefrançois, C. and Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362**, 2105-2121.

Domenici, P., Norin, T., Bushnell, P. G., Johansen, J. L., Skov, P. V., Svendsen, M. B. S., Steffensen, J. F. and Abe, A. S. (2015). Fast-starting after a breath: air-breathing motions are kinematically similar to escape responses in the catfish *Hoplosternum littorale*. *Biol. Open* **4**, 79-85.

Eckles, M. A., Roubik, D. W. and Nieh, J. C. (2012). A stingless bee can use visual odometry to estimate both height and distance. *J. Exp. Biol.* **215**, 3155-3160.

Flores-Abreu, I. N., Hurly, T. A. and Healy, S. D. (2013). Three-dimensional spatial learning in hummingbirds. *Anim. Behav.* **85**, 579-584.

Flores-Abreu, I. N., Hurly, T. A., Ainge, J. A. and Healy, S. D. (2014). Three-dimensional space: locomotory style explains memory differences in rats and hummingbirds. *Proc. R. Soc. B Biol. Sci.* **281**, 20140301.

Fraser, P. J. and Macdonald, A. G. (1994). Crab hydrostatic pressure sensors. *Nature* **371**, 383-384.

Fraser, P. J. and Shelmerdine, R. L. (2002). Fish physiology: dogfish hair cells sense hydrostatic pressure. *Nature* **415**, 495-496.

Fraser, P. J., Cruickshank, S. F., Shelmerdine, R. L. and Smith, L. E. (2008). Hydrostatic pressure receptors and depth usage in Crustacea and fish. *J. Inst. Navig.* **55**, 159-165.

Grobéty, M.-C. and Schenk, F. (1992). Spatial learning in a three-dimensional maze. *Anim. Behav.* **43**, 1011-1020.

Holbrook, R. I. and Burt de Perera, T. (2009). Separate encoding of vertical and horizontal components of space during orientation in fish. *Anim. Behav.* **78**, 241-245.

Holbrook, R. I. and Burt de Perera, T. (2011). Three-dimensional spatial cognition: information in the vertical dimension overrides information from the horizontal. *Anim. Cogn.* **14**, 613-619.

Holbrook, R. I. and Burt de Perera, T. (2013). Three-dimensional spatial cognition: freely swimming fish accurately learn and remember metric information in a volume. *Anim. Behav.* **86**, 1077-1083.

Hurly, T. A., Franz, S. and Healy, S. D. (2010). Do rufous hummingbirds (*Selasphorus rufus*) use visual beacons? *Anim. Cogn.* **13**, 377-383.

Jeffery, K. J., Jovalekic, A., Verriotis, M. and Hayman, R. (2013). Navigating in a three-dimensional world. *Behav. Brain Sci.* **36**, 523-543.

Jordan, M. (1988). Response of *Nautilus* to variation in ambient pressure. *J. Exp. Biol.* **137**, 175-189.

Jovalekic, A., Hayman, R., Becares, N., Reid, H., Thomas, G., Wilson, J. and Jeffery, K. (2011). Horizontal biases in rats' use of three-dimensional space. *Behav. Brain Res.* **222**, 279-288.

Jozet-Alves, C., Boal, J. G. and Dickel, L. (2008). Short-distance navigation in cephalopods: a review and synthesis. *Cogn. Process.* **9**, 239-247.

Jozet-Alves, C., Bertin, M. and Clayton, N. S. (2013). Evidence of episodic-like memory in cuttlefish. *Curr. Biol.* **23**, R1033-R1035.

Karson, M. A., Boal, J. G. and Hanlon, R. T. (2003). Experimental evidence for spatial learning in cuttlefish (*Sepia officinalis*). *J. Comp. Psychol.* **117**, 149-155.

Knight-Jones, E. W. and Morgan, E. (1966). Responses of marine animals to changes in hydrostatic pressure. *Oceanogr. Mar. Biol. Annu. Rev.* **4**, 267-299.

Kramer, D. L. and McClure, M. (1980). Aerial respiration in the catfish, *Corydoras aeneus* (Callichthyidae). *Can. J. Zool.* **58**, 1984-1991.

Lebhardt, F., Koch, J. and Ronacher, B. (2012). The polarization compass dominates over idiothetic cues in path integration of desert ants. *J. Exp. Biol.* **215**, 526-535.

Nieh, J. C., Contrera, F. A. L., Ramírez, S. and Imperatriz-Fonseca, V. L. (2003). Variation in the ability to communicate three-dimensional resource location by stingless bees from different habitats. *Anim. Behav.* **66**, 1129-1139.

Rice, A. L. (1964). Observations on the effects of changes of hydrostatic pressure on the behaviour of some marine animals. *J. Mar. Biol. Assoc. UK* **44**, 163-175.

Shettleworth, S. J. (2010). *Cognition, Evolution, and Behavior*. Oxford, England: Oxford University Press.

Ulmer, K. M., Buresch, K. C., Kossodo, M. M., Mäthger, L. M., Siemann, L. A. and Hanlon, R. T. (2013). Vertical visual features have a strong influence on cuttlefish camouflage. *Biol. Bull.* **224**, 110-118.

Wearmouth, V. J., Durkin, O. C., Bloor, I. S. M., McHugh, M. J., Rundle, J. and Sims, D. W. (2013). A method for long-term electronic tagging and tracking of juvenile and adult European common cuttlefish *Sepia officinalis*. *J. Exp. Mar. Biol. Ecol.* **447**, 149-155.

Webber, D. M., Aitken, J. P. and O'Dor, R. K. (2000). Costs of locomotion and vertic dynamics of cephalopods and fish. *Physiol. Biochem. Zool.* **73**, 651-662.

Williamson, R. and Chrachri, A. (2007). A model biological neural network: the cephalopod vestibular system. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 473-481.

Wolf, S., Roper, M. and Chittka, L. (2015). Bumblebees utilize floral cues differently on vertically and horizontally arranged flowers. *Behav. Ecol.* **26**, 773-781.