4

What Can Studies of Comparative Cognition Teach Us about the Evolution of Dynamic Coordination?

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Abstract

The field of comparative cognition has provided examples of the cognitive abilities of many mammal and bird species, such as some "understanding" of physical properties and the use of episodic-like memory of past events to alter behavior flexibly. Although the seemingly complex behavior exhibited by an animal may be the outcome of cognitive mechanisms, it need not be: often, associative learning principles, or fixed action patterns that form without associative experience ("innate rules"), or a combination thereof are all that is required. Distinguishing experimentally between these accounts is one of the main concerns of comparative cognition. This chapter outlines what is necessary for connecting the field of comparative cognition with the subject of dynamic coordination. Because animal cognition studies are performed on many species from diverse taxa, analyzing the type of coordination required to pass the tasks they include may shed light on the evolution of (dynamic) coordination. Specifically, the convergent evolution of particular cognitive abilities in primates and corvids implies that the type of coordination necessary for these abilities has evolved at least twice. In this respect, one future challenge is to clarify which principles of coordination are shared (and which are different) between mammals, with their laminar cortex, and birds, with a forebrain that is not laminated. Several recent examples of animal cognition are explored and the sort of coordination they require is discussed.

Marrying Comparative Cognition and Dynamic Coordination

A common assumption in cognitive neuroscience is that cognition has evolved in a homologous manner, such that the cognitive abilities exhibited by different

extant species have all developed from the same basic abilities present in their last common ancestor. Like other traits, however, cognitive ones can also evolve through a process of convergent evolution in which distantly related species independently evolve similar solutions to similar problems. When attempting to study cognitive abilities, there is much benefit to be gained from taking a comparative approach to the study of cognition, where many species from diverse phylogenetic taxa are compared for their cognitive abilities. This way we can assess the relative importance to the evolution of cognition of (a) phylogenetic homology (common ancestry) and (b) differences in selection pressures across species and taxa.

Comparing primates and corvids (the crow family) provides one clear case of convergence in cognitive abilities (Emery and Clayton 2004; Seed, Emery et al. 2009). Nonhuman primates and corvids show remarkably similar abilities to behave flexibly in ways suggesting that they understand features in their physical and social worlds. If the reptilian common ancestor of birds and mammals did not possess these abilities, then this supports the hypothesis that cognitive abilities have evolved convergently in these groups. The comparison between the neuroarchitecture of avian forebrains and the mammalian neocortex has suffered from mistakenly attributing a striatal developmental origin to most of the avian forebrain, while in fact most of it is derived from the embryo's pallium (Reiner et al. 2004; see also Balaban et al., this volume). Thus, areas in the avian forebrain are homologous to the mammalian neocortex, to which they also correspond functionally. Although these similarities are now well accepted, there are still major differences in the neuroarchitecure of mammalian and avian forebrains. Most notably, whereas the cortex of primates and other mammals has a laminar organization, the avian forebrain lacks such a laminated organization and is instead nuclear in its organization. This finding, together with the cognitive parallels, implies that it is feasible to evolve similar (computational?) solutions to complex problems, based on different underlying neural mechanisms.

The principles of coordination between different local brain functions may also have evolved convergently, along with cognition. However, in order to begin considering dynamic coordination in a comparative way, at least two routes are possible. First, we may investigate the brains of different species directly to determine how different brain functions are coordinated. This may be done for a small number of species, for which methodology has already been developed and whose brain is relatively well studied. Another, indirect route, is to use the extensive research of (behavioral) comparative cognition in order to draw a general picture of which taxa are likely to exhibit the capacity for dynamic coordination. Marrying comparative cognition and dynamic coordination may allow us to assess the sort of coordination in a very large number of species from diverse taxa. To do so, however, we must first clarify the relation between cognitive abilities exhibited by animals such as primates and corvids, on the one hand, and the (minimal) sort of coordination that is required in

order to exhibit them, on the other hand. This is what we attempt to explore in this chapter. In the following sections we consider the type of coordination necessary in episodic-like memory and in several primate and corvid studies of physical cognition.

Concentrating on such studies requires justification because many, much simpler tasks require some sort of coordination between different local brain functions. In other words, different brain areas, in charge of different computational tasks, have to "talk to each other" to achieve many of the behaviors performed regularly by animals (e.g., grooming; see Balaban et al., this volume). Coordination might therefore be inherently dynamic if it involves the synchronization of oscillating groups of neurons, and many examples of behaviors and basic cognitive abilities (e.g., Gestalt perception, selective attention, and working memory) that involve this type of dynamic coordination have been discussed by both Moser et al. and Engel et al. (this volume). We may need to consider, however, additional or special forms of coordination when trying to understand what makes some species able to solve tasks that others cannot. In this chapter, therefore, we will distinguish between cases in which the coordination required is either prespecified in the brain itself (Phillips et al., this volume), or is specified directly by the outside world, and those tasks in which the solution must somehow come from within the brain. Performing a well-trained skill, such as walking, is an example of prespecified coordination (Phillips et al., this volume), and so is classical conditioning. Even if the stimuli to be associated are novel, precluding a prespecified connection between their representations in the brain, and even if the coordination involves synchronizing oscillations (and is therefore dynamic in that sense), the representations to be connected could be directly specified by external events. In contrast, we will discuss studies in comparative cognition where we suspect that solving the task requires the animal to come up with the solution itself, where the very identity of what should be coordinated, as well as the form of the coordination, needs to come from within the brain. Before we continue, however, we must first clarify how comparative cognition research distinguishes different accounts for flexible behavior.

Different Accounts in Comparative Cognition

Comparative cognition has devoted much empirical effort to distinguishing between different accounts to explain flexible behaviors. Consider the case in which an animal performs behavior *A* in context *a*, whereas it performs another type of behavior *B*, in another context *b*. Perhaps the simplest account for this flexibility in behavior is an "innate rule" that specifies that the type of behavior is dependent on a particular context. Such a rule is "innate" in the sense that its formation does not require the explicit ontogenetic experience with the different outcomes of behaviors *A* and *B* in contexts *a* and *b*, but

instead develops even in an animal naïve to these outcomes, presumably as a result of selection pressures acting on the development of this rule in its ancestors. Another account of flexible behavior is associative learning, whereby the rule for performing *A* in context *a* (and *B* in context *b*), for example, may be created through reinforcing only behavior *A* in context *a* and only behavior *B* in context *b* (for a simple account of how this works, see Dickinson 1980). In comparative cognition research, innate rules and associative learning mechanisms are usually taken as the alternative accounts to a cognitive one. What a cognitive account of the above rule would imply is that the animal has some appreciation of the *reasons* for each behavior being appropriate in a different context. Although it is unclear how this can occur, such an appreciation would be beneficial as it allows much more flexibility in generalization to new contexts. For example, if in a new context *c* the reasons that made behavior *A* beneficial in context *a* remain the same, the animal will be able to transfer to this new context (or new task), whereas depending on associative learning or innate rules will not enable such flexibility.

We hope that we have made clearer the alternative accounts for flexible behavior that the field of comparative cognition addresses, and the empirical ways to distinguish between them. In many cases it is still unclear which account is more plausible in each case (for a simple associative-learning account of what may at first sight appear to be pigeons insightfully stacking boxes on top of one another to obtain food that would otherwise be out of reach, see Epstein et al. 1984), but this is not the focus of our chapter. Instead, we now attempt to consider what kinds of coordination between different brain functions are required to achieve flexible behavior according to these different behavioral accounts. Innate rules seem to require only the coordination that can be prespecified by natural selection. In the case of associative learning, previous experience may prespecify the coordination needed for behavior to be flexible so that it can be adequate in different contexts and tasks. In contrast, behavioral flexibility that is based on an appreciation of reasons that make such flexibility beneficial may require a dynamic coordination which is neither prespecified in the brain nor obvious from observing the outside world. In the following sections we offer a few examples of studies in comparative cognition and discuss their relation to dynamic coordination. In many cases there is still an ongoing empirical debate on whether or not simpler explanations can account for some of the findings and on whether human and animal abilities are comparable. Here, we will not go into these debates, but rather present the findings and their interpretations to make the connection between comparative cognition and particular forms of dynamic coordination. The particular forms to be considered are those involved in episodic memory and in problem solving, and which may require more than the basic forms of associative learning, selective attention, and working memory.

What Coordination Does Episodic-like Memory Require?

To recall a fact, such as "Frankfurt was first founded in the first century," we do not necessarily need to remember when, where, and how we learned this information, and neither do we have to have been there ourselves. In contrast with such factual or "semantic" knowledge about the past, episodic memory contains the specific "what, where, and when" information of a previous event that we have personally experienced (Tulving 1972). For example, UG recalls how, as part of a security check at the Frankfurt airport in the summer of 1994, he was required to exhibit his puny juggling skills to demonstrate that his juggling clubs were indeed what they were. At first sight, it seems that episodic memory would require new coordination in that the memory of a past event can be used to make a later decision. For example, imagine that you realize you have lost your wallet and try to trace your steps back to remember where you have left it. This is essentially different from making a mental note of putting your wallet in the drawer, but does it indeed require a novel coordination between different functions?

Episodic-like memory has recently become an area of research in comparative cognition, starting with experiments showing that western scrub-jays remember the what, where, and when of caching a food item (Clayton and Dickinson 1998, 1999; Clayton et al. 2001, 2003). The term "episodic-like" memory is used when considering animal memory (Clayton and Dickinson 1998) because current definitions of human episodic memory necessitate the subject being consciously aware that the past memories are his or her own and that he or she re-experiences the event when remembering (Tulving 2005), characteristics which cannot be assessed without language and ones that become part of our identity. With study species now including other birds, such as magpies and pigeons, rats, nonhuman primates, meadow voles, and honeybees (reviewed in Crystal 2009; Dere et al. 2006; Schwartz et al. 2005), episodic-like memory seems like a good candidate for exploring the relation between cognitive capacities and the sort of coordination they require. To do this, let us look more closely at some of the first experiments showing episodic-like memory in nonhuman animals.

To study episodic-like memory in western scrub-jays, Clayton, Dickinson and colleagues capitalized on the fact that these birds readily hide food in the lab as well as in the wild (Clayton and Dickinson 1998, 1999; Clayton et al. 2001, 2003). Indeed, western scrub-jays scatter-hoard many types of food in multiple locations and recover them hours, days, or months later (Curry et al. 2002). The types of food cached include various types of nuts as well as invertebrates, which perish much quicker. Thus, these jays might need to form a specific what–where–when memory for each caching event in order to recover the food on time. As mentioned above, distinguishing between cognitive and simpler accounts is a key feature in comparative cognition research. In a study that shows that scrub-jays remember the content of caches they made,

as well as whether they have already recovered them, Clayton and Dickinson (1999) explicitly ruled out a simpler associative account, which is useful for our analysis of the type of coordination needed.

In the first experiment in that study, scrub-jays were first allowed to cache peanuts in one tray and then dog kibbles in another. Before they were allowed to recover from the two trays (simultaneously), they were pre-fed on one type of these food types. Consequently, they preferentially chose to recover from the tray where they had cached the other type of food. This suggests that they remember what they have cached where; however, there was a simpler explanation for these results, based on a classical (Pavlovian) conditioning between each tray and the food type that had been cached in it. According to this account, such an association was formed during the caching phases, such that the stimuli of each tray elicit the representation of a different food type. The motivation to approach one of the food types was decreased due to pre-feeding and therefore the sight of the tray associated with it elicited less approach than the sight of the tray associated with a food type that was still highly valued. For our purposes, it is obvious that the coordination between the representations of location, types of food, and motivation to approach could all be prespecified during the caching session or before then. There is no need, according to this account, for dynamic coordination; that is, for the type of coordination which is "created on a moment-by-moment basis so as to deal effectively with unpredictable aspects of the current situation" (Phillips et al., this volume).

However, a second experiment ruled out this simple account. In this experiment, both pine nuts and kibbles were cached in both trays, but only one food type was subsequently recovered by the jays from each of the trays. Then, the jays were pre-fed one of the food types and consequently chose to recover from the tray that still contained the other food type. This showed not only that jays remember what they had cached where (ruling out the simple conditioning account) but also that they register at recovery that the food they recover is no longer in place. The coordination needed here is obviously more complex, as we discuss below. Before we do that, however, it is worthwhile to consider briefly what else is known about scrub-jay memory for cached items.

Scrub-jays prefer wax moth larva ("wax worms") to peanuts, but after experiencing that worms take a short time to decay (and that peanuts do not decay), the jays searched preferentially for peanuts when allowed to recover both types of food at a time when worms would have already degraded. When allowed to recover after a shorter time had elapsed since caching, short enough for worms to stay fresh, they preferentially search for the worms (Clayton and Dickinson 1998), suggesting that jays remember when and where they cached each type of food. Another study (Clayton et al. 2001) showed that the what, where, and when components form an integrated memory which is retrieved as a whole, and also suggested that the memory of the caching location elicits the two other components; namely, time and content. In addition, the jays are able to incorporate flexibly new semantic information about decay rates,

acquired after caching, and use this information to alter their recovery decisions (Clayton et al. 2003).

Taken together, the above studies depict a complex combination of functions, schematically illustrated in Figure 4.1. For each caching event, episodic information about food type, location, and time of caching is encoded to form an integrated event-specific memory. When deciding which caches to recover, jays take into account semantic information about the decay rates of different food types, e.g., "After 4 days, worms have already perished." This rule can be altered if new information is available, even after caching, providing further support that the jays do not encode their recovery decisions themselves during caching, but rather encode what–where–when information, which is later used when these decisions are made (see Clayton et al. 2003). As mentioned above, jays also remember whether they had already recovered each item (Clayton and Dickinson 1999). Finally, motivation for different food types can be changed through feeding. At recovery, motivation, episodic-like and semantic information are all used to make the correct decision: recover at the site which, according to the decay-rate rule previously experienced, contains a food type that is still edible, and for which there is current motivation.

Episodic-like memory in these jays is thus a complex decision-making system. Dynamic coordination is required between episodic, semantic, and motivational functions (Figure 4.1), and in each caching event a new, event-specific connection must be made between the functions for location, time, and content. However, all of the above does not necessarily require that the *fundamental way* in which these different functions are coordinated be dynamic and change according to the task or between caching and recovery. This is because the sort of coordination needed to make recovery decisions does not in itself need to change when it is time to decide. For example, the possible coordination
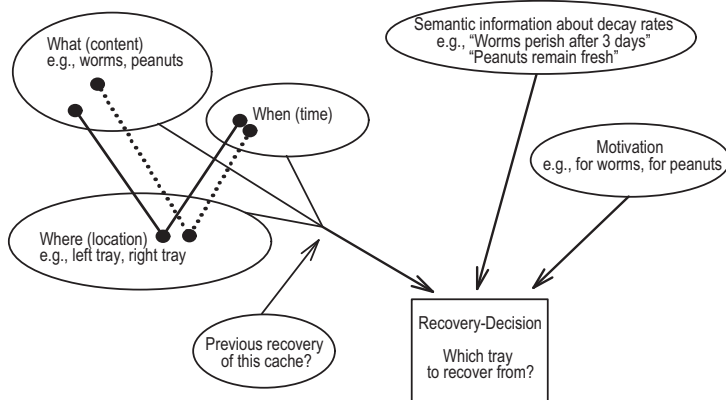

Figure 4.1 Schematic structure of coordination between different brain functions which may be required to solve the episodic-like memory tasks in Clayton and Dickinson (1998, 1999) and Clayton et al. (2001, 2003).

structure given in Figure 4.1 may allow the jays to solve all of the tasks in the above-mentioned experiments without changing anything but the data that is substituted in the different "brain functions." Information about the time that had elapsed since caching can be gained using the episodic-like memory of the caching event, whatever it is; then, this elapsed time could be compared with the semantic information about decay rates, whatever that information may be; motivation, despite changing frequently, will also affect the decision in a constant manner. All this does not change even if the test retention interval between caching and recovery has not yet been experienced by the jays (as in Clayton et al. 2003).

A somewhat different approach to studying episodic-like memory is to ask the subject unexpectedly to report their memory of past events. Zentall et al. (2001) investigated whether pigeons could report on whether they had just pecked a key or not. First they trained them to peck a red key, if they had just pecked, and green if they had not. In a second training phase, two different keys were used: yellow was followed by food whereas blue was not. Finally, the pigeons were given a test: either yellow or blue were presented, with only yellow eliciting a pecking response due to its previous association with food. Immediately thereafter, the bird was to choose between red and green, and they tended to choose the correct key according to their initial pecking or non-pecking action. Note that trials in the second training phase (presenting yellow or blue) did not include the question, "Did you just peck or not?" (i.e., choosing red or green, which was done during other "refreshing trials" in phase 2). In addition, a second test used novel stimuli which the pigeons either pecked or not, again followed by the red/green choice. Therefore, the authors suggest it is very unlikely that the pigeons would encode the correct response to this question (using semantic information) when they peck or do not peck during the tests. Rather, when given this question, they would need to retrieve their memory of what they had just done. While this provides more evidence for episodic-like memory in an animal model, even passing this test does not necessarily require dynamic coordination. The connections between pecking and choosing red (and between refraining and choosing green) were established in the first training phase; the connection between yellow (but not blue) and food was established in the second phase. All of these connections would have to be used during the test, but new ones, or the rearrangement of old ones, are not necessary. In that sense, again, the task does not require the coordination to be created moment-by-moment.

To conclude, passing the above tasks involves coordination of episodic and semantic information and, in some of the experiments, also motivation for different food types. However, as far as we can tell, it seems that episodic-like memory does not necessarily require the structure of coordination to change dynamically. There is, of course, a need for coordination throughout the task; however, the way in which the representations of the different keys relate to one another and to the task at hand do not change. Of course, there is always a

possibility that the *actual* computational manner in which such tasks are solved involves special forms of coordination after all, at least in some species. All we can say at this stage is that they are not necessarily needed in this case. In a similar manner, we shall now try to analyze studies from another realm of cognition, the physical one.

What Coordination Does Physical Cognition Require?

When subjects are able to solve new tasks based solely on their underlying physical properties, this suggests that they appreciate or "understand" something about these physical properties, and that we may bestow the successful subject some "physical cognition" or "causal understanding." While the computational and neuroanatomical details of how such feats are accomplished are largely unclear, physical cognition seems, at first glance, to require the establishment of a novel coordination between the specific properties (affordances) of a new task and some physical "rules" which the subject has already learned. Many studies of physical cognition include an initial training period, where subjects learn to perform a task, and may or may not also learn the physical rules governing this task. Then, "transfer tests" are performed to determine what the subject understands about these physical rules. These tests are most relevant for our purposes, as they include a novel situation which is unsolvable using only the associative learning acquired in the training phase or generalizing from the stimuli in the training task. Rather, the subject has to somehow apply the physical reasons or rules that underlie the success of its behavior in the training phase. The question is whether passing these transfer tests really requires any rearranging of the coordination present before the test. To address this question, we shall explore a few examples of primate and corvid physical cognition and attempt to outline the properties of the coordination they require.

Understanding the Properties of a Trap

A classical example of a physical cognition experiment, first used with primates and recently also with birds, is the trap tube. In the first version of these experiments (Visalberghi and Limongelli 1994), the training phase included a transparent horizontal tube with a trap-hole at its center, next to which a food reward was placed. The idea is to test whether the subject will learn to push the food reward to the correct direction (i.e., away from the trap), using a stick tool. Some of the capuchins, chimpanzees, woodpecker finches, and others tested learned the first task (reviewed in Martin-Ordas et al. 2008). After a subject mastered this task, a transfer test was performed with the tube inverted so that the trap was no longer functional. All primates tested still continued to push the food away from the trap, even when the tube was inverted, whereas one woodpecker did not. It has been rightfully argued that continuing to push

away from the nonfunctional trap bears no cost, and therefore this does not necessarily imply lack of physical understanding (Silva et al. 2005).

Since these studies were conducted, a modification of this task was introduced where two traps are placed in either side of the food reward, but only one is nonfunctional. This allows experimenters to assess what animals understand about the properties of traps, such as when an object will become lodged in a trap as opposed to when it will pass along the top of it or fall through the bottom. Versions of this experiment were conducted with rooks (Seed et al. 2006), and subsequently this design was adopted to test New Caledonian crows (Taylor et al. 2009) and chimpanzees (Seed, Call et al. 2009). The transfer tests suggest that some of the individuals tested have some understanding of the physical rules of the task in all three species. There is not yet a consensus among researchers as to the correct way to interpret success of only a small minority of the subjects. In addition, in some of these studies the transference was not made in the first trial but in the first block or blocks of trials; thus learning cannot be ruled out completely. We might need to wait for more experimental results in order to draw strong conclusions from our analysis. However, at this stage we are only trying to determine what form of coordination passing such transfer tests (on the first trial) seems to require.

In the rook and New Caledonian crow studies, a two-trap tube was used (Seed et al. 2006; Taylor et al. 2009), the configuration of which was altered by the experimenter to make only one trap functional. In the chimpanzee study (Seed, Call et al. 2009), a conceptually similar two-trap box design was used (Figure 4.2), which enabled testing physical cognition without the need for using tools. The subjects could reach the food with their fingers and push it to
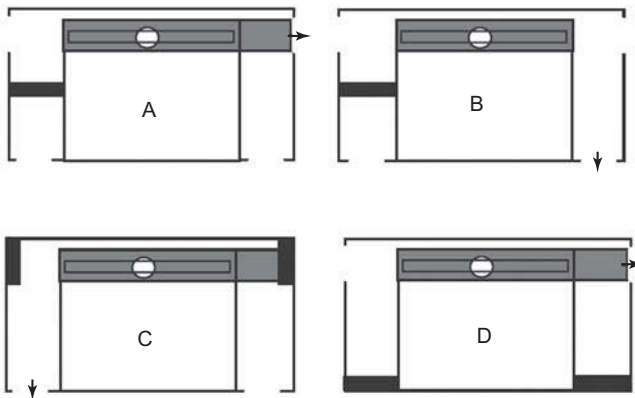

Figure 4.2   The two-trap box design used to test chimpanzees' understanding of physical properties (adapted with permission from Seed, Call et al. 2009). Configurations A and B were used in phase 1; configurations C and D in the transference tests (see text for details). The white circle marks the location of the food reward at the beginning of the trial, and the arrow marks the hole through which the food may be extracted if the subject pushes it in the correct direction.

either side. In configuration A, there was one functional trap (left-hand side of Figure 4.2A); the other trap was made nonfunctional by placing a shelf piece that prevented the food from falling, enabling its extraction through the side exit. In configuration B, the trap was nonfunctional due to the blocking piece being removed so that the food could drop through the bottom exit. Six out of the eight subjects successfully learned these two configurations and were then given the transfer tests (Figure 4.2, configurations C and D) to assess what they had encoded about the task. Note that in these transfer configurations, the blocking pieces which made the trap functional in A and B were removed to prevent a subject from acting according to the rule "push away from the blocking piece" to pass these tests (in D two different blockers were placed at the very bottom of the trap).

Applying such a rule, as well as rules such as "push toward the supporting shelf," does not seem to require any special form of coordination. However, to pass both transfer tests (C and D) the subject must apply some understanding of the fact that the shelf piece prevents the food from falling (e.g., "surface continuity prevents falling"). In C, the conclusion should be to avoid the shelf piece because the only way to get the food is by allowing it to fall through the bottom exit (the side exists are blocked), whereas in D the conclusion should be to push towards the shelf piece to prevent the food from falling and being trapped by the bottom blocker. Thus, an additional rule should have been encoded during the acquisition of A and B, or from previous experiences, to enable transference to both C and D. Namely, something in the form of "objects cannot go through barriers," which would be applied to the side and bottom blockers in configurations C and D, respectively. Such "abstraction from rules" may enable passing transfer tests without any understanding of unobservable forces such as gravity (for further discussion, see Seed et al. 2006; Seed, Call et al. 2009).

The relevant question for our purposes is whether applying such rules requires any special form of coordination between functions operating in these tasks, in the sense that the *type* of coordination between the representations of surfaces, solid objects, and the food item needs to be created moment-by-moment according to the attributes of each transference condition (see above). Our feeling is that there is no such requirement inherent to passing these transfer tests. If, say, the rules (a) "surface continuity prevents falling" and (b) "objects cannot go through barriers" are encoded before the transfer tests are given, then passing the transfer tests "only" requires applying them to the different surfaces and barriers. In other words, once such rules are encoded, a generalization of "barrier" is enough to enable the transference. How such abstract rules are encoded in the first place is another interesting question, and is probably far from being trivial. Evidently, only one rook (Seed et al. 2006) and one or two chimpanzees (Seed, Call et al. 2009) seemed to be able to do so.

"Insightfully" Bending a Wire to Make a Hook

New Caledonian crows are known to manufacture and use tools in the wild (Hunt 1996) and have recently been used in experiments to assess their understanding of physical properties. In one such study, a female crow (Betty) spontaneously shaped a hook tool out of a straight wire (Weir et al. 2002). This occurred during an experiment designed for different reasons, where subjects had to choose a hook tool over a straight one and use it to lift a bucket with a food reward, placed inside a vertical clear tube. In this instance, the provided hook tool was taken by the male, leading the female to shape her own hook from the remaining straight tool; in subsequent trials she (but not the male) continued shaping hooks when provided only with straight wire (Weir et al. 2002). In another study (Bird and Emery 2009), four rooks were first given experience using a hook tool to retrieve a food reward in a similar bucket-lifting task, and subsequently they succeeded in choosing a functional hook tool over a nonfunctional "hook" tool (with a backwards end). Then, they were provided with only a straight wire and spontaneously shaped it into a hook to retrieve the food bucket. It is very unlikely that hook shaping in the above studies could have been prespecified through associative learning or as an innate behavior, given that the rooks have not, in fact, been observed to use tools in the wild and that the birds showed spontaneous manufacture of hook-shaped tools.

In both studies, the subjects had presumably already encoded the connection between a hook tool and lifting the bucket, but not the possibility of bending a straight wire into a hook. Thus, the presentation of the apparatus may have elicited a representation of the appropriate hook tool, but it seems to us that the course of action leading from a straight wire to a hook required a new connection to be made. The fact that the connection is new to the animal means that it cannot be prespecified (Phillips et al., this volume). Perhaps, even more importantly, the type of coordination needed here (leading to the correct solution) is not prespecified either, nor imposed in its entirety by the observable properties of the task, as would be true for an associative learning task (see above). That is, the task affordances suggest a way of action, but do not explicitly specify it. Instead, the subjects must somehow creatively find the right answer. In other words, a form of dynamic coordination is required to solve the task "insightfully," apparently existing at least in these two corvid species. Interestingly, as Bird and Emery (2009) point out, one definition of "insight" states explicitly that it may involve a "sudden adaptive reorganization of experience" (Thorpe 1964:110). Claims for insightful behavior have been documented in primates and birds before, but in some cases simpler explanations involving the "chaining" of preexisting behaviors, which do not seem to require insight, were not excluded (e.g., see the associative account of box-stacking in pigeons by Epstein et al. 1984). Nevertheless, this field appears to hold a promise of providing a good behavioral tool for assessing coordinating abilities in different species, and it will thus be very interesting

to explore what computational mechanisms are enough to enable the insight involved in each case.

Using a Stick to Do a Stone's Job

The four rooks in the above study were also trained to insert a stone into a clear vertical tube in order to collapse a platform at its bottom, so that a food reward placed on the platform will drop (Bird and Emery 2009). In a series of transfer tests, Bird and Emery show that the rooks can choose a stone of correct size for the tube diameter of the tube (both from provided stones and also from stones picked from the ground) and orient it correctly when necessary for insertion. These transfers suggest that during initial training the rooks encoded something about the stone being of correct size compared to the diameter of the tube. It is quite remarkable that they encode this property, especially given the fact that during initial training all stones were of correct size. However, once encoded, a rule such as "compare size of stone to tube diameter" can be applied to solve the above-mentioned transfer tests without requiring insight. Another transfer test, however, seems to require a novel connection to be made. The rooks were given either a heavy stick, which they could drop into the tube to get the reward, or a light stick, which would not collapse the platform if dropped. On the first trial, all four rooks retained their grip of the light stick instead of dropping it, inserted it into the tube and pushed it, providing the force necessary to collapse the platform and get the food reward. This immediate transfer shows that during previous training and testing with the stones, the rooks encoded something about the necessity of collapsing the platform, which they used. However, this representation of the collapse of the platform is not enough to plan how to achieve that with the stick (having only been given experience with dropping stones to do so). Success in this transfer task thus seems to require a novel, "insightful" connection between the properties of the light stick and the way in which it can be used to achieve the collapse of the platform, again suggesting a sophisticated form of dynamic coordination in this corvid.

Open Questions and Future Directions

In addition to the examples analyzed above, there are other areas of research in comparative cognition which may be interesting with respect to the type of coordination they require. "Transitive inference" is the ability to infer a previously unencountered relation between two objects from their relation to one or more other objects (e.g., if A > B and B > C, it can be inferred that A > C). Does this inference of unencountered relations require any special coordination between their representations (through the representations of the relations which have been encountered)? Long thought to be uniquely human, evidence

is accumulating that nonhumans have various degrees of transitive inference (reviewed in Vasconcelos 2008), making the coordination required of even greater interest.

The attribution of mental states (e.g., knowledge, ignorance, motivation, belief) to another individual may also require projecting oneself into another's perspective, but does this require any reorganization of information in a way which is not prespecified? Whether nonhumans are able to attribute mental states is still a matter of controversy (e.g., Penn and Povinelli 2007), with evidence showing that some nonhuman primates and corvids may have such abilities (e.g., Emery and Clayton 2001; Hare et al. 2000). In any case, it could be beneficial to analyze what computational work is needed for one individual to use representations of unobservable states of another, and whether this involved any special form of coordination.

Finally, the ability to "think about one's own thoughts," or metacognition, may require some reorganization of the existing data (i.e., to apply a cognitive function such as "knowing" on one's own knowledge). Recently, evidence has been reported that Rhesus monkeys choose to "opt-out" and not even be given the latter part of a match to sample a test when they do not remember the sample well, suggesting that they "know when they remember" (Hampton 2001).

Regarding the convergent evolution of primate and corvid cognition (and possibly of dynamic coordination), questions remain as to how the structurally different avian and mammalian brains allow comparable cognitive abilities, and whether these structural differences necessarily confer different pathways or constraints in the evolution of cognition and that of dynamic coordination.

Our analysis of the coordination between different cognitive functions in a few animal cognition studies was a very schematic description. This is mainly because little is known about the way in which abstract rules, for example, are encoded in an animal's mind, and which brain functions are involved in such computations. Future research into the mechanisms governing these recently discovered cognitive abilities may enable a more detailed description. However, perhaps even at this early stage there is a better way to represent the coordination required in such behavioral tasks of which we are unaware.

As mentioned above, studies in comparative cognition are usually concerned with distinguishing cognitive explanations from simpler explanations such as associative learning. In addition, many of the studies have been inspired by realms of human cognition and many of the current debates are concerned with whether or not a certain ability that animals exhibit is comparable with its human counterpart (for a discussion of the extent to which episodic-like memory in animals captures the core components of human episodic recall, see, e.g., Tulving 2005). As such, these studies might not easily lend themselves to an analysis of dynamic coordination of the kind we have attempted here. A more productive way to proceed may thus be to design behavioral experiments for the purpose of distinguishing between different types of coordination, and specifically for assessing an animal's capability to reorganize the information it

already has in a novel way which can only be created when it is tested. If such experiments can be implemented in a diverse selection of species, it could enable drawing a phylogenetic tree of coordinating capabilities.

Acknowledgments