A particularly instructive example is an experimental study of public-information use (the ability to assess the quality of a resource on the basis of the success of other individuals) in two closely related species of sticklebacks (Figure 1). Isabelle Coolen and colleagues recently found that nine-spined sticklebacks, after watching conspecific or heterospecific 'demonstrator' fish feeding at two patches, when tested alone, tend to approach the former location of the richer patch. As their observational experience was restricted to the relative success of their demonstrators, and potential alternative explanations could be ruled out, they surmised that nine-spined sticklebacks were capable of public-information use. However, three-spined sticklebacks, when subject to the same test, swam with equal frequency to the former locations of rich and poor patches. These species were collected from the same streams, frequently shoal together, and feed on similar foods. Why should one species and not the other exhibit this specific form of social learning?

The answer to this conundrum comes from a surprising source: mathematical analyses of the adaptive advantages of human culture. Californian anthropologists Rob Boyd and Peter Richerson postulated a *costly information hypothesis*, which proposes an evolutionary trade-off between reliable but costly self-acquired information and potentially less reliable but cheap socially transmitted information. Here, the relative cost of acquiring personal information varies between the two stickleback species, which determines the value of public information. Three-spines have large spines and armoured body plates, robust structural defenses that allow them to sample alternative food patches directly, in relative safety. Such sampling by nine-spines, which have weaker physical defenses, would leave them vulnerable to predation, and hence in fitness terms would be extremely costly. Consequently, nine-spines spend much of their time in refuge, from where selection seemingly has favoured the ability to monitor the foraging success of others. Further research confirms that this species difference is robust.

In fact, considerable evidence is accumulating among fish, birds and mammals that animals will ignore social information under specific and predictable circumstances. For instance, nine-spine sticklebacks will ignore public information if they have reliable, up-to-date personal information, yet switch to exploiting public information if their personal information is unreliable or outdated. Social and personal information are not weighted equally, and animals will toggle between the two in a conditional manner, according to their respective reliability and cost. Evolved rules, labelled *social learning strategies*, dictate the circumstances under which individuals copy others, and when they rely on personal experience. One such rule — copy when asocial learning is costly — has already been described for sticklebacks, but there are likely to be many social learning strategies in nature (conform, copy the most successful individual, copy anyone doing better than you, and so on) and researchers are only now just beginning to investigate them.

The study of animal culture is unmasking a fascinating and rich interplay between two inheritance systems — genes and culture — in which each has, to some extent, been shaped by the other.

Further reading

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Chimpanzees infer the location of a reward on the basis of the effect of its weight

Daniel Hanus and Josep Call

The extent to which animals in general, and non-human primates in particular, understand physical causality is currently unclear [1,2]. One way to assess an animal's causal understanding is to test its ability to analyze a causal chain backwards — to infer cause from an effect [3]. In the study reported here, chimpanzees saw a given outcome (effect) of an action and had to infer the preceding event (cause) in order to solve the problem. More specifically, subjects saw a banana being hidden inside one of two opaque cups mounted on opposite sides of a balanced beam, but they were kept ignorant about the banana's exact location. Subsequently, the subjects witnessed the balance beam tilting to one side after the experimenter released it from its equilibrium position (the Balance condition). The chimpanzees preferentially (and from trial one) selected the lower, compared to the upper, cup. Two control conditions demonstrated that the chimpanzee subjects lacked an intrinsic preference for the lower cup when there was no movement involved (the Wedge condition) or when the balance beam was tilted by the experimenter's action (the Non-causal balance condition). We conclude that the chimpanzee subjects of our experiments demonstrated evidence of causal inference based on an object's weight.

In our experiments, the chimpanzee subjects selected the baited cup significantly above chance in the Balance condition (see the Supplemental data available on-line for details). We compared the Balance condition to two control conditions. In the Wedge condition, the cups were mounted

on opposite sides of a fixed ramp so that they simulated the position of the cups in the titled balance position. This condition allowed us to assess whether subjects simply showed an intrinsic preference for the bottom cup. The subjects performed significantly better in the Balance condition than in the Wedge condition. Analyzing the first trial performance confirmed this result. All eight subjects in the Balance condition selected the bottom cup, but only four out of eight subjects did so in the Wedge condition. It is remarkable that for subjects that began with the Balance condition (group 1), a comparison between the last Balance-block with the first Wedge-block revealed that they significantly decreased their performance by 30% (Figure 1). In contrast, subjects that began with the Wedge condition (group 2) significantly improved their performance by 18% when comparing the last Wedge-block to the first Balance-block. We tested the Non-causal balance control condition on a new group of subjects. In this condition subjects witnessed the same beam movement as in the Balance condition, except that the movement was caused by the experimenter pushing down the balance beam, not by the weight of the reward. This condition allowed us to assess whether subjects simply preferred the cup that followed a downward trajectory independently of its cause. Subjects performed significantly better in the Balance than in the Non-causal balance condition (Figure 2). In general, there was no significant improvement in performance across blocks of trials within any of the three conditions.

Our results suggest that chimpanzees inferred the location of the reward based on the movement and the resultant final position of the balance on which the cups were mounted. This result was not due to an intrinsic preference for the bottom cup, because subjects lacked such a preference in the first trial of the Wedge condition. Arguably, subjects may have been particularly attracted by falling (rather than raising) trajectories, as shown for cotton-top tamarins and human infants younger than 2.5 years of age [4,5]. We can rule out that explanation, however,

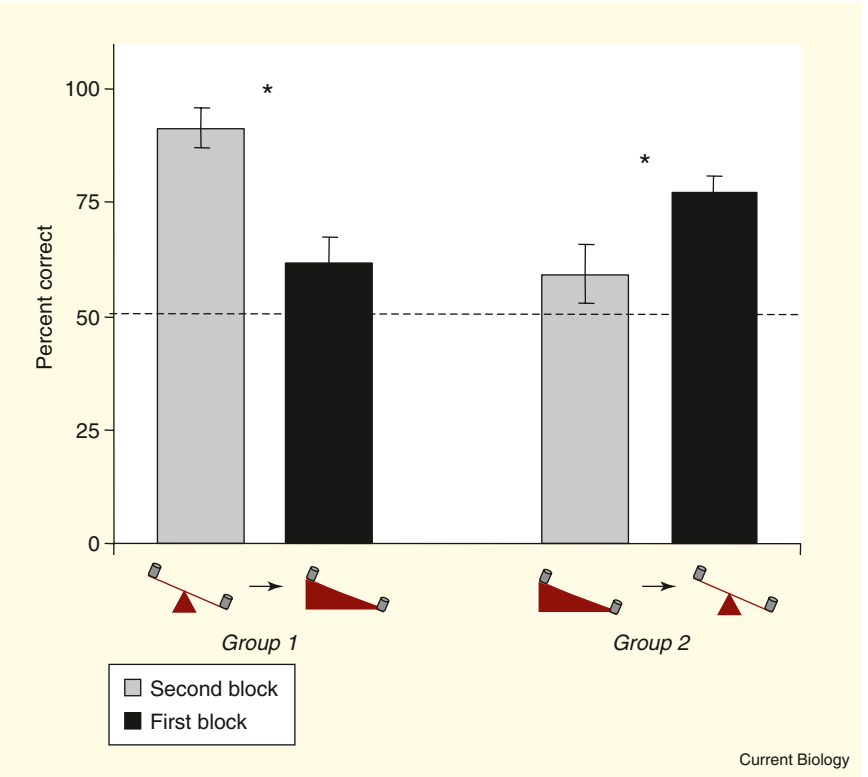

Figure 1. Mean percent of trials (±SEM) in which subjects selected the lower cup for subsequent testing blocks of different conditions.

For group 1, performance of the last balance-block (trial 17–32) is compared with the first wedge-block (trial 33–48). For group 2, the performance of the last wedge-block (trial 17–32) is compared with the first balance-block (trial 33–48). Asterisk: $p < 0.05$.

because subjects did not show such preference in the Non-causal balance condition. Therefore, it is conceivable that subjects selected the bottom cup because they inferred that the presence of the reward, and its weight in particular, caused the balance to tilt. These data support the notion that chimpanzees more easily solve tasks whose elements hold a causal rather than an arbitrary relation [2,6]. Subjects' flawless performance in the first trial ruled out the possibility that they learned to respond in this way during the course of the experiment.

Furthermore, the chimpanzee subjects that received the Wedge condition first increased their performance when confronted with the Balance condition, whereas the subjects that were tested with the Balance condition first decreased their subsequent performance upon encountering the Wedge condition. This shows that the chimpanzee subjects clearly detected the difference between the two conditions. More importantly, these results make a 'choosing the lower cup' heuristic untenable, because once the subjects were already choosing the bottom cup in the Balance condition, it is unclear why they would decrease their preference for the bottom cup drastically in the following Wedge condition.

A typical approach to investigating causal understanding in non-human animals is to test their ability to anticipate the effect that their *own* action will have on certain elements of the physical world. If they understand the underlying causal principle then they are expected to act accordingly towards a wanted outcome — in most cases, access to food [3,7]. In general, tool-using behavior is a typical example for the 'productive' aspect in causal reasoning. According to the definition of Visalberghi and Tomasello [7], 'comprehensive' or 'postdictive' abilities can be postulated when subjects solve a problem by inferring the preceding event (the cause), on the basis of

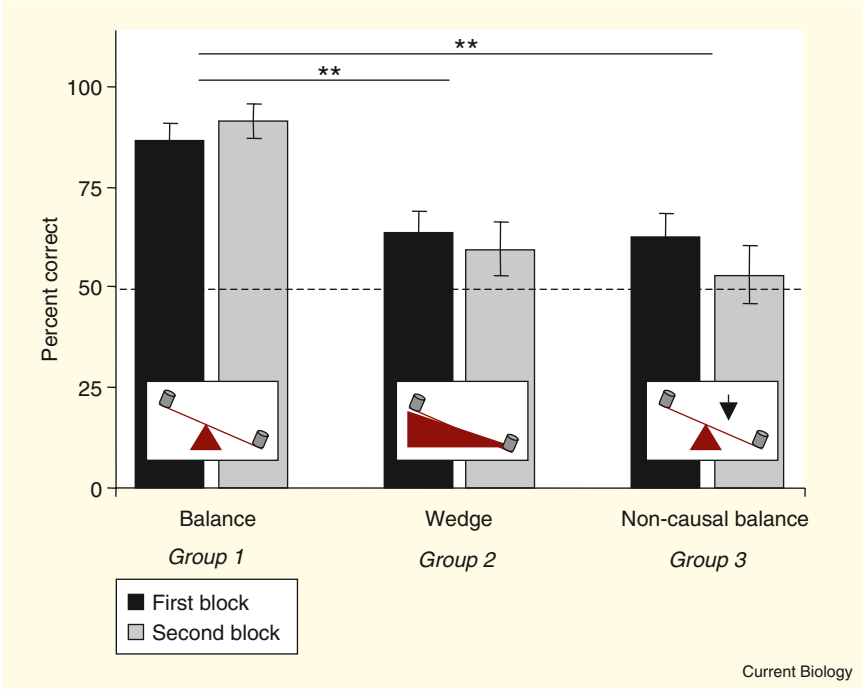

Figure 2. Mean percent of trials (±SEM) in which subjects selected the lower cup as a function of condition.

Only the first 32 trials for each group are included, with the first block containing trial number 1–16 and the second block containing trial number 17-32. Double asterisk: $p < 0.001$.

a given outcome (the effect). We argue that the current study revealed evidence that chimpanzees can engage in the 'comprehensive' aspect of causal reasoning with regard to object weight. Further research is needed to clarify whether such basic comprehensive aspect of causal reasoning represents a precursor of more sophisticated forms of physical reasoning found in adults involving abstract concepts such as gravity.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/9/R370/DC1

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Fasting or feasting in a fish social hierarchy

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Understanding why and how subordinates of many social animals remain consistently smaller than dominants is important for determining the mechanisms underlying the structure and stability of hierarchical societies. Here we show that competition over food and conflict over social rank are ultimately responsible for the regulation of subordinate growth in the group-living reef fish, *Paragobiodon xanthosomus* (Gobiidae). Subordinates benefit from reducing their own food intake, and hence growth, when they approach a size where they risk conflict with dominants. Dieting appears to be a behavioural mechanism ensuring that subordinates remain smaller than dominants within the hierarchy.

P. xanthosomus is a goby that lives in colonies of the coral *Seriatophora hystrix*. Inside colonies, they form groups of up to 20 gobies: a breeding male and female (dominant breeders) plus several smaller non-breeding females (subordinate non-breeders) [1]. Subordinate non-breeders are organised into a size-based hierarchy with each female remaining consistently smaller than the one ranked above it [2]. Hierarchies function as queues for breeding. When a dominant dies, all subordinates below it grow and shift up in rank. Only when they reach the front of the queue can they breed [2].

Traditionally, subordinate growth regulation in size-based hierarchies has been viewed as a non-adaptive consequence of competition over limiting food resources — subordinates are out-competed by dominants, obtain less food and grow more slowly [3]. More recently, an alternative adaptive perspective has emerged — in hierarchies where body size determines dominance rank and rank determines reproductive opportunity, conflict over rank between dominant and subordinates is thought to select for social regulation of subordinate growth [2,4,5]. We tested the relative effects of both processes by training subordinate