

Cognitive Imitation: Insights into the Development and Evolution of Social Learning

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The Oxford Handbook of Comparative Evolutionary Psychology

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Print Publication Date: Feb 2012 Subject: Psychology, Social Psychology

Online Publication Date: Sep 2012 DOI: 10.1093/oxfordhb/9780199738182.013.0025

Abstract and Keywords

What is cognitive imitation and what does it tell us about the development and evolution of imitation and cultural learning? Here, evidence is reviewed demonstrating dissociations between different forms of social learning; Specifically, dissociations between the copying of end-results (i.e., emulation) and the copying of actions (i.e., imitation), as well as between the imitation of ordinal rules (cognitive imitation) and the copying of motor-spatial rules (motor imitation), in human and non-human populations that typically fail to learn in motor imitation paradigms. Together, this body of research suggests that imitation is a multifaceted faculty with numerous domain-specific copying mechanisms. These mechanisms are predicted to be both developmentally and phylogenetically discontinuous; a result of unique selection pressures favoring certain copying mechanisms over others.

Keywords: Imitation, cognitive imitation, social learning, primates, children, autism, cognitive evolution

Introduction

What can animals imitate, if anything at all? This question has baffled comparative psychologists for more than a century (Fragaszy & Visalberghi, 2004; Subiaul, 2007; Thorndike, 1898, 1911; Tomasello & Call, 1997; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Toward the end of the twentieth century, the comparative sciences have moved in the direction of describing different phylogenetically ancient processes that may contribute to social learning (Call & Carpenter, 2002; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009; Zentall, 2006). These processes include attentional and motivational systems that are triggered by the presence of conspecifics, accelerating individual, trial-and-error learning, and, ultimately, behavior matching. Such “lower-level” processes include stimulus (Spence, 1937), local (Thorpe, 1956), and social (Clayton, 1978) enhancement. Other comparative scientists have pointed to “higher-level” social learning processes that result in behavior matching. For example, mimicry has been defined as

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copying specific actions, while remaining ignorant of the model's goals or intentions. So when parrots say “hello” or “good-bye” they are reproducing a vocal response learned from their keepers without an understanding of the significance of these responses (Zentall, 2006).

Tomasello and colleagues (Nagell, Olguin, & Tomasello, 1993; Tomasello, Davis-Dasilva, Camak, & Bard, 1987), among others, including Whiten (Whiten & Ham, 1992; Whiten, McGuigan, et al., 2009) have promoted various forms of emulation as an alternative to imitation. *Emulation* refers to copying the results of actions or their causal structure (e.g., emulation *sensu stricto*) the movement of objects (e.g., object-movement reenactment), or the goals motivating actions (e.g., goal emulation). (p. 475) According to this view, individuals emulate when they reproduce goals, results, or causal structure while ignoring the precise actions used by the model to achieve that result. These social learning mechanisms are seen as being distinct from imitation, which is typically defined as copying the actions and goals of a model to achieve a specific action (Call & Carpenter, 2002; Tomasello & Call, 1997).

The Legacy of Morgan's Cannon

Historically, a comparative perspective on imitation has adhered closely to Morgan's canon (Morgan, 1903). This has meant that, if behavior-matching may be explained by a “lower” or simpler process, then we should reject any “higher” or presumably more-complex processes (e.g., emulation or imitation) as an explanation for a given behavior. Such assumptions have led to a number of pervasive assumptions in the comparative study of social learning. First, researchers, although regularly “controlling” for stimulus/local enhancement, have largely failed to study these processes in their own right. Those that have studied the role of stimulus enhancement on social learning have reported rather sophisticated forms of learning, including the transmission of “traditions” (Matthews, Paukner, & Suomi, 2010). Second, social learning theorists have largely assumed that if one mechanism explains behavior-matching (e.g., emulation) then other, presumably more complex behavior-matching mechanisms (e.g., imitation) must be excluded. However, imagine you have two groups of children: one group is exposed to a model demonstrating both a given action (e.g., picking up a ring and placing it on a peg) and the end-result of that action (e.g., a ring around a peg). A second group sees only the end result of the model's actions (e.g., a ring around a peg) but never sees the model executing this action. After being exposed to one of these events, children are presented with both a ring and a peg and allowed to interact with them. Comparative psychologists will argue that children who pick up the ring and place it around the peg are imitating if and only if children fail to place the ring on the peg in the end-result condition. The argument is straightforward: if children can reproduce a given event when provided with just the end-result of actions, then there is no reason to assume that, in the condition where a model is present, the child is reproducing the model's actions. The more parsimonious explanation is that

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children are independently reproducing the outcomes of actions (emulation). They need not reproduce the actions *and* results (imitation) they observed the model execute.

Though reasonable enough, such a parsimonious explanation assumes that these conditions are equivalent; the only difference is that the model is missing in the results only condition. However, these conditions are not equivalent because the *nature* of the information are inherently different. The presence of a human model almost certainly changes the informational signal, making behavior-matching an implicit-pedagogical-expectation (e.g., natural pedagogy: Csibra & Gergely, 2009). As such, rejecting imitation as a mechanism in the condition where participants observed both actions (by the model) and their consequences (i.e., results), though parsimonious, is probably incorrect. What is more likely is that individuals possess two distinct mechanisms, one that is activated when observing actions and results together as when executed by a model and another that is activated to achieve behaviormatching when observing only results. Horner and Whiten (2005) elegantly pointed to such a dissociation in a study with chimpanzees (albeit between subjects). Chimpanzees were presented with models interacting with two different types of boxes, providing different types of information. In one case, models demonstrated both actions and results; in the other case, models demonstrated only actions (results were occluded). Results revealed that when chimpanzees were allowed to see only the actions of the model, they copied the model's actions and goals (e.g., imitation). However, when they saw both actions and results, chimpanzees copied only the end-result of the model's actions, using their own idiosyncratic techniques (e.g., emulation). Such emulation/imitation switching suggests that behavior-matching can be achieved by multiple and independent social learning mechanisms that may be dissociable within-subjects.

The ghost control is another experimental paradigm that has been problematic. In this control condition, participants observe objects move toward a goal autonomously, as if being moved by a ghost. This paradigm is considered to be a control for object movement reenactment (Hopper, 2010) because participants are provided with only two types of information: results and object movements. The absence of a model precludes the ability to copy actions directly. As in our first example, if participants learn in this ghost condition in addition to the standard demonstration condition with a live model, then imitation is excluded as the primary learning mechanism. Despite the fact that it (p. 476) had long been argued that primates are emulators— copying either end results only or the movements or objects only (Tomasello & Call, 1997)—few studies have reported evidence of learning in ghost controls. Specifically, neither monkeys (Subiaul, Cantlon, Holloway, & Terrace, 2004) nor apes (Hopper, et al., 2007) learned when provided with just results and object movements. Children, however, some as young as 18 months, did learn under such conditions (Huang & Charman, 2005; Subiaul, Lurie, Klein, Holmes, & Terrace, 2007; Thompson & Russell, 2004). Since the publication of these studies, Klein and Zentall (2003), working with birds, as well as Hopper and colleagues, working with captive chimpanzees, have employed an “enhanced” ghost control that highlights specific aspects of the object movement event; drawing attention to object affordances. Learning was achieved in these enhanced ghost conditions, but performance was relatively impover-

ished in comparison to learning in a standard “social” condition in which a model demonstrates the action (for a review see: Hopper, 2010; Hopper, Flynn, Wood, & Whiten, 2010).

These studies, although interesting, leave many questions unanswered. What does it mean when someone learns under such strange conditions? Under such circumstances, it is unclear whether dedicated social learning mechanisms are involved. It is also unclear *how* information is being processed and understood by the participant. Herein lies the crux of the problem for comparative psychologists: while the focus has been to isolate *what* information is being used by subjects using subtractive experimental methods (e.g., Call & Carpenter, 2002), these researchers have paid little to no attention to *how* neural-cognitive mechanisms process such information and whether these purported mechanisms of social learning actually map unto known neural circuits.

In the cognitive sciences, most higher-order cognitive skills such as memory, language, and theory of mind are believed to consist of multiple dedicated mechanisms that make specific computations on restricted content domains (Pinker, 1997; Carruthers, 2006; Leslie, 1994)—for example, personal (episodic) memories versus general (semantic) facts, speech versus nonspeech ambient noises, and agency-attribution versus false beliefs, respectively. Some of these mechanisms may be highly encapsulated and automatic such as the perception of agency (Leslie, 1994). Others may be less encapsulated and may take as input a wider range of content types such as episodic memory (Carruthers, 2006). In the following section, I will argue that the architecture of imitation also consists of multiple mechanisms or systems, each dedicated to representing information in a format that allows that information to be reproduced or imitated, matching that which was observed (Subiaul, 2010).

The Multiple Imitation Mechanisms (Mim) Hypothesis

The Many Faces of Imitation

Imitating *is* copying. The core question for a cognitive science of imitation is then to address not just *what* is copied but *how* any copying is achieved by the brain and the mind. From a comparative perspective, we are also interested in whether these mechanisms are homologous or whether copying is achieved through analogous processes. As already noted, there are likely to be alternate, noncopying or nonimitative processes that can result in two behaviors resembling one another (i.e., behavior matching). Indeed, there is evidence demonstrating that fairly low-level attentional mechanisms may ultimately lead to behavior matching (Bonnie & de Waal, 2007; Fritz, Bisenberger, & Kotrschal, 2000; Matthews, et al., 2010). The difference between a copying mechanism that is part of the imitation faculty and these alternative (lower-level) processes is that imitation mechanisms are *dedicated* copying mechanism. That is, they are specialized neural-cognitive information processors that perform specialized forms of computations on particular types of stimuli. The result of these computations is sent as output to other mechanisms that

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may perform additional computations, execute specific motor response(s) or both (Car-ruthers, 2006; Leslie, 1994, 2000). As such, the multiple imitation mechanisms (MIM) hypothesis (Subiaul, 2010) views imitation as consisting of various imitation mechanisms, each involved in the copying of specific types of information. Together, these various systems comprise the imitation faculty.

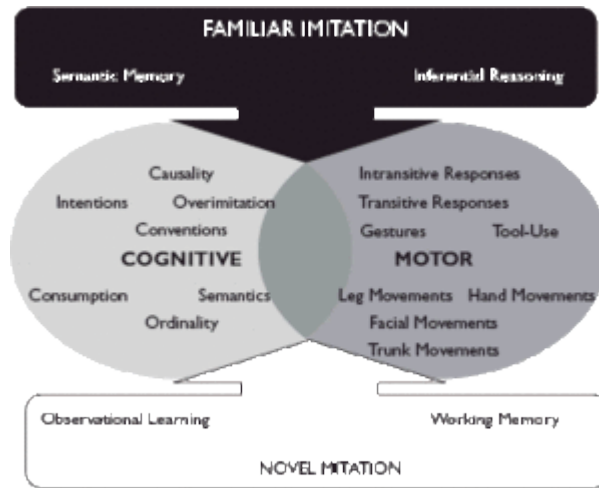


Figure 25.1 Multiple Imitation Mechanism (MIM) Model. Schematic includes two super-ordinate imitation mechanisms (familiar and novel) as well as two sub-ordinate imitation mechanisms (cognitive and novel) and various hypothesized domain-specific imitation mechanisms encompassed in the broader “cognitive” and “motor” domain. The sub-ordinate “motor” and “cognitive” imitation mechanisms interact with each other and with the two superordinate imitation mechanisms: “familiar” and “novel” imitation. These mechanisms provide specific computational constraints on imitation-specific mechanisms matching them with previously learned information from a semantic store (i.e., familiar imitation) or developing a matching response in working memory (i.e., novel imitation).

In the MIM model, the imitation faculty is conceptualized as consisting of various subsystems, each specializing in the copying of a specific class of stimuli. These subsystems are, in some cases, independent of other subsystems as may be the case with cognitive and motor-spatial imitation. However, in other instances, subsystems are likely to be interdependent, taking as input the output of other subsystems. For example, the observational learning system likely provides necessary input to various novel imitation systems, as there is no knowledge (p. 477) or existing memory trace to serve as the basis for a matching response. The familiar imitation system is unlikely to take input from the observational learning system. Instead, it is expected to rely on semantic memory stores to generate a matching response (see Figure 25.1). This view of imitation fundamentally differs from the widely held domain-general view of imitation (Brass & Heyes, 2005; Catmur, Walsh, & Heyes, 2009). These theorists and researchers view the imitation faculty as a domain-general mechanisms that operate across different domains and content types, allowing indi-

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viduals to learn everything from motor rules, such as how to use chop sticks, to vocal rules, such as how to say *spaghetti*, to abstract rules, such as how to cook your favorite French dish. Given what is known about the imitation skills of human children and other primates, it appears that the environment of early hominids favored individuals who were versatile and adaptive imitators, capable of copying a wide range of behaviors and responses: from using chop sticks, among other tools, to saying *spaghetti*, among other novel sounds, to cooking steak au poivre, among other procedural rules. However, the representation of auditory stimuli (such as *spaghetti*) for the purposes of reproducing that sound must be fundamentally different than the representation of a motor action (such as using chop sticks) for the purposes of copying that action. A general-purpose imitation mechanism capable of performing these different tasks seems unlikely if not improbable. What is more likely is that selection sifted through individuals with varying imitation skills and a unique cognitive-neural imitation profile capable of identifying, representing, and copying these different types of information. This process would have produced distinct imitation skills mediated by specific imitation mechanisms dedicated to representing and copying specific types of stimuli. From this it follows that humans are good imitators relative to other primates, not because we have an imitation mechanism that primates lack, but because our species has evolved a whole suite of distinct imitation mechanisms or “imitation instincts” that together result in an impressive ability to copy all sorts of responses in a flexible and adaptive fashion.

(p. 478) This view of imitation suggests that the imitation faculty represents a specialized psychological system with input from a number of domain-general or “central” systems like attention, reasoning, and in some cases, associative learning as well as domain-specific “core knowledge” that include “theory of mind,” “naïve physics” and “naïve biology” (Carey, 1985; Spelke, 2000). Through this kind of domain-specificity, the imitation faculty can copy responses across different domains in a flexible and adaptive fashion.

Like other faculties, the imitation faculty can be divided by its various functions. These functions are best captured by superordinate and subordinate imitation mechanisms associated with the processing of specific types of stimuli. The superordinate imitation mechanisms include, (1) “familiar imitation,” or the copying of familiar rules or responses and (2) “novel imitation,” or the copying of novel rules or responses; the latter is often referred to as “imitation learning,” which is distinguished from “familiar imitation” because it requires observational learning. That is, the ability to learn through vicarious (rather than direct) reinforcement (Bandura, 1977). Various researchers have made similar class distinctions, recognizing that different mechanisms likely mediate the learning and copying of novel behavior(s) and the copying of behaviors that already exist in an individual's repertoire (Byrne & Russon, 1998; Heyes, 2001). However, these investigators have tended to argue that these skills are not related and, consequently, have used different names to describe these skills. The likely reason for this is that many of these researchers believe that imitation is a single unitary cognitive process that animals either have or lack entirely; this is a notion that dates back to Thorndike (1898). A similar point is raised by Smith and colleagues in chapter 15 of this volume, who question the usefulness of viewing metacognition as a unitary system, a view that neglects the possibility that some

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species may have evolved some components of a metacognitive system and not others. In the MIM framework, familiar and novel imitation mechanisms are brought together as part of the same cognitive faculty that mediates the ability to copy rules or responses across contexts. Moreover, subsumed within those two broad functional concepts are subordinate mechanisms of imitation that specify the type of stimuli that is reproduced by either novel or familiar imitation.

All the proposed imitation mechanisms are characterized by flexibility *and* specificity. The flexibility requirement means that the behavioral rule that is copied is deliberate or replicable. That is, it can be elicited in multiple contexts on multiple occasions; it is not the result of happenstance or trial and error learning. The specificity requirement emphasizes that individuals must copy a specific “rule” or response. The term *rule* is broadly defined as a structured response that is hierarchically organized to achieve a matching response. The requirement that any type of imitation be rule governed and flexible is necessary in order to differentiate imitation from either perceptual or motivational mechanisms that, in association with rapid trial-and-error learning, may represent an ancestral learning mechanism that predates (and may, perhaps, co-exist) with the imitation faculty, providing critical input to the mechanism mediating familiar imitation, for example. The same is true of narrow species-specific skills such as copying mate preferences, which, although impressive, do not extend beyond a very narrow context (i.e., mating) and is dependent on specific stimuli (i.e., females) (Bshary & Grutter, 2006; Paz, Bond, Kamil, & Balda, 2004). Nevertheless, such mechanisms provide important clues into the origins of the primate imitation faculty; highlighting, for instance, how selection for multiple content-specific observational learning skills could be aggregated by natural selection resulting in a domain-specific imitation faculty.

However, what evidence is there that there are specialized mechanisms for copying specific forms of information? One way of addressing this problem is by demonstrating a within-subject dissociation between the copying of two different content domains. For example, Rumiati, Tessari, and colleagues (Rumiati & Tessari, 2002; Rumiati, et al., 2005) demonstrated that the copying of meaningful (familiar) actions is dissociable from the copying of meaningless (novel) actions. Another approach is to isolate certain forms of imitation in special populations like monkeys or individuals with autism that have limited social learning repertoires. In what follows, I describe a number of studies with monkeys, typically-developing children, and individuals with autism, which provide some of the earliest evidence for specialized imitation learning mechanisms in these different populations; providing hints about the different selection pressures acting upon the imitation faculties of human and nonhuman primates, respectively.

Cognitive Imitation in Monkeys

Although much has been written about motor imitation as well as vocal imitation in mammals (p. 479) (Janik & Slater, 2000), little has been written about the imitation of nonmotor, nonvocal rules in these populations. Subiaul (2010) and colleagues (Subiaul, et al.,

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2004; Subiaul, Lurie, et al., 2007; Subiaul, Romansky, Cantlon, Klein, & Terrace, 2007) were the first to demonstrate that the copying of cognitive—ordinal—rules can be isolated from the imitation of motor rules. The studies conducted on novel cognitive imitation were analogous to copying someone's password at an automated teller machine (ATM) after looking over that person's shoulder while they punched in their personal identification number or PIN. Because the observer already knows how to enter numbers on the keypad, no motor learning is necessary. However, in the task employed—the simultaneous chaining paradigm (Terrace, 2005)—a set of pictures appeared simultaneously on a 45 X 4 grid of a touchscreen. From trial to trial the position of the pictures changed. This would be like showing up to an ATM and the numbers being in a different spatial configuration each time.

Nonetheless, the ATM example illustrates the two different rules that individuals might learn when observing someone enter their PIN. For instance, when copying someone's password, observers may copy a spatial/motor rule (e.g., up, down, left, right); ignoring the sequence of numbers being pressed. Conversely, someone might copy the actual numbers pressed (e.g., 2, 8, 4, 6), disregarding the specific motor responses corresponding with each number's location on the touch pad. In both instances, the observer is copying a rule; the principle difference is the type of rule: spatial/motor versus cognitive/ordinal that is learned and copied by the observer.

In one experiment (Subiaul et al., 2004), two rhesus macaques were given the opportunity to execute serial chains involving novel lists of pictures in one of two ways: by trial and error (baseline) or by observing an “expert” macaque execute the same list in an adjacent chamber (sociallearning condition). When the monkeys' performances in the baseline and in the social-learning conditions were compared, results revealed that naïve “student” macaques who observed an “expert” executing a new list during the social-learning condition learned significantly faster than in a baseline condition in which they had to learn new lists entirely by trial and error.

In a second experiment (Subiaul et al., 2004), student macaques were given the opportunity to observe an expert execute a list (e.g., list A). At the end of 20 trials, the student was tested on a *different* list (e.g., list B). Students in this social-facilitation condition could not learn from the expert because both students and experts executed different lists of arbitrary pictures. As in the social-learning condition, performance in the social-facilitation condition was compared to baseline in which subjects had to learn new lists entirely by trial and error. In this experiment, any difference between a student's rate of learning in the social-facilitation and the baseline conditions would be the result of social facilitation (Zajonc, 1965) rather than of novel imitation. Yet, the rate of learning in the social-facilitation and the baseline conditions did not statistically differ.

In all three conditions, computer feedback was available to students. For example, every time the monkey touched an item on the screen, a black border flashed around the picture item. As such, student monkeys in experiment 1 could have learned from the computer feedback alone, rather than from the actions of the model, to discover the ordinal posi-

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tion of list items. To test whether performance in the social-learning condition could be replicated by providing naïve students with computer feedback only, in experiment 3 all features of the social-learning condition were maintained, except that, during the computer feedback condition, no monkey was present in the adjacent chamber and the computer automatically highlighted the target items in the correct serial order. This control condition was analogous to the “ghost controls” described earlier. After 20 trials, the student was tested on the same list. As was done in the previous experiments, students' performance in this “ghost control” was compared with performance in the baseline condition. Results demonstrated that monkeys did not benefit from computer feedback alone, as evidenced by the fact that the rate of learning in the ghost condition did not differ from the rate of learning in the baseline condition. However, a similar test given to typically developing human children and individuals with autism showed that all participants learned in the ghost control (Subiaul, Romansky, et al., 2007); a result that has been replicated in numerous motor imitation studies with children (Huang & Charman, 2005; Thompson & Russell, 2004). And, as was previously noted, while earlier studies failed to demonstrate similar learning in nonhuman great apes (Hopper, et al., 2007; Tennie, Call, & Tomasello, 2006), more recent work by Hopper and colleagues has shown that, under certain experimental conditions, apes can learn in ghost conditions. Though learning in ghost controls by nonhuman great apes is poor when compared with the performance of human children in similar conditions (p. 480) and when compared with great apes' performance in a standard social condition with a live model (Hopper, 2010).

The fact that learning in ghost controls may come as naturally to humans as learning in standard social learning conditions raises a number of interesting questions that beg for an explanation. One hypothesis is that the difference may rest on the propensity of human subjects (but not nonhuman animals) to generate powerful percepts about agency, goaldirectedness, and/or intentionality whenever an inanimate object moves autonomously and with goaldirectedness (Csibra, Gergely, Biro, Koos, & Brockbank, 1999; Michotte, 1946; Premack, 1990). Such percepts may aid imitation learning in ghost controls. (Subiaul, Vonk & Rutherford, In Press) This potentially unique human ability has been reported in human infants, who attribute intentionality and/or goaldirectedness to a ball that jumps over a barrier and navigates around obstacles (Csibra, et al., 1999). Thus far, no comparable evidence exists for monkeys (Cheney & Seyfarth, 1990) or other animals. The spontaneous generation of such percepts in ghost conditions may focus human participants' attention on the relevant actions and their consequences in ways that facilitate learning. The success of nonhuman animals in “enhanced” versions of the ghost controls is consistent with such an “attentional hypothesis,” but note that the mechanisms underlying learning are different. Whereas both children and animals (under “enhanced” conditions) learn in ghost controls, the underlying mechanisms are unlikely to be the same. Whereas children's attention is guided by internal percepts of agency and animacy-generating representations about goals and/or possible (imagined) actions, nonhumans' performance appears to be primarily guided by external factors that call attention to the most relevant features of the task-promoting learning.

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In summary, there are reasons to suspect that, although aspects of the primate imitation faculty are ancient and widely distributed, as expected by common descent, other features of the imitation faculty are likely to be species-specific (Subiaul, 2007, 2010). Using the simultaneous chaining (computer) paradigm (Terrace, 2005), monkeys, a population that typically does poorly on motor imitation paradigms, demonstrated the ability to flexibly copy novel cognitive rules. This result suggests that monkeys have a novel motor imitation deficit rather than a general novel imitation deficit. That is, an impairment for copying new rules and responses. Additionally, given that some evidence exists for familiar motor imitation but none exists for novel motor imitation in monkeys is further evidence that the motor planning and execution systems of apes might be more derived than those of monkeys and other animals, perhaps as a result of apes' long history using tools (Mercader, et al., 2007; Mercader, Panger, & Boesch, 2002). Nevertheless, additional research is necessary in order to better understand monkey's motor imitation limitations.

Given the results of Subiaul and colleagues, what might be the function of cognitive imitation in more ecologically valid settings? One possibility is that novel cognitive imitation is critical for learning and copying social rules that provide individuals with the tools to manage dominance hierarchies, kin relationships, and socio-political relationships or alliances at low costs. That is, costs are too high if not impossible to manage without a social learning mechanism. However, in addition to these benefits, novel cognitive imitation may also be critical for learning what foods are palatable. After all, Reader and Laland (2002) note that anecdotal reports of innovation and social learning are most common in foraging. In a number of studies, Visalberghi and colleagues explored this very question using a captive population of capuchin monkeys. Capuchin monkeys are, in many regards, an ideal species with which to study the cognitive imitation of novel food preferences because, although they are moderately neophobic of new foods, captive capuchins sit near each other during feeding and closely attend to what others are eating (Fragaszy & Visalberghi, 2004). Capuchins are also very tolerant, allowing conspecifics to take small bits of food they have dropped (Fragaszy & Visalberghi, 2004). Given these characteristics, it seems that their behavioral and motivational states are optimal for observational learning and novel cognitive imitation. Fragaszy and Visalberghi (2004) reasoned that there are at least three mechanisms by which individuals could acquire novel food preferences. These mechanisms range from (1) a general (arousal/motivational) mechanism that increases feeding overall without regard to particular food items, to (2) a more subtle mechanism whereby subjects are attracted to novel items in general (e.g., neophilia), to (3) cognitive imitation, whereby individuals acquire a dietary rule(s) pertaining to the palatability of particular foods.

Fragaszy and Visalberghi (2004) cite a number of studies that suggest that capuchin monkeys use a general (motivational or arousal) mechanism that increases feeding, particularly when presented with novel foods (i.e., neophilia). For Fragaszy (p. 481) and Visalberghi, this precludes any evidence for novel cognitive imitation. These conclusions are buttressed by a number of studies showing that monkeys are more likely to eat when in the presence of others than when alone (Galloway, 1998 as cited by Fragaszy & Visalberghi, 2004; Addessi & Visalberghi, 2001). For example, Addessi and Visalberghi (2001)

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presented capuchins with novel food items (consisting of different food products that were mashed and differentially colored) in three different conditions: (1) alone, (2) in the presence of noneating group members, and (3) in the presence of eating group members. They reported that, as group size increased, so did the consumption of the novel food product by the observing monkey. Moreover, the sight of a conspecific eating a novel colored food was sufficient to increase food consumption (independently of condition) for two of the three different types of novel food products presented. Although these results provide important insights into the feeding behavior of capuchin monkeys, they are not designed as social learning experiments per se because subjects are not provided with a choice, for example, between a “palatable” and a “nonpalatable” food item. However, Fragazy and Visalberghi (2004) cite unpublished data (i.e., Addessi & Visalberghi, 2001) that suggests that, even when provided with a choice, capuchin monkeys do not show a preference for the “palatable” food. However, in studies that changed the palatability of a familiar food item, there was no difference between a social condition (with a model eating the now unpalatable food) and an individual learning condition, in which subjects discovered the palatability of the food item by happenstance (Addessi & Visalberghi, 2001).

In contrast to capuchins, Hopper and colleagues (in press), using a token economy, demonstrated that apes imitate the dietary preferences of others. Hopper and colleagues trained two groups of chimpanzees to exchange inedible tokens for either a high value (grape) or a low value (carrot) reward. Before gaining access to the tokens, group members observed a high ranking individual in their group choose one of the two types of tokens. In one group this token earned the high reward. In the other group the same token was associated with the low reward. Groups conformed to the dominant individual's preference. This was particularly striking in the group that observed the model choose the low reward. After discovering that the other token led to a higher valued reward, they continued to imitate the high-ranking model's preference. Hopper and colleagues argue that this type of cognitive imitation resulting in group-specific dietary conventions is critical for the maintenance of group relations.

Certainly there are very few studies that systematically explore the learning of novel dietary rules. Given this limited evidence, the results of studies by Addessi & Visalberghi (2001) and Hopper and colleagues (in press) tentatively suggest a potential phylogenetic divide between apes' and monkeys' ability to imitate a novel cognitive rule in the dietary domain. Specifically, whereas monkeys appear to rely on a domain-general arousal mechanism, apes appear to rely on a domain-specific dietary mechanism. This more specialized cognitive imitation mechanism allows them to vicariously learn and reproduce specific dietary rules that specify group-wide food preferences, food palatability or both.

Cognitive Imitation In Children

A number of studies suggest that, by 14 months, children imitate flexibly, seemingly alternating between emulation (copying only goals or endresults) and imitation (copying both actions and goals and/or endresults) depending on context (Buttelmann, Carpenter, Call,

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& Tomasello, 2008; Gergely, Bekkering, & Kiraly, 2002). The evidence from great apes is mixed, however. Some have demonstrated that apes can alternate between copying actions and copying endresults (e.g., Horner & Whiten, 2005) and enculturated apes imitate “rationally” (Buttelmann, Carpenter, Call, & Tomasello, 2007). But, subsequent research by some of these same authors has revealed that peer-reared apes neither rationally nor flexibly imitate others' actions (Buttelmann, et al., 2008). What accounts for these differences? Some of these differences have been explained by differences in rearing histories (Tomasello & Call, 1997)—for example, apes that are reared by humans as opposed to those reared by kin or those reared by their mothers. However, the dominant argument in the comparative sciences has been that the differences between human and nonhuman imitative performance has to do with great apes' inability (or difficulty) inferring psychological states like goals and intentions; something humans do from a very early age (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Tomasello & Call, 1997). These differences in imitation performance appear early in the ontogeny of human and chimpanzee infants (Tomasello & Carpenter, 2005). Specifically, Tomasello and colleagues have argued that underlying these differences in imitation and cultural learning are a suite of (p. 482) skills present in human infants but missing almost entirely in nonhuman great apes including the ability to engage in the joint sharing of attention and intention with others (Tomasello & Carpenter, 2005; Tomasello & Carpenter, 2005).

Although a failure to infer goals and intentions of others' actions would limit imitation performance, so would a failure to understand actions themselves. It is possible that one reason why apes do not understand goal-directed actions is because they have a limited understanding of functional capability, that is, the notion that the limbs of others are to some degree specialized, capable of doing some actions but not others. Vonk and Subiaul (2009) for example, demonstrated that chimpanzees failed to distinguish between two experimenters who were differentially capable of executing a given action. Across five different studies, chimpanzees as a group failed to distinguish between an experimenter who could give them a reward from one who was incapable of doing so because either their hands, feet, upper body, or lower body were occluded. A failure to appreciate the function and capability of limbs would seriously affect one's ability to imitate others' actions. Related work in the developmental sciences has demonstrated that 3-month-old infants who fail to appreciate goal-directed reaching action because of limited motor capabilities can eventually understand goal-directed actions following a training session in which they are rendered capable of “grabbing” a desired toy when their hands were affixed with “sticky mittens” (Sommerville et al., 2005). These studies have suggested that, to understand goals, one must be able to both execute the observed action and experience the results of a given goal. In other words, action understanding is an embodied experience involving an appreciation of not just goals but functional capability.

The cognitive imitation paradigm described throughout this text overcomes some of these potential differences between how human and nonhuman primates understand actions because subjects must copy neither a motor nor a vocal rule but rather a “cognitive” rule. In one study, Subiaul, Romansky, and colleagues (2007) compared the performance of monkeys described earlier to that of healthy, typically developing 2.5-year-olds. Results

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showed that children, like monkeys, learned from the model; they copied the ordinal rule demonstrated. However, since we were interested in whether monkeys and children used homologous, rather than analogous cognitive mechanisms to learn by trial and error and cognitive imitation, we compared the frequency of two types of errors. Specifically, we analyzed the rate of perseveration (i.e., repeating the same error multiple times before the first correct trial) and backward errors (i.e., touching an earlier item in the sequence: A→B→A) made by both monkeys and children while executing novel lists of pictures by trial and error (baseline) and cognitive imitation (social).¹ Both monkeys and children made significantly more perseverative errors in baseline than in the social (cognitive imitation) condition. Similarly, both monkeys and children made very few backward errors in baseline and the social condition. These results are consistent with the hypothesis that the monkeys and children used homologous learning mechanisms.

Williamson, Jaswal, and Meltzoff(2010) have built on this research and asked how children might employ cognitive imitation in the course of typical development. To do this, they asked whether children can learn and copy a categorization (i.e., cognitive) rule demonstrated by an adult. Sorting and categorization strategies are important because they can be applied across different contexts. In a series of studies, children were shown models who sorted different objects based on visually distinctive features such as color or acoustic features such as the sound they made when placed in a box. A control group was simply given the objects to sort however they saw fit. Results demonstrated that children adopted the sorting strategy employed by the model. Importantly, this strategy differed from the one preferred by children who did not see a model sort the objects. As in Subiaul et al.'s paradigm, children could not imitate the actions of the model per se. Rather, they had to abstract the model's responses into an overarching cognitive (categorization) rule, dividing objects into nonobvious categories used by the model (e.g., shape).

Individuals with autism have also been studied using this cognitive imitation paradigm because some have suggested that this population has a domain-specific imitation impairment (Williams, Whiten, & Singh, 2004). Specifically, a meta-analysis of various studies using different methods and tasks revealed that individuals with autism have a pervasive difficulty copying meaningless or novel motor responses on the body or actions directed toward objects (e.g., tool/object use). Such a result indicates that this population suffers from a general difficulty copying novel rules from others. That is, a primary feature of autism seems to be imitation *learning*.

To address whether individuals with autism had a specific problem copying novel or unfamiliar (p. 483) rules, Subiaul, Lurie, and colleagues (2007) used the cognitive imitation paradigm described earlier and tested a group of typically developing 3- and 4-year-olds as well as a group of individuals with autism. Participants were tested in a baseline (trial and error) control condition and three different vicarious learning conditions: social + computer feedback, social only, and computer only (i.e., ghost control). Results showed that individuals with autism had no difficulty learning in any of the conditions. Specifically, as a group, individuals with autism performed significantly above-chance levels on the very first trial in the social + computer feedback, the social only, and the computer only

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(ghost) condition. The same was true for the typically developing 3- and 4-year-olds. When these two groups were compared, there was no statistically significant difference between their performances. These results indicate that individuals with autism are capable of learning novel (unfamiliar) ordinal rules from a model and, like typically developing children, they learned when provided with just social cues as well as nonsocial (computer) cues—evidence of flexibility in imitation learning.

This body of research, though small, indicates that humans and other primates differ in their ability to understand, attend to, and subsequently copy motor responses; particularly motor responses that appear to be arbitrary or meaningless (Subiaul, Romansky, et al., 2007). Yet, a fundamental aspect of social learning, the ability to understand global rules pertaining to the ordinal structure of an event (e.g., Subiaul et al., 2004; Subiaul, Romansky, et al., 2007) and perhaps the ability to copy categories (e.g., Williamson et al., 2010), may represent phylogenetically ancient skills that likely served as a pre-adaptation for more derived imitation skills such as novel motor imitation.

Discussion and Conclusions

The work summarized in this chapter has a number of implications for the study of imitation that are both conceptual and methodological. Evidence demonstrating that apes as well as children can alternate between emulation and imitation learning (Buttelmann et al., 2008; Gergely et al., 2002; Horner & Whiten, 2005) and that monkeys and children with autism—two populations that typically fail to evidence imitation in motor paradigms—can nonetheless, learn novel and arbitrary novel cognitive rules (Subiaul et al., 2004; Subiaul, Lurie, et al., 2007; Subiaul, Romansky, et al., 2007) suggests that the imitation faculty, like other psychological faculties, consists of many discrete mechanisms. These mechanisms are specialized copying systems that have been shaped by species-specific evolutionary factors to reproduce ecologically meaningful information in the environment. From this, it follows that humans and nonhuman animals differ not in whether they can imitate but *what* they are capable of copying (Subiaul, 2007). That is, each species should have a unique imitation faculty. Some of these faculties will have many different copying mechanisms, as appears to be the case with humans, but others are likely to have just a few copying mechanisms, as may be the case with other mammals and primates.

The conceptualization of imitation as a domain-specific faculty leads to a number of novel questions that are yet to be fully explored. In the section that follows, I highlight some of the major outstanding questions in the comparative study of imitation. Answers to these questions will bring us closer to understanding what is truly unique about human imitation and cultural learning.

Future Directions

- *Are there within-subject dissociations in the imitation of different content (task) types?* Researchers have generally assumed that imitation performance in one content domain should transfer to other content domains, assuming comparable levels of complexity. However, few studies have experimentally tested this assumption. The MIM hypothesis, predicts that there will be differences in imitation performance depending on content type. Of significance to comparative researchers interested in the question of cognitive evolution is whether humans and other primates excel and fail in the same way in the course of their development.
- *What underlies the ability to learn in ghost controls?* It is a curious fact that children readily learn in ghost controls. Yet, nonhuman animals, generally fail to learn under similar conditions (Hopper et al., 2010). This result is surprising because historically it had been argued that apes generally copied only results. That is, whereas humans are imitators, copying actions and results, monkeys and apes are emulators, copying only results. However, success of human children in the ghost controls remains to be explained. Given that certain manipulations lead to apes successfully learning in ghost controls, we are now in a position to ask whether apes and (p. 484) human children learn under such conditions using homologous or analogous mechanisms. Specifically, do children learn because they are guided by percepts of goaldirectedness or by more general learning principles?
- *Is there something special about the imitation of tool use?* Great apes have a long history using tools (Mercader, et al., 2007; Mercader, et al., 2002) and humans have been developing tools made of nonperishable materials such as stone for at least two million years. The complexity of the most primitive forms of human tool use, the Oldowan (stone) tradition, lacks any parallel in the tools of nonhuman great apes. Experimental evidence has demonstrated that stone tools are difficult if not impossible for nonhuman apes to produce (Whiten, Schick, & Toth, 2009). Why can apes produce all sorts of tools from perishable materials but are unable to make relatively simple stone tools? The MIM hypothesis predicts that apes cannot produce stone tools because they lack the requisite imitation mechanisms. Such a mechanism is likely to be the product of the co-evolution of a suite of cognitive and motor-skills associated with understanding, planning, and executing actions with folk physical (i.e., physical property of objects) and folk psychological mechanisms (i.e., joint attention and intention sharing) as well as specialized imitation mechanisms (i.e., cognitive and motor) that would have facilitated the learning and copying of tool-specific actions.

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Notes:

(1.) The rationale for this analysis was that different mechanisms, when stressed, should produce distinct error signatures as a result of the unique computations they perform on incoming stimuli. That is, as mechanisms differ, so do their error signatures.

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