

9. Fiorito, G., and Scotto, P. (1992). Observational learning in *Octopus vulgaris*. *Science* 256, 545–547.
10. Hochner, B., Shomrat, T., and Fiorito, G. (2006). The octopus: a model for a comparative analysis of the evolution of learning and memory mechanisms. *Biol. Bull.* 270, 308–317.
11. Squire, L.R., and Alvarez, P. (1995). Retrograde amnesia and memory consolidation: a neurobiological perspective. *Curr. Opin. Neurobiol.* 5, 169–177.
12. Hochner, B., Brown, E.R., Langella, M., Shomrat, T., and Fiorito, G. (2003). A learning and memory area in the octopus brain manifests a vertebrate-like long-term potentiation. *J. Neurophysiol.* 90, 3547–3554.
13. Di Cosmo, A., Paolucci, M., and Di Cristo, C. (2004). N-methyl-D-aspartate receptor-like immunoreactivity in the brain of *Sepia* and *Octopus*. *J. Comp. Neurol.* 477, 202–219.
14. Lima, P.A., Nardi, G., and Brown, E.R. (2003). AMPA/kainate and NMDA-like glutamate receptors at the chromatophore neuromuscular junction of the squid: role in synaptic transmission and skin patterning. *Eur. J. Neurosci.* 17, 507–516.
15. Johnston, D., Williams, S., Jaffe, D., and Gray, R. (1992). NMDA-receptor-independent long-term potentiation. *Annu. Rev. Physiol.* 54, 489–505.
16. Nicoll, R.A., and Schmitz, D. (2005). Synaptic plasticity at hippocampal mossy fibre synapses. *Nat. Rev. Neurosci.* 6, 863–876.
17. Burrell, B.D., and Sahley, C.L. (2004). Multiple forms of long-term potentiation and long-term depression converge on a single interneuron in the leech CNS. *J. Neurosci.* 24, 4011–4019.
18. Xia, S., Miyashita, T., Fu, T.F., Lin, W.Y., Wu, C.L., Pyzocha, L., Lin, I.R., Saitoe, M., Tully, T., and Chiang, A.S. (2005). NMDA receptors mediate olfactory learning and memory in *Drosophila*. *Curr. Biol.* 15, 603–615.
19. Glanzman, D.L. (2007). Simple minds: the neurobiology of invertebrate learning and memory. In *Invertebrate Neurobiology*, G. North and R.J. Greenspan, eds. (New York: Cold Spring Harbor Laboratory Press), pp. 347–380.

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Animal Cognition: Rooks Team up to Solve a Problem

A recent study has found that rooks team up to get food in a cooperative instrumental task, but they may have difficulties in understanding when cooperation is necessary and how it works.

Thomas Bugnyar

For us humans, cooperation is a fundamental feature of our life, essential for our societies and cultural achievements. No wonder that explaining the evolution of human cooperation, its maintenance and its cognitive underpinnings is one of the hottest topics in science [1]. In the animal kingdom, cooperation can take many forms [2], from interactions of genetically related individuals, exemplified in eusocial insects such as bees, ants and termites, to interactions between different species, such as the mutualisms observed between ants and plants. Of particular interest for cognitive scientists are systems in which individuals flexibly decide whether or not to cooperate in a given situation and selectively choose among potential cooperation partners that possess different qualities. Such flexible decisions have been described for species of different taxonomic groups, ranging from mammals to birds and fish, that team up for accessing food, raising young, avoiding predators and defending resources [3–5]. Well-known examples are the cooperative hunting of carnivores [6] and coalition formation during fights in primates [7]. The difficulty with these types of naturally occurring cooperation is teasing

apart different phenomena like mutual attraction towards a resource, coordination among individuals, and understanding of the others' roles.

Experimental work on the cognitive aspects of cooperation has focused on problem solving in the foraging context, with individuals working together to gain access to food [8,9] or taking turns in producing and sharing food [10]. In these experiments manipulations were made to: the accessibility of food, so that it can be reached without the help from others; the distribution of food, so that it can or cannot be shared with ease; and the role and availability of partners, so that different strategies are possible [11]. Depending on the paradigm, individuals are thus tested for their understanding of when cooperation is necessary (if a goal can be achieved alone), how cooperation works (who is taking which role) and who is an effective cooperation partner. Surprisingly perhaps, studies have only been conducted with a limited number of species, mostly non-human primates.

Seed *et al.* [12] have now reported a novel and important advance in our understanding of the cognitive underpinnings of cooperation: they have shown that the rook, a member of the crow-family *Corvidae*, is capable

of solving a cooperative instrumental task (Figure 1) but apparently shows little sensitivity to the need for a partner. These results are interesting in two ways: on the one hand, they support the idea that corvids are able problem solvers; but on the other hand, they challenge the idea that the birds have an understanding of the problem. The latter is surprising: over the past decade studies on social cognition have described capacities in corvids, such as tactically deceiving others or judging the others' perspective [13,14], which rival those found in non-human primates, even apes [15]. Importantly for the new study [12], rooks live in societies that differ from those of most primates. They form long-term affiliative relationships with one or two individuals, who tend to support one another during fights and regularly share food [16]. Seed *et al.* [12] therefore argue that rooks could be expected to cooperate when accessing food in an experimental setting. But their reliance on a relatively small network of valuable relationships raises the possibility that their understanding of cooperation is different from that of primates such as chimpanzees, who have access to a large biological market [17], forming short- and long-term relationships with a varying number of individuals.

In their study, Seed *et al.* [12] provided rooks with food on a platform that was placed outside their cage but could be reached by pulling on a string. Because the string was threaded through metal loops on the platform, with both ends extending into the test-compartment, pulling from only one end was ineffective and resulted in an unthreaded string; to successfully

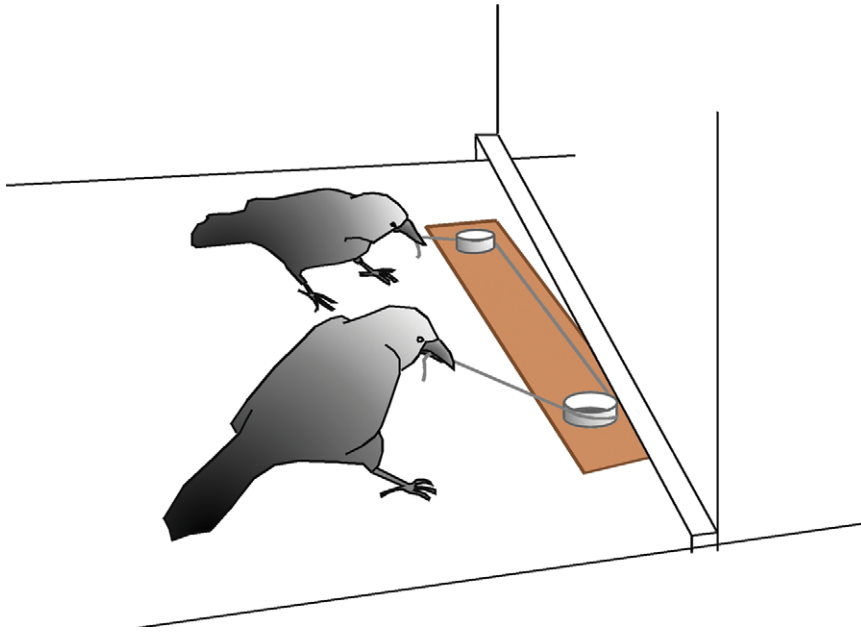


Figure 1. Two rooks working together to pull a platform containing two food bowls into their test-cage.

(Illustration made by Johanna Kramer from a photo courtesy of Amanda Seed.)

move the platform, individuals had to pull on both ends of the string simultaneously [8]. Each of the eight rooks participating in the experiment was tested in two dyadic combinations. Impressively, all pairs were able to solve the task within a short time period. Moreover, in a similar way to primates [18], the pairs' success in reaching the reward by simultaneously pulling the strings correlated with the pairs' mutual tolerance in a food-sharing test, which was conducted before and after the cooperation test. But unlike primates [18,19], the rooks' propensity to cooperate was not affected by the distribution of food on the platform — that is, by how easily one individual could monopolize all items.

What is the cognitive mechanism underlying the cooperation in this set-up: do rooks understand that they need a partner? A possible alternative would be that tolerant individuals merely direct their actions simultaneously towards the reward and successfully solve the task without any understanding of the other's behaviour. Seed *et al.* [12] performed two follow-up experiments to address this question. In the delay test, one bird of a dyad faced some resistance in entering the experimental room, so that the bird already at the apparatus should delay pulling the string for the

period of time it took his partner to join him. In the choice test, individual rooks could choose between two platforms, one having the two ends of the string next to each other, so that it could be picked up by a single bird, and the second having the two ends of the string far apart, so that a cooperation partner would be needed. In both experiments, the rooks performed as if they did not understand the requirements of the task. In the delay test, all birds pulled the string without waiting for the partner. In the choice test, four out of six birds showed no preference for the apparatus that could be manipulated alone over the apparatus that required the action of two birds. The authors contrast the behaviour of rooks with that of chimpanzees, which did wait for a partner in a delay test [20], and interpret the findings with a difference in understanding of the partner's action.

Of course, it is difficult to draw firm conclusions from a single study. Critics might argue that the findings in rooks and chimpanzees are hardly comparable, because the time required to wait for a partner was much shorter in the apes than in the birds. Moreover, two of the rooks did perform well in the choice test, which, because of the small sample size, corresponds to one third of the individuals tested. Since

a high inter-individual variation is typical for cognitive tasks, a bigger sample size could have produced different results. Although the authors openly address these problems in the paper, there is the danger that a simplified interpretation like 'primates understand, corvids do not' prevails as the take-home message. Nonetheless, Seed *et al.* [12] are to be congratulated for opening up the field for comparative research. Investigating the cognitive underpinnings of cooperation in mammalian and avian species with similar paradigms is relevant for our understanding of convergent evolution [15]. Notably, linking the species' cooperative abilities with the ideas of biological market theory [17] has a high potential and has already become the topic of recent international funding programmes.

References

1. Hammerstein, P. (2003). Genetic and Cultural Evolution of Cooperation (Cambridge, Mass.: MIT Press).
2. Dugatkin, L.A. (1997). Cooperation Among Animals (Oxford: Oxford University Press).
3. Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296, 69–72.
4. Connor, R.C. (1996). Partner preferences in by-product mutualism and the case of predator inspection in fish. *Anim. Behav.* 51, 451–454.
5. Bshary, R., and Grutter, A.S. (2006). Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441, 975–978.
6. Packer, C., and Rutan, L. (1988). The evolution of cooperative hunting. *Am. Nat.* 132, 159–198.
7. Harcourt, A.H., and de Waal, F.B.M. (1992). Coalitions and Alliances in Humans and Other Animals (Oxford: Oxford University Press).
8. Hirata, S., and Fuwa, K. (2007). Chimpanzees learn to act with other individuals in a cooperative task. *Primates* 48, 13–21.
9. De Waal, F.B.M., and Berger, M.L. (2000). Payment for labour in monkeys. *Nature* 404, 563.
10. Hauser, M.D., Chen, M.K., Chen, F., and Chuang, E. (2003). Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. R. Soc. Lond. B* 270, 2363–2370.
11. Noë, R. (2006). Cooperation experiments: coordination through communication or acting apart together. *Anim. Behav.* 71, 1–18.
12. Seed, A.M., Clayton, N.S., and Emery, N.J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proc. R. Soc. Lond. B* 275, 1421–1429.
13. Bugnyar, T., and Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proc. R. Soc. Lond. B* 272, 1641–1646.
14. Clayton, N.S., Dally, J.M., and Emery, N.J. (2007). Social cognition by food-caching corvids. The Western scrub-jay as a natural psychologist. *Phil. Trans. R. Soc. Lond. B* 362, 507–522.
15. Emery, N.J., and Clayton, N.S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* 306, 1903–1907.

16. Emery, N.J., Seed, A.M., von Bayern, A.M., and Clayton, N.S. (2007). Cognitive adaptations to social bonding in birds. *Phil. Trans. R. Soc. Lond. B* 362, 489–505.
17. Noë, R., and Hammerstein, P. (1995). Biological markets. *Trends Ecol. Evol.* 10, 336–339.
18. Melis, A.P., Hare, B., and Tomasello, M. (2006a). Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Anim. Behav.* 72, 275–286.
19. De Waal, F.B.M., and Davis, J.M. (2003). Capuchin cognitive ecology: cooperation based on project returns. *Neuropsychologia* 41, 221–228.
20. Melis, A.P., Hare, B., and Tomasello, M. (2006b). Chimpanzees recruit the best collaborators. *Science* 311, 1297–1300.

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Motor Control: From Joints to Objects and Back

A new study shows that the nervous system has the flexibility to learn dynamics in object-centered coordinates – up to a limit.

Olivier White and Jörn Diedrichsen

The primary task of the nervous system is to guide action. But in order to move the body gracefully, the brain needs to anticipate the forces and torques that act on the joints. For example, when we move only the lower arm, we need to anticipate and counteract the induced torques that act on the upper, non-moving part of the arm, to ensure stability of the shoulder. This is a complicated problem, as these torques depend on the relative position of the joints, body orientation with respect to gravity, and on the dynamics of tools or other objects we manipulate.

How does the brain solve this problem? One suggestion is that the brain learns an internal model of the body's dynamics by associating the state of the body — its position, velocity, joint angles, and so on — with forces that arise depending on the state of the limbs. This process has been extensively investigated using dynamic force fields. In a typical experiment, participants move a handle to a target position, while a robotic device generates a position- or velocity-dependent force on the arm. At first, participants make large errors that gradually decrease with further exposure to the force field. If the force field is unexpectedly removed, the hand path deviates in the opposite direction, indicating that the motor control system learned to actively compensate for the expected forces [1].

But what exactly did the brain learn? How we generalize learning from one task to another can help to uncover the structure of the learned

representations. In a typical generalization experiment, participants learn to compensate for a force field in one arm position, and then perform similar movements in an unvisited part of the workspace. If participants learned to associate certain movement velocities (\dot{x}) with forces (F) in 'extrinsic' coordinates (Figure 1A), then they should expect the same forces in

Cartesian space even in a new joint configuration (grey). If, on the other hand, participants learned to associate changes in joint angles (θ) with torques on those joints (τ) — they learned in an 'intrinsic' reference frame — then they should expect forces that are rotated with the joint configuration (Figure 1B). For learning of force fields within a limb, the evidence favours the idea that people learn in an intrinsic coordinate system [1–3].

Thus, learning of force fields can be thought of as the tuning of weights between neuronal populations that code for joint position and velocity, and elements that code for joint torques or muscular forces [4] (Figure 1C). In this

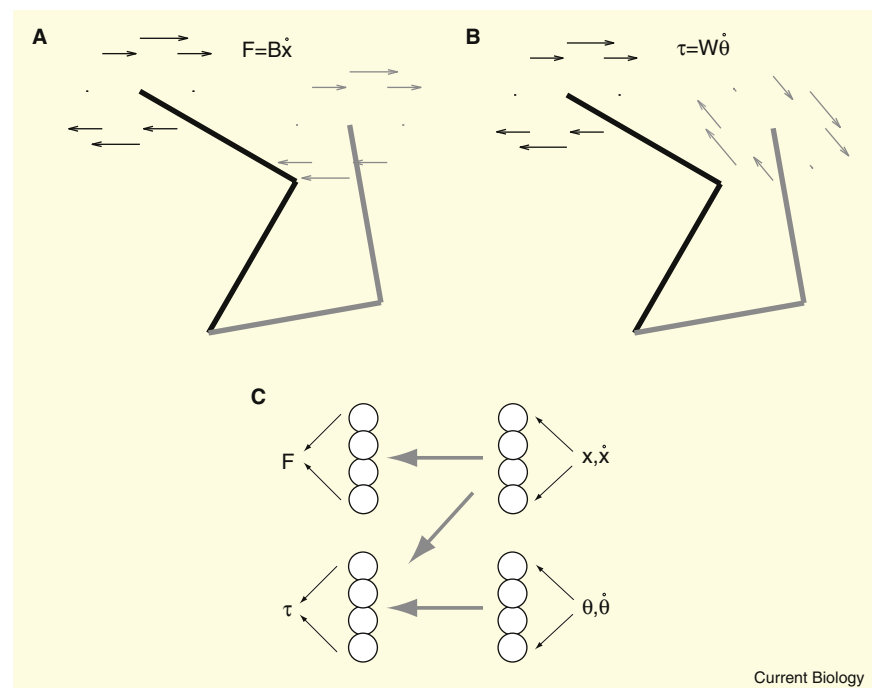


Figure 1. Learning to compensate for force fields.

A force field (black arrows) pushes the hand rightward for upward movements and leftward for downward movements. (A) If participants learn that a force field depends on movement direction in extrinsic space, changes in arm position (grey) do not lead to a directional change of anticipated forces (grey arrows). (B) Conversely, when the forces are learned in terms of joint coordinates, the anticipated forces rotate with the arm configuration. (C) Force fields can be learned as associations between neural elements with preferred directions in external space (x, \dot{x}), joint angles ($\theta, \dot{\theta}$), and neural assemblies indicating forces in external space (F) and torques (τ).