Current Biology 21, 460–462, March 22, 2011 ©2011 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2011.01.052

Report

Octopus vulgaris Uses Visual Information to Determine the Location of Its Arm

Tamar Gutnick,[1,*] Ruth A. Byrne,[3] Binyamin Hochner,[1,2] and Michael Kuba[1,2]
[1]Department of Neurobiology, Institute of Life Sciences
[2]Interdisciplinary Center for Neuronal Computation
Edmond J. Safra Campus, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel
[3]Division of Rheumatology, Clinic of Internal Medicine III, Medical University of Vienna, Währinger Gürtel 18-20, 1090 Vienna, Austria

Summary

Octopuses are intelligent, soft-bodied animals with keen senses that perform reliably in a variety of visual and tactile learning tasks [1–6]. However, researchers have found them disappointing in that they consistently fail in operant tasks that require them to combine central nervous system reward information with visual and peripheral knowledge of the location of their arms [6–8]. Wells [6] claimed that in order to filter and integrate an abundance of multisensory inputs that might inform the animal of the position of a single arm, octopuses would need an exceptional computing mechanism, and "There is no evidence that such a system exists in *Octopus*, or in any other soft bodied animal." Recent electrophysiological experiments, which found no clear somatotopic organization in the higher motor centers, support this claim [9]. We developed a three-choice maze that required an octopus to use a single arm to reach a visually marked goal compartment. Using this operant task, we show for the first time that *Octopus vulgaris* is capable of guiding a single arm in a complex movement to a location. Thus, we claim that octopuses can combine peripheral arm location information with visual input to control goal-directed complex movements.

Results

We designed an operant task in the form of a visually cued three-choice maze (Figure 1) to test learning that required single-arm control. The maze shape, a narrow central tube opening into three choice compartments (Figure 1), was based on the natural probing movement that octopus arms often perform when exploring and hunting in small crevices and under rocks. In order to reach the food reward, octopuses had to reach a single arm through the tube, out of the water (thus preventing chemical cueing), and into the water of the goal compartment (Figure 2; see also Movie S1 available online). A black disk in the goal compartment visually marked the presence of a small piece of food, which was moved between choice compartments in a random sequence. Animals performed ten trials a day in which they had to make a choice within 3 min and were not allowed a second choice. All trials were videotaped and later analyzed by observer agreement of two to three experimenters (for details, see Supplemental Experimental Procedures).

All but one of the seven *Octopus vulgaris* tested reached the criterion for learning of five correct trials in a row within 61–211 trials (Table 1). Completing the operant task required the animals to associate a visual cue with their own voluntary motor actions. In the first 20 trials of the experiment, animals performed at chance level (n = 120, $\chi^2 = 0$, p = not significant [NS]). Performance in the last 20 trials up to reaching the criterion was significantly above chance level (n = 120, $\chi^2 = 12.15$, $p < 0.001$). Using the same procedure with an identical opaque maze, the animals' performance fell back to chance level (n = 120, $\chi^2 = 0.935$, p = NS) (Table S1).

When solving the task, octopuses used different sitting positions in the tank and on the support stems, which afforded them different views of the maze and its compartments. A binary logistic regression ($R^2 = 0.136$, n = 5, correlation −0.923, p = 0.00) showed a strong correlation between not seeing the target and failing to complete the task (Movie S2). Animals learned to orient themselves to get an unobstructed view of the target and were in view of the target significantly more often in the last 20 trials (binomial n = 109, $p < 0.05$). Even though the animals learned the task, they did not improve in speed. Interestingly, in the last third of the experiment, successful trials were significantly longer than unsuccessful trials from first contact with the maze until choice (Mann-Whitney n = 225, p = 0.013, z = −2.478), and the same trend was kept from arm insertion into the tube until choice (Mann-Whitney n = 184, p = NS, z = −1.295). We investigated the arm movement inside the central tube and into the choice compartment and defined two different arm use strategies: straight and search. Straight movements involve the unrolling or pushing upward of a bend through the central tube and opening it into the choice compartment. Search movements involve probing and crawling in the central tube and above the choice compartments of the maze before entering the water of a choice compartment. In successful trials, search was used significantly more often than straight in the last 20 trials (30 search to 14 straight, binomial p = 0.023), but not in the first 20 trials (13 search to 19 straight, binomial p = NS), and search was used more in the last 20 trials than the first 20 (30 search to 13 straight, binomial p = 0.014).These movements proved to be distinct in their duration from arm insertion into tube until choice, with straight taking an average of 3.66 ± 2.83 s (n = 207), whereas the average duration for search of 6.50 ± 5.03 s (n = 303) was significantly longer (Mann-Whitney n = 501, $p < 0.001$, z = −10.777).

Discussion

Our study clearly shows the ability of octopuses to learn to complete an operant task requiring them to control the movement of a single arm. The essence of this learning is the development of an association, by reinforcement, between a stimulus and a voluntary motor action that is not the direct inherent response to the reinforcement [10]. Our findings

*Correspondence: tamar.gutnick@mail.huji.ac.il

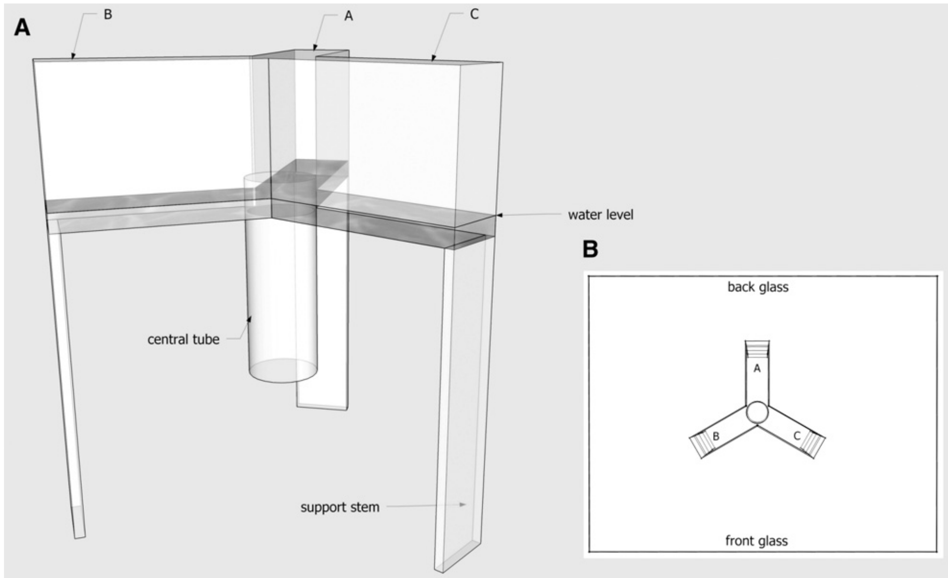

Figure 1. Three-Choice Maze

The octopus had to insert a single arm through the central tube, out of the water, and into the water of the cued compartment.

(A) Side view of maze showing the central tube surrounded by the three choice compartments. On the bottom of each compartment is a support stem that provides the octopus with a place to sit when performing the task.

(B) Top view of maze that is fitted as a tank lid.

show that octopuses are capable of remembering and repeating a series of motor actions that lead them to a desired goal. In order to complete the task, animals identified the target, associated it with a positive reward, positioned themselves with a clear view of the target, inserted the arm into the central tube, and attempted to guide their arm toward the goal compartment. Successful trials took longer to complete, from contact with the maze until choice, suggesting that animals needed more time to correctly position themselves for a clear view of the maze and to visually control the search movements that were more prevalent when they had learned.

The clearly visual nature of the task, as demonstrated both by the opaque control maze and by the importance of animal positioning, requires central nervous system (CNS)

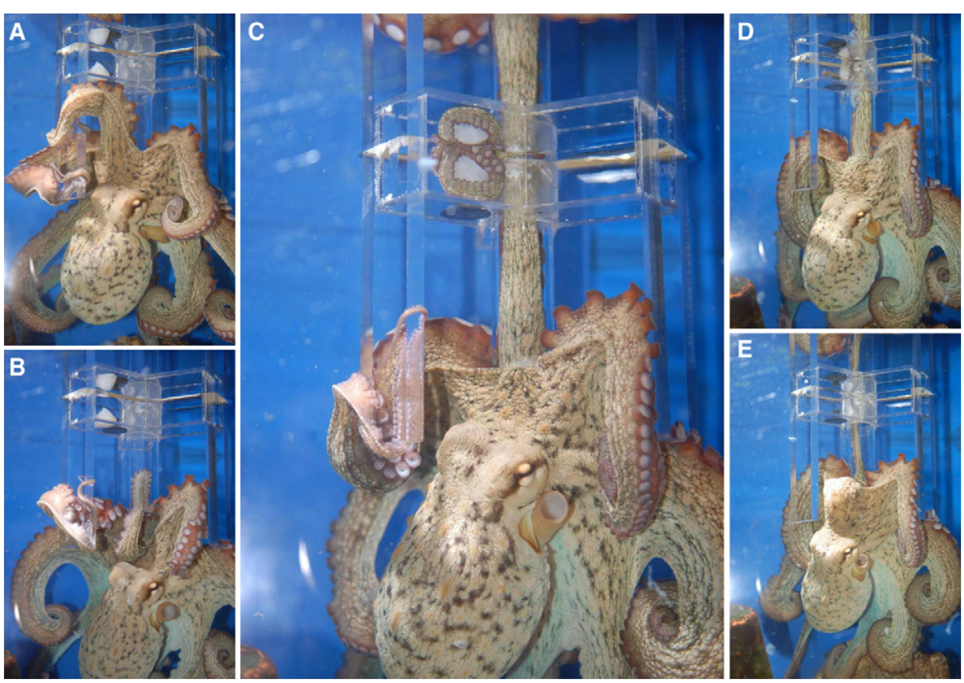

Figure 2. Octopus Performs the Task Correctly and Retrieves the Food Reward

Octopus approaches maze (A), inserts a single arm (B), makes a correct choice using the straight strategy (C), and retrieves the food reward (D and E).

Table 1. Number of Trials to Reach Criterion for Learning

	Trials	Sex
Animal 1	211	male
Animal 2	157	female
Animal 3	69	female
Animal 4	103	male
Animal 5	110	female
Animal 6	61	male

Seven adult *Octopus vulgaris* from the Mediterranean Sea were used for the experiment. Six of the seven animals reached the criterion for learning of five correct trials in a row.

processing. The results of this experiment strengthen the hypothesis of Zullo et al. [9] that octopuses might indeed be capable of multimodal integration in their central nervous system.

The movement toward the goal compartment through the maze might be controlled in one of two ways, either a simple feed-forward command or a set of movements requiring online control. In the feed-forward control scheme, only an initial global command from the CNS would be required to activate the movement, the details of which are prescribed. Visually directing a movement does not necessarily require online feedback. Previous works have centered on movements that might be controlled in a strictly feed-forward manner, such as the reaching movement that is performed by bend propagation [11, 12]. The straight movements that octopuses used in our task might be a case of such feed-forward control. Even though the average duration of such movements (3.66 ± 2.83 s) was longer than movements observed in bend propagation (about 1.5 s, according to [13]), such a difference might be explained by the physical impairment of performing the movement through a tube, because constrained movements have been shown to possess different kinematic profiles [13]. However, when the task was learned, the more prevalent method of arm movement was the search movement. Search movements, such as those used by octopuses during exploration and hunting, might require little or no central control and could be performed by local reflexes of the peripheral nervous system (PNS) relying on tactile and chemical information [6, 14, 15] (Movie S3). However, the ability to use visual information to control a single arm during such exploration movements has significant advantages, especially when following an escaping prey or when avoiding noxious stimuli. The control experiment reinforces our claim that local tactile and chemical information are not used by the animal in solving this task and that visual CNS information is required. The "crawling and probing" nature of the search movements makes it unlikely that such complex movement is controlled in a feed-forward manner.

The specific demands of our maze suggest that there might be an online exchange of information between the CNS and the PNS. This result is even more intriguing in light of a recent study showing the lack of somatotopic representation of the body in the higher motor centers as well as the inability to elicit single-arm responses in stimulation experiments [9]. The ability to control a specific arm raises the question of whether a representation might exist at a lower level of motor center [16], or perhaps the octopus has a unique solution that is based on the properties of the higher motor centers. This study is the first to show that octopuses can determine the position of their arm and learn to visually guide it to a location in a set of movements that are not restricted to a few degrees of freedom.

Supplemental Information

Supplemental Information includes one table, Supplemental Experimental Procedures, and three movies and can be found with this article online at doi:10.1016/j.cub.2011.01.052.

Acknowledgments

This work was supported by Project OCTOPUS, a European Commission 7th Framework Programme (FP7). We thank R. Hammer and I. Zweimüller for valuable statistical advice.

Received: November 5, 2010
Revised: December 19, 2010
Accepted: January 21, 2011
Published online: March 10, 2011

References

1. Sanders, G. (1975). The cephalopods. In Invertebrate Learning, Volume 3: Cephalopods and Echinoderms, W.C. Corning, J.A. Dyal, and A.O.D. Willows, eds. (New York: Plenum Press), pp. 1–101.
2. Boal, J.G. (1996). A review of simultaneous visual discrimination as a method of training octopuses. Biol. Rev. Camb. Philos. Soc. *71*, 157–190.
3. Mather, J. (1995). Cognition in cephalopods. In Advances in the Study of Behavior 24, P.J.B. Slater, J.S. Rosenblatt, C.T. Snowdon, and M. Milinski, eds. (London: Academic Press), pp. 317–353.
4. Anderson, R.C., and Mather, J.A. (2010). It's all in the cues: Octopuses (Enteroctopus dofleini) learn to open jars. In Proceedings of the Third International Symposium "Coleoid Cephalopods Through Time," Ferrantia 59, D. Fuchs, ed. (Luxembourg: Musée National d'Histoire Naturelle), pp. 8–13.
5. Hochner, B. (2008). Octopuses. Curr. Biol. *18*, 897–898.
6. Wells, M.J. (1978). Octopus: Physiology and Behaviour of an Advanced Invertebrate (London: Chapman and Hall).
7. Crancher, P., King, M.G., Bennett, A., and Montgomery, R.B. (1972). Conditioning of a free operant in *Octopus cyaneus Gray*. J. Exp. Anal. Behav. *17*, 359–362.
8. Dews, P.B. (1959). Some observations on an operant in the octopus. J. Exp. Anal. Behav. *2*, 57–63.
9. Zullo, L., Sumbre, G., Agnisola, C., Flash, T., and Hochner, B. (2009). Nonsomatotopic organization of the higher motor centers in octopus. Curr. Biol. *19*, 1632–1636.
10. Thorpe, W. (1963). Learning and Instinct in Animals (London: Methuen).
11. Gutfreund, Y., Flash, T., Fiorito, G., and Hochner, B. (1998). Patterns of arm muscle activation involved in octopus reaching movements. J. Neurosci. *18*, 5976–5987.
12. Yekutieli, Y., Sagiv-Zohar, R., Hochner, B., and Flash, T. (2005). Dynamic model of the octopus arm. II. Control of reaching movements. J. Neurophysiol. *94*, 1459–1468.
13. Gutfreund, Y., Flash, T., Yarom, Y., Fiorito, G., Segev, I., and Hochner, B. (1996). Organization of octopus arm movements: A model system for studying the control of flexible arms. J. Neurosci. *16*, 7297–7307.
14. Altman, J.S. (1971). Control of accept and reject reflexes in the octopus. Nature *229*, 204–206.
15. Mather, J.A. (1998). How do octopuses use their arms? J. Comp. Psychol. *112*, 306–316.
16. Chittka, L., and Niven, J. (2009). Are bigger brains better? Curr. Biol. *19*, 995–1008.