“Causal Reasoning in Non-Human Animals” by Christian Schloegl and Julia Fischer

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Chapter 34

Causal Reasoning in Non-Human Animals

Christian Schloegl and Julia Fischer

Whether or not we grant non-human animals (hereafter: “animals”) the ability to think, or reason, depends very much on the time we live in, and the scientific school we belong to (Menzel & Fischer, 2011; Wild, 2008). Radical US behaviorists, for instance, questioned whether the “inner processes” that underlie animal behavior were amenable to scientific investigation (Watson, 1913); they assumed that animal behavior could largely be explained by the formation of stimulus–response patterns. Ethologists, in contrast, were much more interested in innate components, such as instincts, and, to a lesser degree, emotions. The cognitive revolution of the 1960s paved the way for the view that animals were capable of storing, processing, and retrieving information, and thus for cognitive approaches to animal behavior (Menzel & Fischer, 2011). But even before this turn of the tide, a handful of scientists who studied animal intelligence, such as Wolfgang Köhler (1917/1963) and Robert Yerkes (1916) were interested in the reasoning abilities of animals.

The purpose of this chapter is to provide an overview of the studies on animal causal reasoning. After a brief introduction into the history of the field and the terminology used, we discuss the developments over the last two decades; we will begin with an overview of studies on important prerequisites for causal reasoning, namely the ability to tune into causally relevant features and sensitivity for disruptions of causal regularities. Next, we will discuss inference by exclusion and various forms of reasoning about object–object relationships before turning toward reasoning about the outcome of one’s own actions. As the reader will see, not all animal taxa (i.e., groups of phylogenetically related species) have attracted the same amount of attention. Great apes tend to be the stars of the show, but considerable work has also been done in monkeys, and more recently in corvids and dogs. We conclude with a discussion of the limitations when it comes to reconstructing the evolution of cognitive abilities, and will provide some suggestions for future research.

A Little Bit of History

Wolfgang Köhler (1917/1963) was interested in the problem-solving abilities of chimpanzees (*Pan troglodytes*). In a series of now famous experiments, he was able to demonstrate that chimpanzees are able to combine tools to gain access to otherwise out-of-reach food. In another classical experiment, the animals stacked several boxes on top of each other to reach a banana attached to a string several meters above their head. Köhler did not use the term “causal reasoning”, however, and rather spoke of “insight”, although he clearly assumed that the chimpanzees understood causal relationships between objects. Similarly, other scientists who studied animals’ understanding of causal relationships at that time did not refer to causal understanding or reasoning (e.g., Grether & Maslow, 1937; Klüver, 1933).

Apart from these initial studies, the topic of causal reasoning was largely neglected until Premack and Premack (1994) published their seminal study on causal understanding in chimpanzees. The authors conducted a series of experiments to distinguish between three “[l]evels of causal understanding in chimpanzees and children,” with causal reasoning regarded as the deepest level, defined as an individual “solving problems in which he sees the outcome of a process but not its cause, and must infer or reconstruct the missing events” (p. 348). At the intermediate level, the subject would need to be able to decompose “intact causal sequences” (p. 348), such as an actor using a tool to manipulate an object, and to label the different components accordingly. At the “most superficial level” (p. 348), an individual would be able to “complete an incomplete representation of a causal action, by selecting the correct alternative” (p. 348). Premack and Premack then set out to test if their chimpanzees would reach the highest level. In the first task, the apes first learned to run down a path to a spot where food was hidden. After they had comprehended this task, the experimenter hid a rubber snake in the hiding spot at random intervals on 15% of the trials, which greatly disturbed the animals. In the test, the subject was able to see another chimpanzee, which had just completed the task, either after having encountered the food, or a snake. At stake was the question of whether the subject would be able to infer from the (positive or negative) emotional state of the other chimpanzee what would be found in the hide. None of the four chimpanzees was able to do this.

In the second task, the chimpanzees first observed how an experimenter hid an apple and a banana under two boxes. The subject was then distracted from the boxes for two minutes before seeing another person eating either an apple or a banana. Here, the question was whether the chimpanzee would infer that the second person had raided one of the boxes and that they should better approach the alternative box to obtain a reward. One of the four test subjects solved this second task instantaneously, while one always chose the container that held the food the other person had been eating. The other two chimpanzees erred on the first trials, but then started to solve the task. Hence, the results of only one chimpanzee suggest that it is within the species' realm to reach the highest level of causal reasoning.

From these findings, Premack and Premack (1994) concluded that learning may be found in numerous species, but reasoning, at least at the highest level, only in a very few. But possibly, reasoning about the cause of an emotional state may be very different from reasoning about the causal relationships resulting in the eating of fruit. Failures to reason may therefore be due to a lack of understanding of a very specific causal relationship, rather than a lack of the ability to reason per se. Interestingly, in violation of expectancy paradigms, human infants detect some violations of causality at an earlier age than other violations (Baillargeon, 2004; Muentener & Bonawitz, Chapter 33 in this volume); similarly, animals may not understand all causal relationship as causal and thus may not be able to reason about them.

Prerequisites for Causal Reasoning: Identifying Causally Relevant Features and Detecting Violations of Causality

A first step in the exploration of causal reasoning in animals is to assess whether they are sensitive to causal relationships. O'Connell and Dunbar (2005) showed chimpanzees and bonobos (*Pan paniscus*) videos of causally plausible and implausible events. For instance, in one set of videos, a banana was either lifted by a hand or was flying upward before the hand touched it. If the apes had seen the causally plausible event several times until they lost interest ("habituation"), and were then presented with the implausible event, they looked longer at the screen than if they had been shown the videos in reverse order. The authors interpreted this as sensitivity to causal plausibility (see Cacchione & Krist, 2004, for similar findings). Hanus and Call (2011) found that chimpanzees learn discriminations faster if these are based on causal rather than on arbitrary cues; for instance, when searching for food in opaque bottles, they learned to discriminate between lighter and heavier bottles faster than to discriminate between bottles of different colors, suggesting that chimpanzees are tuned to attend to causally relevant cues.

Among monkeys, capuchin monkeys (*Sapajus libidinosus*) received the most attention. This species is a highly proficient tool user (Fragaszy, Visalberghi, & Fedigan, 2004) and uses stones as a hammer to crack nuts, which they position on hard surfaces ("anvils"). They are therefore seen as prime candidates for some understanding of causality. Like chimpanzees, capuchin monkeys quickly learn in nut-cracking tasks to attend to the weight of tools and to select heavier stones as hammers (Schrauf, Call, Fuwa, & Hirata, 2012; Schrauf, Huber, & Visalberghi, 2008). Visalberghi, Fragaszy, and colleagues demonstrated that the monkeys also considered several other causally relevant features when selecting tools (i.e., mass of the stone, friability, distance to transport, features of the anvils; Fragaszy, Greenberg, et al., 2010; Fragaszy, Pickering, et al., 2010; Liu et al., 2011; Massaro, Liu, Visalberghi, & Fragaszy, 2012; Visalberghi et al., 2009).

Besides primates, corvids (ravens, crows, magpies, and jays) are famous for their large brains (Emery & Clayton, 2004) and advanced cognitive abilities (e.g., Bugnyar & Heinrich, 2005; Clayton & Dickinson, 1998; Dally, Emery, & Clayton, 2006). Rooks (*Corvus frugilegus*), for instance, showed indications of surprise and looked longer at pictures of causally implausible spatial relationships (e.g., objects suspended in mid-air above a surface) than at plausible illustrations (Bird & Emery, 2010). New Caledonian crows (*Corvus moneduloides*) belong to the most prolific tool users in the animal kingdom (Hunt, 1996, 2000; Weir, Chappell, & Kacelnik, 2002); like capuchin monkeys

(Fragaszy, Greenberg, et al., 2010; Visalberghi et al., 2009) and chimpanzees (Sabbatini et al., 2012), they attend to causally relevant features and select tools of the appropriate, but not necessarily optimal, length (Chappell & Kacelnik, 2002) and diameter (Chappell & Kacelnik, 2004). Similar to chimpanzees (Hanus & Call, 2011), these crows also quickly learned to select causally relevant tools when presented with a novel situation (Taylor et al., 2011; see Jelbert, Taylor, Cheke, Clayton, & Gray, 2014, for similar findings in a different task).

While the aforementioned examples focused mainly on physical causal relationships, some studies investigated the sensitivity to cause–effect relationships in social actions and events. For instance, chimpanzees and bonobos were shown a video in which either a human pushed another person from a chair to obtain a fruit, or one person simply fell off a chair and the fruit moved by itself to the other person (O'Connell & Dunbar, 2005). In another video, they either saw chimpanzees hunting and killing a colobus monkey or they saw the same video played backward. In test trials, the apes looked longer if they had been habituated to the causally plausible video than vice versa, again suggesting an understanding for causal plausibility and surprise upon seeing an implausible event. In a study on free-ranging African elephants (*Loxodonta africana*), Bates et al. (2008) placed a mix of fresh urine and earth in the path of traveling groups and found that the animals inspected the urine samples longer if they stemmed from a female traveling behind them, indicating that they were surprised to detect the scent of this animal in a causally impossible location.

An indication for an innate preference for "causal agents" comes from a study with chicks (*Gallus gallus*). Right after hatching, chicks are imprinted on their parents and begin to constantly follow them. In the absence of their parents, chicks can also be imprinted on other individuals or even moving objects. Mascalzoni, Regolin, and Vallortigara (2010) showed freshly hatched chicks a so-called Michotte's launching event, in which one moving object A touches another object B, which subsequently begins to move. These launching events elicit strong impressions of causality in humans, (i.e., that A causes B to move; White, Chapter 14 in this volume). Even though both objects had moved identical distances, chicks preferred object A when subsequently presented with a choice between both objects; in other words, they preferred the self-propelled over the not self-propelled object. As these chicks did not have any previous experiences with moving objects, it appeared that the chicks have an innate sensitivity for causal agents.

Taken together, these studies indicate that several species are sensitive to causally relevant features or cues in their environment (e.g., the weight or length of a tool), may be innately tuned to (at least some) of these features, and act as if surprised if causally sound relations are violated (e.g., objects floating in mid-air). Nevertheless, there is considerable variation between the tasks. In the study of O'Connell and Dunbar (2005) mentioned earlier, the strength of the dishabituation in the test trial was strongest with the hunting sequence shown in reversed order and lowest in case of a banana suspended in mid-air. In the work of Cacchione and Krist (2004), the apes looked equally long at a scene in which an apple was resting on a horizontal board and a scene in which the apple was touching a vertical board but was otherwise floating. Interestingly, many species also fail at solidity tasks. The general principle here is that a reward cannot pass through a solid barrier and the subjects are asked to search for the reward; most subjects, however, including non-human primates and dogs (*Canis familiaris*), often search behind the barrier, suggesting that they assume that the reward could have passed through the barrier (see Müller, Riemer, Range, & Huber, 2014, and references therein, and also Kundey, De Los Reyes, Taglang, Baruch, & German, 2010, for positive evidence in dogs).

There are also notable species differences. In a task to assess if capuchin monkeys and chimpanzees are attentive to the functional, causally relevant features of tools, they were trained to insert a stick into a tube to obtain a reward hidden inside the tube (Sabbatini et al., 2012; see Figure 34.1). The animals could choose between sticks of different lengths (with only the longest stick long enough to reach the reward) and different handles. During a transfer phase, the handles were switched between the tools. Only the chimpanzees attended to the functional features and continued to use the tool with the appropriate length, whereas the capuchin monkeys needed considerably more training to do so. Capuchin monkeys tested by Fujita, Kuroshima, and Asai (2003) had to choose between two rewards and two hooked tools to pull in the reward (designed after the original study by Brown, 1990). On each trial, the location of the reward, the presence of a trap into which a reward could fall, and the orientation of the hook ensured that only one tool was functional; hence, only the choice of the correct tool would enable the monkeys to obtain the reward. The monkeys, however, were not able to incorporate the orientation of the hook, the location of the reward, and the location of a trap in their decisions at the same time. These limitations are in stark contrast to the monkeys' performances in the nut-cracking tasks mimicking a natural foraging situation (see earlier discussion). Possibly, the capuchin monkeys' attention to causally relevant features is restricted and attuned to their natural tool-using behavior.

[INSERT FIGURE 34.1 about here]

Causal Reasoning

Given that at least some species are sensitive to causally relevant features, one may probe if they are indeed able to make causal inferences, that is, if the animals can use their understanding of (certain) causal relationships to make deductions about unobservable reasons for outcomes they have observed. Within the faculty of reason, differences seem to exist in the levels of complexity of the tasks, as well as the mental processes required to solve them. In the following, we will discuss different types of causal reasoning.

Inference by Exclusion

One relatively simple form of causal reasoning is the ability to select the correct option by excluding potential alternatives. This corresponds to the “superficial level” identified by Premack and Premack (1994), and has been extensively studied in animals. To our knowledge, the first experiment on inference by exclusion was conducted in the 1930s to test “insight” in monkeys. Grether and Maslow (1937) confronted seven different species with two cups, with food hidden underneath one of them. The empty cup was then lifted to show that nothing was underneath it. Some subjects instantaneously selected the alternative cup, suggesting that they grasp the relationship that because one cup is empty, the reward must be hidden in the other cup.

In the 2000s, the research community rediscovered Grether and Maslow’s (1937) task, and a modified version quickly became popular in animal cognition research. Call (2004), for instance, again hid a food reward in one of two cups, but now confronted the subjects not only with a condition in which they were informed that one cup was empty (and the exclusion could be made), but also with control conditions. In these, the animals either saw the content of the baited cup, of both cups, or of none of the cups. In a plethora of studies, success in this task could be demonstrated in the great apes (Call, 2004; Hill, Collier-Baker, & Suddendorf, 2011), capuchin monkeys (Paukner, Huntsberry, & Suomi, 2009; Sabbatini & Visalberghi, 2008), olive baboons (*Papio hamadryas anubis*) (Schmitt & Fischer, 2009), ravens (*Corvus corax*) (Schloegl et al., 2009) and Clark's nutcrackers (*Nucifraga columbiana*) (Tornick & Gibson, 2013).

Although most of the tested species solved this task, performances differ as several species seem to be highly susceptible to modifications of the experimental procedures. Sheep (*Ovis orientalis aries*) and dwarf goats (*Capra aegagrus hircus*) were distracted by the hand movements of the experimenter when he lifted the empty cup to reveal its content. When the setup was changed to control for the distracting movement cues, a few individual goats could solve the task (Nawroth, von Borell, & Langbein, 2014; see Erdöhegyi, Topál, Virány, & Miklósi, 2007, for parallel results in dogs). Similarly, only one out of six carrion crows (*Corvus corone corone*) managed to avoid the empty cup when its content was shown, whereas three birds significantly preferred the empty cup (two other birds were indifferent). When the experimenters controlled for the movement during the lifting of the cup, those birds that had been previously distracted now managed to avoid the empty cup, whereas the indifferent birds continued to choose at random (Mikolasch, Kotrschal, & Schloegl, 2012). Kea (*Nestor notabilis*), a parrot species, failed in the visual task, but did not appear to be distracted by hand movements (Schloegl et al., 2009); a follow-up study using a different paradigm suggested, however, that the experimenter’s manipulations may nevertheless have prevented the keas from solving the task (O’Hara, Gajdon, & Huber, 2012).

Although it was originally assumed that success in this task would be based on “inferential reasoning by exclusion” (e.g., Call, 2004; Erdöhegyi et al., 2007), this interpretation is no longer upheld. To assume that the animals indeed reason, it would be necessary that they first exclude the empty cup and then *logically infer* that the other cup must be baited (Aust, Range, Steurer, & Huber, 2008; Paukner et al., 2009; Schmitt & Fischer, 2009). Unfortunately, the animals could also simply avoid the empty cup and choose the other cup. This “avoidance” strategy is now considered as the more parsimonious explanation for success in these tasks.

Reasoning About Object–Object Relationships: Noise as Causal Predictor

A more complex level would be achieved if subjects were capable of (mentally) completing a cause–effect relationship (i.e., to infer the cause of an effect, or vice versa). To tackle this question, several tasks have been developed, among them an acoustic version of the “empty cup” task (Call, 2004). Here, the content of the cups must be inferred from the sound the bait is making: after baiting, the experimenter shakes the baited or the empty cup, or both; a rattling noise indicates the presence, a silent shaking the absence of the reward. Importantly, several control conditions are required, among them one in which the cups are not shaken but the rattling noise is played back (e.g., Call, 2004; Schloegl, Schmidt, Boeckle, Weiß, & Kotrschal, 2012). The reasoning behind this control condition is that the animals should *not* select the noisy cup if they understood that, in the test condition, the noise is a causal consequence of the food’s presence in the cup and its movement due to the shaking. In contrast, the animals *should* select the noisy cup if they had learned an association between the noise and the presence of the food. So far, only the great apes, grey parrots, and a group of noise-experienced capuchin monkeys chose the other cup if they witnessed a silent shaken cup, and passed all the control conditions (Call, 2004; Hill et al., 2011; Sabbatini & Visalberghi, 2008; Schloegl et al., 2012). In tests with wild boars (*Sus scrofa scrofa*) and pigs (*Sus scrofa domesticus*), only the domestic pigs that lived in an enriched environment with frequent contact with humans preferred the "noisy" cup, but controls suggested that they responded to the shaking movement, but not the noise (Albiach-Serrano, Bräuer, Cacchione, Zickert, & Amici, 2012). Bräuer, Kaminski, Riedel, Call, and Tomasello (2006) reported similar results for dogs, which also chose a non-moving cup from which an arbitrary, causally irrelevant sound was played. Monkeys received considerable attention, but are usually unsuccessful (Heimbauer, Antworth, & Owren, 2012; Paukner et al., 2009; Schmitt & Fischer, 2009) or require extensive experience (Sabbatini & Visalberghi, 2008). This suggests that only very few species solve this task through reasoning, whereas most fail entirely or attend to other cues (e.g., shaking movement). For some, this may have to do with sensory differences, as Plotnik, Shaw, Brubaker, Tiller, and Clayton (2014) recently suggested that the acoustic domain is inappropriate for tests with Asian elephants (*Elephas maximus*), but that these animals may solve such tasks if olfactory cues are provided. Similarly, monkeys' problems with this task reflect the general pattern that these animals have enormous difficulties in solving operant conditioning tasks involving noises (in contrast to visual stimuli); the reason for this remains unclear, as monkeys in the wild rapidly learn to associate specific sounds with the appearance of predators

(Fischer, 2002). It is also noteworthy that one study found tentative evidence for a better performance of two lemur species when acoustic rather than visual cues were provided (Maille & Roeder, 2012).

Reasoning About Object–Object Relationships: The Predictive Value of Covers

That monkeys have rather limited skills in tasks requiring a deeper understanding of cause–effect relationships than simply avoiding an empty cup became also evident in a study on long-tailed macaques (*Macaca fascicularis*). These monkeys had to find food that was either hidden under a small board or a hollow cup (Schloegl, Waldmann, & Fischer, 2013). If the reward was hidden under the board (which consequently was then inclined), the monkeys did locate the reward (Figure 34.2). If the reward was under the cup (which obviously did not alter its appearance), the animals chose at random. Apparently, the monkeys could not use the absence of an inclination of the board to exclude this option, and to infer in a second step that the food must be under the cup. This finding parallels the results in the auditory exclusion task: here, many animals, including most monkey species, fail to use the absence of the noise from the silent shaken cup to exclude this option, and to infer that the food must be in the other cup.

[INSERT FIGURE 34.2 about here]

The study by Schloegl, Waldmann, and Fischer (2013) had been inspired by similar work with chimpanzees: when one board was inclined and the other one was lying flat on the ground, the apes demonstrated a clear preference for the inclined board. Thus, the apes seemed to be aware that objects influence the orientation of other objects (Call, 2007). In a next step, they were allowed to choose between a small piece of highly preferred banana and a large piece of much less preferred carrot. The chimpanzees clearly preferred the banana. If, however, the same pieces of food were hidden underneath two boards, the chimpanzees failed to incorporate the strength of the inclination to infer where the small banana and where the large piece of carrot must be hidden; instead, they went for the stronger inclination (Call, 2007). Interestingly, these findings mirror those of the long-tailed macaques, which also tended to show the same bias for the stronger inclination (Schloegl et al., 2013). In a striking study, chicks that were a few days old, were imprinted on objects and then were asked to find these objects underneath and behind occluders. In contrast to the apes and monkeys, the chickens were not distracted by the strength of inclination and approached the board with the imprinted object underneath even in the presence of another, stronger inclined board (Chiandetti & Vallortigara, 2011).

When dogs were confronted with an inclined and a flat board, they preferred the inclined board, but only if they had observed the human experimenter hiding the reward and manipulating the boards; this is in contrast to chimpanzees, which chose the inclined board regardless of whether they had seen an experimenter manipulating it beforehand (Bräuer et al., 2006). Finally, in tests with wild boars and domesticated pigs, only the pigs living in a *less* enriched environment (i.e., living mainly on concrete floor) showed a preference for inclined boards (Albiach-Serrano et al., 2012). Taken together, species differences, rearing history, and experience may influence performance in these tasks.

A very different approach was taken by Waldmann, Schmid, Wong, and Blaisdell (2012), who trained rats (*Rattus norvegicus*) to expect a reward when a light turned on. In the following extinction phase, for half of the rats, the access to the reward was blocked by a cover, whereas the other rats experienced that no reward was available from the dispenser. In a subsequent test phase, the access to the dispenser was open for all rats, and those animals that had experienced a blocked access in the extinction phase showed a stronger expectancy for the reward than the other group. This was then interpreted as support for the assumption that rats can distinguish between the absence of events and the lack of evidence for the absence of events.

Reasoning About Object–Object Relationships: Weight and Food Trails as Causal Predictors

Similar to shape, weight can also be used as a predictive cue for the presence of an object or a reward. In one study, a banana was hidden in one of two containers and both containers were placed on a balance; the balance subsequently tipped toward the heavier, baited container. The observing chimpanzees used this information to infer where the banana must have been hidden (Hanus & Call, 2008). Likewise, when a baited and an empty container could be pulled up by a string, chimpanzees quickly learned to (a) pull both containers to compare their weight and then (b) to choose the heavier container (Schrauf & Call, 2011). Long-tailed macaques, in contrast, had considerable difficulties in a similar study (Klüver, 1933); it seemed as if they did not pay attention to the weight initially, and started to compare the two different containers only after the experimenter had increased the weight difference dramatically to highlight the relevance of the weight.

Some authors argued that performances may increase if tasks are modified (reviewed by Seed & Call, 2009; Shettleworth, 2010) or if their cognitive load is reduced (Seed, Seddon, Greene, & Call, 2012). Völter and Call (2014) proposed that many of the previously mentioned tasks required a relatively elaborate technical understanding and therefore physical knowledge, which may interfere with pure causal knowledge. To test the latter only, they designed a task in which a small bowl of yogurt was hidden underneath one of two cups. The bowl was “leaking” and lost some yogurt. When the baited and the non-baited cup were displaced, the baited cup left a visual trail of yogurt. The tested apes used the trail to identify the baited cup; in control conditions, they also were attentive to the temporal component of the cause–effect sequence and ignored yogurt trails that had been visible before the cups were displaced (Völter & Call, 2014).

Reasoning About Actions of Social Agents

Whereas the previously mentioned studies focused on physical relationships, a number of studies also incorporated social actions. One example mentioned earlier is the apple–banana–task by Premack and Premack (1994). In this task, the animals had to infer the social cause (the experimenter removing the apple) of the observed effect (experimenter eating the apple). These results were replicated in all great ape species (Call, 2006), and one grey parrot (but six others failed; Mikolasch, Kotrschal, and Schloegl, 2011). Subsequently, the performance of grey parrots in this task was increased when the cups used for hiding the rewards had different colors (Pepperberg, Koepke, Livingston, Girard, & Hartsfield, 2013). One (out of six) Clark’s nutcrackers was also successful in this task, but only when non-food objects had been hidden (Tornick & Gibson, 2013).

Based on the results of an entirely different paradigm, it was assumed that New Caledonian crows are able to reason about hidden causal agents (Taylor, Miller, & Gray, 2012). Captive crows were allowed to retrieve a food reward from a box mounted on a table. Next to the box was a hide, and before the crows could retrieve the reward from the box, they saw a wooden stick protrude from the hide and move back and forth; the stick then disappeared again in the hide (Figure 34.3). Importantly, the stick was moving in a position where the bird's head would be when retrieving the food (i.e., this stick could potentially hit the bird in the head). The authors created two conditions. In the first condition, the birds had seen a human agent disappear behind the hide right before the stick appeared; after the stick's movement, the human agent left the hide. In the second condition, no human agent walked behind the hide. Thus, in the first condition it appeared as if the human was responsible for the stick movement, whereas in the second condition the cause for the stick's movement remained unclear. After the stick had disappeared and the birds had descended to the table to retrieve the reward from the box, the authors measured how often the birds inspected the hide to check if the stick might reappear. These inspections were significantly more frequent in the second condition, which raises the possibility that the birds did indeed reason about the causes for the stick's movement (but see Boogert, Arbilly, Muth, & Seed, 2013; Dymond, Haselgrove, & McGregor, 2013; Taylor, Miller, & Gray, 2013a, 2013b, for a discussion of these findings).

[INSERT FIGURE 34.3 about here]

Cheney, Seyfarth, and Silk assessed the responses of chacma baboon females (*Papio ursinus*) to seemingly normal and anomalous interactions of other group members. When high-ranking animals approach lower-ranking ones in a benign fashion (because they want to inspect the subordinate's infant, for instance), they frequently utter grunts, to which the subordinate sometimes responds with fear barks. Using playback experiments, causally consistent (dominant individual grunts, subordinate fear barks) and inconsistent (subordinate individual grunts, dominant fear barks) call sequences were played to females. The subjects looked significantly longer in the direction of the calls when an inconsistent call sequence compared to a consisted one was played; this finding was interpreted as an indicator of the baboons' understanding of the causes of this unlikely scenario (i.e., that a rank-reversal must have occurred; Cheney, Seyfarth, & Silk, 1995).

Diana monkeys (*Cercopithecus diana*) are hunted by chimpanzees, and both species are preyed upon by leopards. If the monkeys see or hear chimpanzees, they usually retreat silently. When they hear chimpanzee alarm screams (which may indicate the presence of leopards), in contrast, they respond with their own specific leopard alarm calls. The authors took this to indicate that the Diana monkeys understand the underlying causal structure (i.e., that the chimpanzees scream because they have seen a leopard; Zuberbühler, 2003). The problem with this interpretation is, however, that it cannot be excluded that the monkeys living in chimpanzee territory simply learned to associate the chimpanzee alarm scream with the presence of leopards.

Taken together, these studies suggest that several animal species can make inferences about physical- as well as social-causal relationships, with the great apes and some bird species demonstrating particularly advanced skills. It seems, however, that many performances may not be very robust, as several species appear susceptible to sometimes only small modifications of the test conditions. In some cases, this may be due to sensory preferences of a species (i.e., some species may have problems in dealing with certain sensory modalities such as acoustic cues), but in other cases may reflect only weak causal understanding. However, species differences may also reflect evolutionary patterns, which we will discuss later in detail.

Reasoning About the Outcome of One’s Own Actions: Tool Use

As mentioned earlier, tool users receive considerable attention, as these species appear predestined to possess causal reasoning skills. Therefore, a number of studies assessed if tool-using animals, for instance, apes (e.g., Mulcahy & Schubiger, 2014; Seed et al., 2012), New Caledonian crows (e.g., Hunt & Gray, 2003; Weir et al., 2002), and capuchin monkeys (e.g., Moura & Lee, 2004; Visalberghi et al., 2009), can predict the effect their own actions will have, and if a sophisticated understanding of cause–effect relations is the basis for their behavior. Researchers had noted that chimpanzees appear to modify tools “with a plan” (e.g., Boesch & Boesch, 1990), as if they knew in advance what to do to a tool to make it functional. This led to the suggestion that chimpanzees reason causally (Visalberghi & Limongelli, 1994), in the sense that they have at least a rudimentary understanding for the causally relevant characteristics of a given tool.

Capuchin monkeys were trained to use a stick to push a food reward out of a horizontal, non-movable tube. After they had learned how to solve this task, the tube was modified and a trap (i.e., a floored hole in the tube, similar to the pockets in a pool-billiard table; see Figure 34.4) was added to its middle. Now, the animals needed to pay attention to the position of the trap and to push the reward away from the pocket. Would they be able to predict the effect of their actions? In the inaugural study using this now-famous experimental design, only one of four capuchin monkeys avoided the trap (Visalberghi & Limongelli, 1994). When, however, the tube was rotated so that the trap was *above* the reward and therefore non-functional, the monkey still avoided the trap;

thus, capuchin monkeys may use tools *without* an understanding for cause–effect relationships. Similar results were also obtained in chimpanzees (see Seed, Call, Emery, & Clayton, 2009, and references therein) and woodpecker finches (*Cactospiza pallida*) (Tebbich & Bshary, 2004; see also Emery & Clayton, 2009, for a review). Yet, several studies found that small modifications to the original design, such as allowing chimpanzees to move the reward with their fingers instead of a stick, can significantly alter the outcome (Seed et al., 2009). Furthermore, Silva, Page, and Silva (2005) demonstrated that human adults, just like capuchin monkeys, also continue to avoid the non-functional trap, leaving the diagnostic value of a failure to avoid the trap unclear.

[INSERT FIGURE 34.4 about here]

[INSERT FIGURE 34.5 about here]

In an improved version of the trap tube (Figure 34.5), non-tool-using rooks were tested with four different versions of a two-trap tube: here, the birds had to identify in advance which of the two traps is functional, and to pull the reward in the other direction. Seven of eight rooks learned to solve the first two versions, and one of them managed to transfer this instantaneously to two novel versions. Thus, this bird may indeed have understood the causal properties of each trap and could predict what would happen if it pulled the reward toward the traps (Seed, Tebbich, Emery, & Clayton, 2006). In a similar task, three (of six) New Caledonian crows learned to solve an initial two-trap tube task and transferred their skills in two (of three) modified tasks and to another trap-table task; the trap-table is functionally similar, but visually distinct from the trap-tube. Because all three crows also solved the trap-table task, it was suggested that the crows may solve this through causal and potentially also analogical reasoning (Taylor, Hunt, Medina, & Gray, 2008).

An especially prominent example of the assumed cleverness of crows is Aesop's (ca. 620–560 B.C.) fable "The Crow and the Pitcher." In this fable, a thirsty crow cannot reach the water at the bottom of a pitcher, and starts dropping stones into it until the water level is raised sufficiently for the bird to reach the water. When orangutans (*Pongo abelii*) were confronted with an analogous task in which a peanut was floating in a water-filled tube out of reach of the apes' hands, they obtained water from a dispenser and spit the water into the tube to raise the water level. All subjects solved the task on the first trial and, on average, within less than 10 minutes; again, this suggests that they quickly understood how to solve the task (Mendes, Hanus, & Call, 2007). Rooks also solved the task instantaneously — this time, just as in the fable, by dropping stones into a water-filled tube (Bird & Emery, 2009b). Subsequent studies with Eurasian jays (*Garrulus glandarius*) and New Caledonian crows suggested, however, that the birds must first learn to drop stones into a tube with water for the water to rise (Cheke, Bird, & Clayton, 2011; Taylor et al., 2011). Learning seemed to be facilitated if causal cues were available: for instance, jays and crows learned to drop stones into the tube, but did not learn to select one of two differently colored tubes in the same number of trials (Cheke et al., 2011), or to select a tube based on the size of a stone placed in front of it (Taylor et al., 2011). This led Taylor and colleagues to propose a "causal learning account", according to which correlations between stimuli are easier learned if they are causally relevant; in other words, dropping a larger stone into a tube with water is causally relevant, because it raises the water level, whereas the stone in front of the tube is an arbitrary feature and causally irrelevant. The birds must then have a predisposition for (or be attuned to) causal features (see also Hanus and Call, 2011, for a similar argumentation for chimpanzees).

Reasoning About the Outcome of One's Own Actions: Causal Reasoning in Rats

In the previous section we have seen that tool-using species seem to have an understanding of what the outcome of their tool-related actions might be. They may not do so through sudden "insight," but their predispositions to attend to causally relevant features may facilitate learning. But is this a specific skill of tool-using or large-brained species? In a highly influential study, Blaisdell and colleagues (2006) explored causal reasoning in rats. Using Pavlovian conditioning, the rats first learned to associate a light cue with a following tone and, in a second step, an association of the light and a following food reward. The idea was that the rats would acquire a common cause model in which the light causes the tone and the food; as a consequence, the tone should also be predictive for the presence of the food reward. In a second training step, the rats were split into two groups. One group was confronted with a lever, which, upon being pressed by the rat, caused the same tone as during the first training period. The other group was also confronted with a lever, but the occurrence of the tone was independent from pressing the lever. In the final test, then, the authors measured the rats' expectancy to obtain a reward after hearing the tone in the absence of the light (expectancy was measured by the frequency of rats poking their nose in the food dispenser). The rats that were confronted with the lever causing the tone (group 1) expected food less frequently than the rats whose lever presses had no observable effect (group 2). This suggests that the rats had some form of causal understanding: during training, the tone was predictive for the presence of food (via the light); in the test, this causality still held for the rats in the second group, even though they could not observe the light (actually, the light was off, but the rats may have assumed that they could not observe it). For the first group, however, this causality did not hold any more, as a new cause for the tone was introduced: their own lever pressing (Blaisdell et al., 2006; but see, for instance, Dwyer, Starns, & Honey, 2009, or Penn & Povinelli, 2007, for alternative views). Similar to the results of Blaisdell and colleagues, Beckers, Miller, De Houwer, and Urushihara (2006) could demonstrate that conditional forward blocking in rats is sensitive to experimental modifications that are not accounted for by classical associative theories, but can be expected from a causal reasoning perspective (see also Boddez, De Houwer, & Beckers, Chapter 4 in this volume).

Inferring a Required Action from Observation

So far, we have talked about animals' ability to reason about the outcome that their own actions will or should have. While at least some species may be able to do so, this may not be a result of "insight," but rather they may have to learn about the outcome of their actions before applying them correctly. But would animals also know what to do from observation alone? Tomasello and Call (1997) rejected this idea, and suggested that after having seen fruits falling off a tree shaken by the wind, apes would not get the idea of having to shake a tree themselves to reproduce this effect. Interventions in this sense are seen as a pinnacle of human causal understanding (Taylor et al., 2014), but have received relatively little attention in the animal cognition literature. Inspired by work by von Bayern and colleagues (von Bayern, Heathcote, Rutz, & Kacelnik, 2009), in which the authors demonstrated that New Caledonian crows can transfer a cause–effect relationship to novel types of tools, Taylor et al. (2014) investigated if these birds would find a novel solution to reproduce an effect they had previously observed. In their experiment, the birds (and 24-month-old children) were confronted with a plastic block inside an apparatus. If they accidentally touched the block, it could fall on a platform, which, in turn, would lead to a reward. In the following test, the plastic block was located outside the apparatus, but could be inserted through a hole. According to the authors, operant conditioning should cause the subjects to act on the block, but only an intervention would allow them to infer that they must insert the block into the apparatus so that it would act on the platform to repeat the effect of obtaining the reward. Only the children, but not the crows, came up with an idea of how to solve the task, while a control group of crows was able to learn the task through operant conditioning. Importantly, for the children this was also not an easy task; nearly 20% of the children did not create an intervention, and those who did needed several observations to understand what was required (but see Jacobs, von Bayern, Martin-Ordas, Rat-Fischer, & Osvath, 2015; Taylor et al., 2015, for a discussion of these findings, and Bonawitz et al., 2010, for a study reporting toddlers' problems in such tasks). In sum, there is so far no convincing evidence that animals truly understand the causal structure of interventions.

Evolutionary Patterns

From an evolutionary view, a goal is to reconstruct the origins of different cognitive abilities. At what point in evolutionary history did the ability for causal reasoning evolve? Did it evolve several times? What are the selection pressures promoting its evolution? So far, only few taxonomic groups have been studied in sufficient detail to allow for some very sketchy outlines of the potential evolution of causal reasoning abilities. The available evidence suggests a convergent evolution of reasoning abilities in birds and mammals (e.g., Emery & Clayton, 2004; Pepperberg et al., 2013; Schloegl et al., 2012; Taylor et al., 2012); in the following, we will largely focus on differences within the primate lineage, domestication effects, and the evolution of reasoning in birds.

Thompson and Oden (2000) argued that a cognitive divide exists between "paleological" monkeys and "analogical" apes, as only the latter can perceive relations between relations: for instance, if having seen a sample of two identical objects, and subsequently being tasked to identify a pair of objects that have the same relationship, they chose a pair of identical objects (but different from the sample) over a pair of non-identical objects; monkeys, in contrast, can only form categorizations on the basis of shared physical attributes (e.g., same shape or color). In support of convergent evolution in birds and mammals, hooded crows (*Corvus corone cornix*) have recently been shown to understand relations between relations in an analogical reasoning task (Smirnova, Zorina, Obozova, & Wasserman, 2014) like the apes did in the previously mentioned example; at the same time, the debate about the cognitive gap between apes and monkeys has been fueled by similar findings in monkeys (e.g., Fagot & Maugard, 2013; Flemming, Thompson, & Fagot, 2013). Still, monkeys seem to fail in a number of tasks that apes solve. For instance, apes master the acoustic version of the "empty cup" task introduced before, even though not all subjects are successful and the task in general is challenging (see Call, 2004). Studies on monkeys, in contrast, typically produced negative results (Heimbauer et al., 2012; Schmitt & Fischer, 2009), or required experience training (Sabbatini & Visalberghi, 2008; but see Maille & Roeder, 2012, for tentative positive evidence in lemurs, which had been explained as an ecological adaptation). Likewise, using weight as a causal predictor seems to be easier for apes than for monkeys (Hanus & Call, 2008, 2011; Klüver, 1933; Schrauf & Call, 2011), even though the tool-using capuchin monkeys seem to distort the picture (Fragaszy, Greenberg, et al., 2010; Visalberghi et al., 2009).

Another distinction has been drawn between “causal apes” and “social dogs” (Bräuer et al., 2006), arguing that apes are sensitive to causal information, whereas dogs pay more attention to social cues (i.e., pointing, gazing). Dogs’ priority for social information is supposed to be a result of domestication, as dogs may have been selected to pay attention to signals provided by humans (Hare, Brown, Williamson, & Tomasello, 2002; see Hare et al., 2010; Udell, Dorey, & Wynne, 2010; Udell & Wynne, 2010, for a discussion of this domestication hypothesis). In a comparative study with wild boars and domesticated pigs, however, it seemed as if differences might be explained best by individual life histories (Albiach-Serrano et al., 2012). It thus is unclear whether the “social dogs” hypothesis can be expanded to domesticated animals in general.

Two different evolutionary explanations have been proposed for corvids. Taylor and colleagues stressed that New Caledonian crows may possess superior reasoning skills as adaptations to their elaborate tool use (e.g., Taylor et al., 2008; Taylor et al., 2011; Taylor et al., 2012). Others have wondered if the performance in exclusion tasks could be linked to caching behavior (e.g., Mikolasch et al., 2012; Schloegl, 2011), as food-caching species may be more attentive to the presence or absence of rewards in hidden locations (Tornick & Gibson, 2013; but see Shaw, Plotnik, & Clayton, 2013, for a different view).

Open Questions

The debates about the cognitive underpinnings of exclusion or causal reasoning in rats mentioned earlier illustrate one of the key issues in this field of research. On the functional level, the evidence for causal reasoning in animals is increasing. On the mechanistic level, however, it often remains unclear whether the animals indeed have a deep understanding of the causal relationships or whether they respond to covariations (see also Le Pelley, Griffiths, & Beesley, Chapter 2 in this volume). In other words, do they understand that one event causes the other, or did they learn that these two usually occur together (e.g., Penn, Holyoak, & Povinelli, 2008; Penn & Povinelli, 2007)? Völter and Call (2012) have shown that great apes learn to solve mechanical problems faster if they can observe the mechanism underlying the problem, but the authors were cautious about interpreting this as evidence for causal understanding. Instead, they argued that the apes might have only learned "*what* caused the beneficial outcome but not necessarily *how* it was caused" (p. 935, emphasis theirs). New Caledonian crows were tested in a task in which a reward was placed on a platform at the bottom of a tube. To obtain the reward, the platform had to be collapsed (e.g., by pushing it down; von Bayern et al., 2009; see also Bird & Emery, 2009a). Interestingly, for two birds, the experience of having collapsed the platform themselves by pushing it down with their beak was sufficient to solve the task later by dropping stones into a tube and onto the platform from above. Thus, in this case it seems possible that they may have understood *how* to cause an effect.

But is this evidence for "insightful" problem-solving based on causal understanding? For a long time, one of the standard tests for "insightful" problem-solving was the so-called string-pulling task, which has a long tradition in avian research (e.g., Pepperberg, 2004; Vince, 1961; see Jacobs & Osvath, 2015, for an extensive review). Here, a string, with food attached to it, is hanging from a branch. To obtain the food, the birds have to grasp the string with their beak, pull up the string, hold it in a loop, step on the loop with a foot, grasp the string, and pull again. This sequence can be repeated multiple times. Because of the complexity of the string-pulling behavior and its lack of an equivalent in the birds' daily behavior, its spontaneous occurrence had long been interpreted as a textbook example of "insight" (e.g., Heinrich, 1995). This view has been challenged recently (Taylor et al., 2010) by the demonstration that New Caledonian crows fail in this task if they are prevented from the visual feedback of the food moving closer to the puller. Thus, perceptual-motor feedback may be required, and this may facilitate the acquisition of the task's solution through operant conditioning (but see also Jacobs & Osvath, 2015).

This uncertainty about the cognitive mechanisms is partly due to the problem that researchers studying animal cognition, just like developmental psychologists, cannot ask their non- or pre-linguistic subjects about their understanding of a task or for the reason why they behaved as they did. It is therefore difficult to differentiate between what Kummer (1995; cited by Visalberghi & Tomasello, 1998) had called "weak causal knowledge" (which is based on learning and acquired through numerous repetitions of a task), "strong causal knowledge" (which is based on rapid or even a priori interpretations of a situation), and "non-causal knowledge" (i.e., associatively learned covariations without an understanding of the underlying cause–effect relationships). Researchers have tried to answer these questions by designing increasingly complex tasks with numerous control conditions, but critics have kept up with this development by offering more elaborate alternative explanations. Despite their generally skeptical stance, Penn and Povinelli (2007, p. 97) acknowledged that current comparative evidence “does not fit comfortably into [. . .] the traditional associationist” accounts. Nevertheless, they reject the notion of human-like causal reasoning skills in animals. But even if animals were to be able to reason causally, the immediately following question would then be whether they also would have “meta-knowledge about the concept of causality” (Blaisdell & Waldmann, 2012, p. 179), or if that is, as Penn et al. (2008) have suggested, a uniquely human capacity.

A related issue is the question of how to extrapolate from individual task performances. If an individual animal could be shown to reason in a human-like fashion in a single study, what would this tell us about *general* reasoning abilities? Do such general reasoning abilities exist at all? There seems to be considerable doubt, as evidenced by the performance differences between species. Seed and Call (2009) deemed it unlikely that causal understanding would constitute a singular ability; similarly, Taylor et al. (2014) suggested that “causal understanding is not based on a single monolithic, domain-general cognitive mechanism” (p. 5).

So far, most studies have focused on relatively simple, all-or-nothing decisions (i.e., they tested if animals can exclude *one* wrong option to infer *one* correct option). In real life, however, one is often forced to base decisions on reasoning about probabilities, but very little is known about animals’ abilities to choose between options by inferring the *likelihood* of each option being correct. When apes had to choose between two buckets filled with different ratios of highly valued banana pellets and lowly valued carrots, they preferred the bucket from which a banana pellet would be drawn with higher probability (Rakoczy et al., 2014). However, chimpanzees have also been confronted with two sets of cups of varying number, of which some would be baited and others would be not. Then, one cup was drawn from each set, and they could choose between these two cups. Whether the chimpanzees would identify the cup with the higher probability of reward was highly dependent on the ratio of baited to non-baited cups in each set (Hanus & Call, 2014). Finally, when chimpanzees had to choose between two partially occluded tools, they failed to identify the tool with the higher probability of being intact (Seed et al., 2012; see also Mulcahy & Schubiger, 2014, for similar findings with orangutans).

Even though cause–effect reasoning and effect–cause reasoning can both be based on the same causal relationships, research suggests that human subjects are sensitive to directional differences (Waldmann & Hagmayer, 2013); furthermore, the direction may have consequences on the cognitive demands (Fernbach, Darlow, & Sloman, 2011; Waldmann & Hagmayer, 2013). Human children aged 3.5–4.5 years seem to perform better in cause–effect reasoning than in effect–cause reasoning (Hong, Chijun, Xuemei, Shan, & Chongde, 2005). Given that animals may not understand all causal relationships, just as human infants may not develop an understanding for all causal relationships at the same time (Muentener & Bonawitz, Chapter 33 in this volume), it seems plausible to expect different performances in animals depending on the direction of reasoning. To our knowledge, however, this prediction has never been investigated, as we are not aware of any study using the same task to explore both reasoning directions.

In the future, further emphasis should be placed on the development of formal models that are explicit about the logical operations required, and experiments that rule out generalization and associative learning. At the same time, we may note, however, that from an evolutionary perspective, it does not really matter whether the animal reasons, associates, or expresses innate behavior, as long as it gets the job done.

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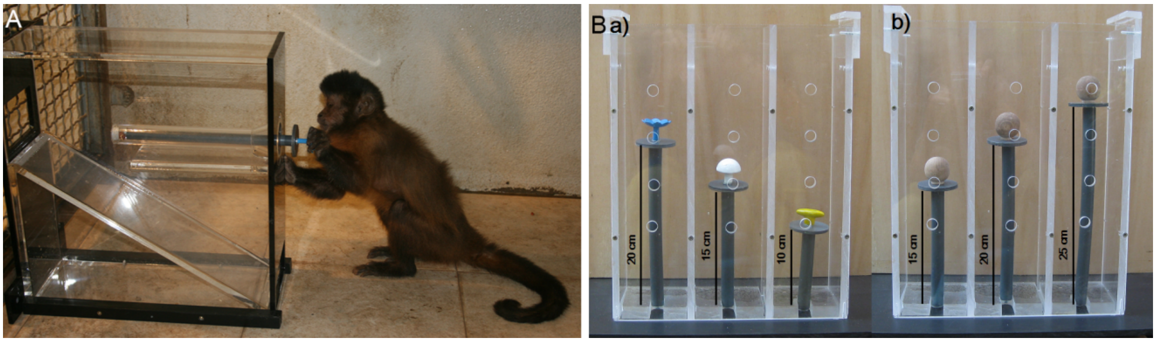
Figure 34.1.



(a) A capuchin monkey solving the tube task of Sabbatini et al. (2012); a reward is located at the end of the tube; if pushed with the tool, the reward drops on the sloped board underneath and can be accessed by the monkey. (b) (1) Tools with different handles as used in the training phase; (2) tools with the new handles used in one transfer phase; for details, see Sabbatini et al. (2012).

Photo (A) by Elisabetta Visalberghi; (B) reprinted with permission from Sabbatini et al. (2012).

Figure 34.2.

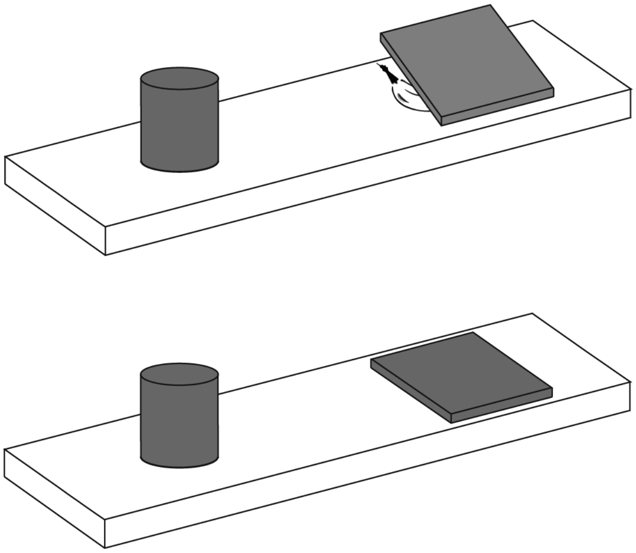


Illustration of the setup used in the study by Schloegl, Waldmann, and Fischer (2013) with long-tailed macaques. In the upper panel, a food reward was hidden underneath the board, which then was inclined (note that the food reward was not visible for the monkeys, but is shown here for illustration purposes). The monkeys could use the inclination to find the reward. In the lower panel, the reward was hidden in the cup; the monkeys failed to infer the location of the reward based on the absence of an inclination of the board.

Figure 34.3.

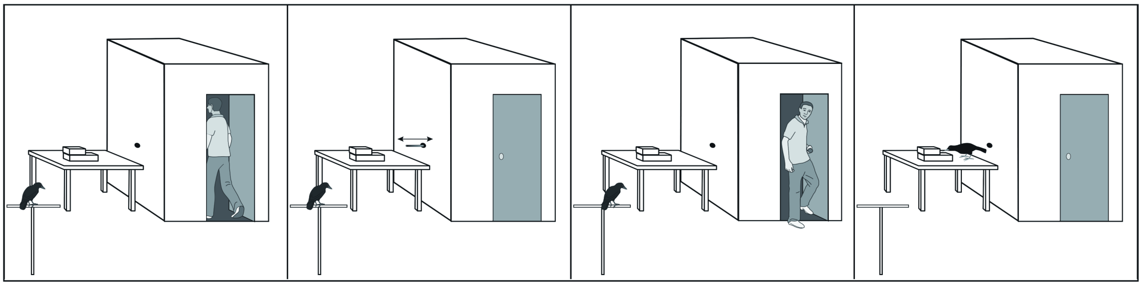
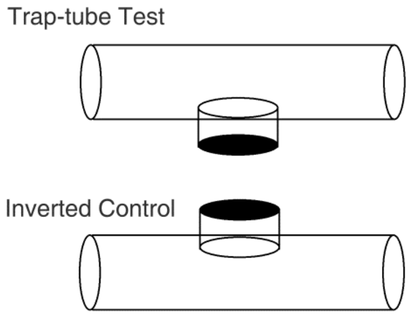


Illustration of the setup used by Taylor et al. (2012) to investigate New Caledonian crows’ reasoning about hidden causal agents. In this condition, the agent enters a hide (left panel), a stick probes through a hole in front of the block the crow could feed from (second panel from left), the agent leaves the hide (second panel from right), and the crow approaches and retrieves food from the block (right panel).

Figure by Alex H. Taylor; reprinted with permission from Taylor (2014).

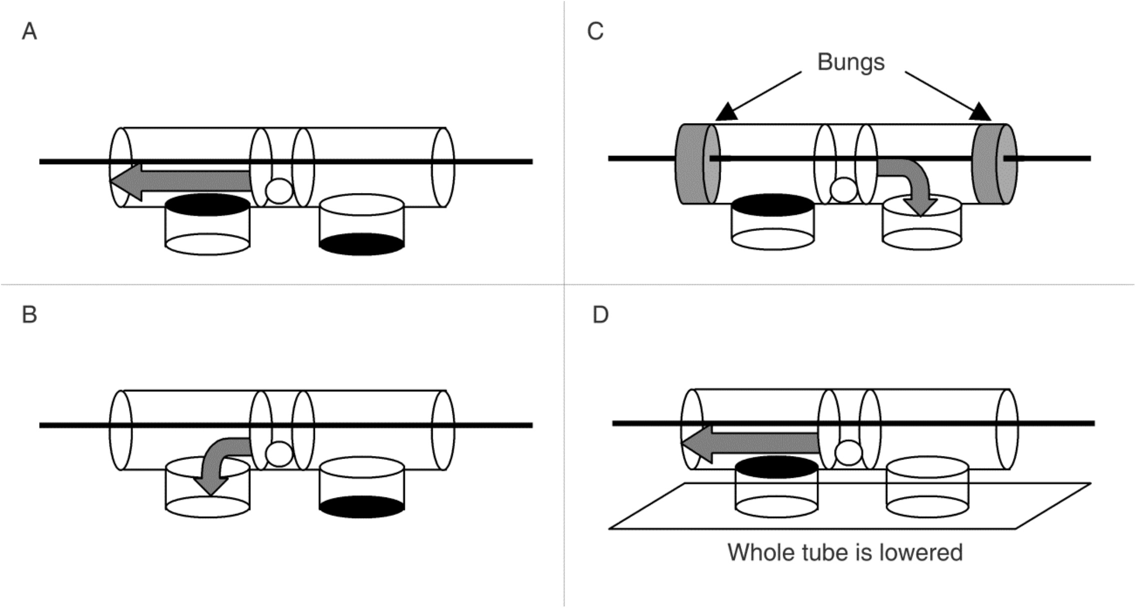
Figure 34.4.



The trap-tube task as used in earlier studies with, for instance, capuchin monkeys and woodpecker finches.

Figure by Amanda Seed; reprinted with permission from Seed et al. (2006).

Figure 34.5.



Modified versions of the trap-tube task introduced by Seed et al. (2006) in their study with rooks. The stick is already inserted in the tube and the reward is located between two clear Perspex discs. Moving the stick causes the discs (and thereby the reward) to move. Horizontal black discs indicate closing of the traps. Arrows represent the correct solution in each condition.

Figure by Amanda Seed; Reprinted with permission from Seed et al. (2006).