cell may have closer parallels to the dynamic action of vertebrate Kif7.

References

- Wong, S.Y., and Reiter, J.F. (2008). The primary cilium at the crossroads of mammalian hedgehog signaling. Curr. Top Dev. Biol. 85, 225–260.
- Endoh-Yamagami, S., Evangelista, M., Wilson, D., Wen, X., Theunissen, J.W., Phamluong, K., Davis, M., Scales, S.J., Solloway, M.J., de Sauvage, F.J., et al. (2009). The mammalian Cos2 homolog Kif7 plays an essential role in modulating Hh signal transduction during development. Curr. Biol. 19, 1320–1326.
- Cheung, H.O., Zhang, X., Ribeiro, A., Mo, R., Makino, S., Puviindran, V., Law, K.K., Briscoe, J., and Hui, C.C. (2009). The kinesin protein Kif7 is a critical regulator of Gli transcription factors in mammalian hedgehog signaling. Sci. Signal 2, ra29.
 Liem, K.F., Jr., He, M., Ocbina, P.J., and
- Liem, K.F., Jr., He, M., Ocbina, P.J., and Anderson, K.V. (2009). Mouse Kif7/Costal2 is a cilia-associated protein that regulates Sonic hedgehog signaling. Proc. Natl. Acad. USA 106, 13377–13382.
- Whittle, J.R. (1976). Clonal analysis of a genetically caused duplication of the anterior wing in *Drosophila melanogaster*. Dev. Biol. 51, 257–268.
- Saunders, J.W., and Gasseling, M. (1968). Ectodermal-mesenchymal interaction in the origin of limb symmetry. In Epithelial-Mesenchymal Interaction, R. Fleischmayer and R.E. Billingham, eds. (Baltimore: Williams and Wilkins). pp. 78–97.
- Wilkins), pp. 78–97.
 Kalderon, D. (2004). Hedgehog signaling: Costal-2 bridges the transduction gap. Curr. Biol. 14, R67–R69.
- 8. Farzan, S.F., Ascano, M., Jr., Ogden, S.K., Sanial, M., Brigui, A., Plessis, A., and

Robbins, D.J. (2008). Costal2 functions as a kinesin-like protein in the hedgehog signal transduction pathway. Curr. Biol. 18, 1215–1220.

- Tay, S.Y., Ingham, P.W., and Roy, S. (2005). A homologue of the Drosophila kinesin-like protein Costal2 regulates Hedgehog signal transduction in the vertebrate embryo. Development *132*, 625–634.
- Varjosalo, M., Li, S.P., and Taipale, J. (2006). Divergence of hedgehog signal transduction mechanism between Drosophila and mammals. Dev. Cell 10, 177–186.
- Wolff, C., Roy, S., and Ingham, P.W. (2003). Multiple muscle cell identities induced by distinct levels and timing of hedgehog activity in the zebrafish embryo. Curr. Biol. 13, 1169–1181.
- Chen, M.H., Gao, N., Kawakami, T., and Chuang, P.T. (2005). Mice deficient in the fused homolog do not exhibit phenotypes indicative of perturbed hedgehog signaling during embryonic development. Mol. Cell Biol. 25, 7042–7053.
- Merchant, M., Evangelista, M., Luoh, S.M., Frantz, G.D., Chalasani, S., Carano, R.A., van Hoy, M., Ramirez, J., Ogasawara, A.K., McFarland, L.M., et al. (2005). Loss of the serine/threonine kinase fused results in postnatal growth defects and lethality due to progressive hydrocephalus. Mol. Cell Biol. 25, 7054–7068.
- Svard, J., Heby-Henricson, K., Persson-Lek, M., Rozell, B., Lauth, M., Bergstrom, A., Ericson, J., Toftgard, R., and Teglund, S. (2006). Genetic elimination of Suppressor of fused reveals an essential repressor function in the mammalian Hedgehog signaling pathway. Dev. Cell 10, 187–197.
- Lunt, S.C., Haynes, T., and Perkins, B.D. (2009). Zebrafish ift57, ift88, and ift172 intraflagellar transport mutants disrupt cilia but do not affect hedgehog signaling. Dev. Dyn. 238, 1744–1759.

- Aanstad, P., Santos, N., Corbit, K.C., Scherz, P.J., Trinh le, A., Salvenmoser, W., Huisken, J., Reiter, J.F., and Stainier, D.Y. (2009). The extracellular domain of Smoothened regulates ciliary localization and is required for high-level Hh signaling. Curr. Biol. 19, 1034–1039.
- Litingtung, Y., Dahn, R.D., Li, Y., Fallon, J.F., and Chiang, C. (2002). Shh and Gli3 are dispensable for limb skeleton formation but regulate digit number and identity. Nature 418, 979–983.
- Haycraft, C.J., Banizs, B., Aydin-Son, Y., Zhang, Q., Michaud, E.J., and Yoder, B.K. (2005). Gli2 and Gli3 localize to cilia and require the intraflagellar transport protein polaris for processing and function. PLoS Genet. 1, e53.
- processing and function. PLoS Genet. 1, e53. 19. Jia, J., Kolterud, A., Zeng, H., Hoover, A., Teglund, S., Toftgard, R., and Liu, A. (2009). Suppressor of Fused inhibits mammalian Hedgehog signaling in the absence of cilia. Dev. Biol. 330, 452–460.
- Collier, L.S., Suyama, K., Anderson, J.H., and Scott, M.P. (2004). *Drosophila* Costal1 mutations are alleles of protein kinase A that modulate hedgehog signaling. Genetics 167, 783–796.

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Animal Cognition: Aesop's Fable Flies from Fiction to Fact

A new study shows that rooks are able to spontaneously drop stones into a tube of water to obtain a floating worm. This sophisticated problem solving raises intriguing questions about the use of imagination in animals.

Alex H. Taylor and Russell D. Gray

Do Aesop's fables (Figure 1) reflect the behaviour of real animals? While talking foxes and racing tortoises may be unlikely, Bird and Emery's recent findings suggest there may be a kernel of truth to one of Aesop's most famous stories. In the fable of the crow and the pitcher, a clever crow drops stones into a jug of water in order to raise the level and ease its thirst (Figure 1) [1]. The rooks in the experiment reported recently in Current Biology by Bird and Emery [2] did something strikingly similar - they dropped stones into a tube of water in order to bring a floating worm within reach. Two of

the four rooks tested were able to spontaneously solve this problem on the first trial. The rooks were then able to rapidly learn to drop big stones, rather than small ones, into the tube. They also rapidly learnt to drop stones only into tubes containing water, and not those containing sawdust.

At first glance, the way the birds solved these tasks seems remarkably insightful and human-like. The rooks only put in sufficient stones to bring the worm within reach, and then did not continue to add stones once the worm had been removed. The rooks also appeared to examine the problem before putting stones into the tube, consistent with the idea that they initially assessed the task. One interpretation of these results is that the rooks had immediate causal knowledge of the task [3]. That is, they understood how the stones would interact with the water and therefore could estimate how high the water would rise once a certain number of stones were put into the tube. As the fable tells it, the crow put the stones into the pitcher because it *knew* that this would cause the water level to rise.

However, the follow-up experiments preclude the use of such human-like causal knowledge. If the rooks had understood how stones interact with water they should have also known that bigger stones would displace more water. In contrast to this expectation, the rooks did not immediately use large stones when presented with a choice between small and large stones, although they quickly learnt to do so. The rooks also did not seem to have knowledge of the peculiar causal



Figure 1. In Aesop's fable of "The Crow and the Pitcher", the thirsty crow drops stones into a jug of water in order to raise the level and ease its thirst. From [1].

characteristics of water. When presented with a choice between a tube with water and one with sawdust, the rooks had to learn to choose the water-filled tube. The follow-up experiments carried out by Bird and Emery [2] therefore exemplify the common paradox found in studies of animal cognition. Animals can behave in apparently complex ways that lead us to believe they have cognitive abilities just like us. But when we start to probe their performance with more revealing tasks, they make mistakes that indicate that they are solving these tasks using simpler cognitive mechanisms. What exactly, then, were the rooks thinking when they solved the problem?

In the past, spontaneous problem solving has been suggested to be based on 'insight', a rather murky term that has both folk meaning in human language and several technical definitions. Thorpe's [4] commonly cited definition of insight is, "the sudden production of new adaptive responses not arrived at by trial behaviour or the solution to a problem by the sudden adaptive reorganization of experience". However, use of this term leaves us with a cognitive black box. What kind of cognitive mechanisms allow the sudden reorganisation experience? How does the animal know that this reorganisation is adaptive?

A related idea that avoids such vagaries is Dennett's [5] conception

of a 'Popperian creature'. According to Dennett, Popperian creatures have imagination and so can mentally simulate the real world and the causal regularities in it. Thus, when these creatures are faced with a novel problem, they can engage in a process of mental conjectures and refutations to try out various solutions. Given the results of experiments 2 and 3 of Bird and Emery [2], it seems unlikely that the rooks were using such complex cognition. As the crows did not understand the differential effects of large and small stones on water, or the effects of stones on water and sawdust, it seems likely that they did not imagine how the stone would interact with the water before they dropped the stone into the water for the first time. Thus, the riddle of exactly how they managed to spontaneously solve the problem without trial and error learning still remains.

An alternative explanation for the spontaneous problem solving resides in the rooks' previous experience. The birds in this experiment all had previously dropped stones into a tube with a platform in order to collapse it and release food [6]. On their first trial with the new experiment they could have generalised this past experience to the new apparatus and dropped the stone down the water-filled tube. The stone dropping had a positive effect: the water rose and the worm moved closer. This would have reinforced the stone-dropping behaviour and so set up a perceptual-motor feedback cycle. The crows therefore continued to put stones into the tube until the worm rose within reach. Perceptual-motor feedback cycles of this type may also be able to explain other cases of apparently insightful problem solving in birds, such as spontaneous string pulling to obtain food in ravens [7] and keas [8].

What about our close primate relatives? Orangutans have recently been shown capable of solving a very similar problem to the one Bird and Emery [2] presented to the rooks. Mendes *et al.* [9] presented orangutans with a tube quarter-filled with water. Floating on the surface of the water was a peanut. To solve the problem the apes needed to collect water from a drinking container in their mouths and spit it into the tube in order to raise the water level and gain the peanut. After trying to reach the peanut with their fingers or mouths, the orangutans spat water into the tube in order to raise the level and so gain the reward on the first trial. Interestingly, the apes also solved a control task where there was no water in the tube, which suggests that the sight of water was not necessary for the solution of the problem. However, as the apes were already experienced water spitters, testing with naïve individuals is needed to confirm this conclusion.

The crucial issue for the interpretation of the orangutan problem solving is the first spitting attempt. As Mendes et al. [9] note, it is unclear if the apes spat the water, saw the effect it had on the peanut and then repeated it, or if the apes had fully formed the solution to the problem in their minds before spitting the first mouthful. In other words, was this a randomly generated behaviour that was then reinforced, or did the apes imagine the solution and so seek out the water in order to spit into the tube? Given the novelty of the task and the fact that the apes had never used water to solve other problems, the evidence for imagination is stronger than that in the rook study. However, the future experiments with opaque tubes and naïve subjects proposed by Bird and Emery could provide more compelling evidence for imagination in corvids.

References

- 1. Aesop, The Aesop for Children, Illustration by Milo Winter, Project Gutenberg etext 19994, http://www.gutenberg.org/etext/19994.
- Bird, C.D., and Emery, N.J. (2009). Rooks use stones to raise the water level to reach a floating worm. Curr. Biol. 19, 1410–1414.
- Kummer, H. (1995). Causal knowledge in animals. In Causal Cognition. A Multidisciplinary Debate, D. Sperber, D. Premack, and A.J. Premack, eds. (Oxford, UK: Clarendon Press), pp. 26–39.
- Thorpe, W.H. (1964). Learning and Instinct in Animals (London: Methuen).
- Dennett, D.C. (1996). Kinds of Minds: Toward an Understanding of Consciousness. (New York: Harper Collins/Basic Books).
- Bird, C.D., and Emery, N.J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. Proc. Natl. Acad. Sci. USA 106, 10370–10375.
- Heinrich, B. (1995). An experimental investigation of insight in ravens (Corvus corax). Auk. 112, 994–1003.
- Werdenich, D., and Huber, L. (2006). A case of quick problem solving in birds: string-pulling in keas (Nestor notabilis). Anim. Behav. 71, 855–863.
- Mendes, N., Hanus, D., and Call, J. (2007). Raising the level: orangutans use water as a tool. Biol. Lett. 3, 453–455.

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