The imitation faculty in monkeys: evaluating its features, distribution and evolution

Francys Subiaul

The George Washington University, Department of Speech & Hearing Science, Mind, Brain & Evolution Cluster, 2115 G Street, NW # 204, Washington, DC 20052
e-mail: subiaul@gwu.edu
website: www.subiaul.com

Summary - *Despite more than 100 years of research, there is no agreement among experts as to whether or not monkeys can imitate. Part of the problem is that there is little agreement as to what constitutes an example of 'imitation.' Nevertheless, recent research provides compelling evidence for both continuities and discontinuities in the psychological faculty that mediates imitation performance in monkeys and apes, including humans. For instance, a number of studies have shown that monkeys are capable of copying familiar responses but not novel responses that require the use of a tool, for example. And, while these studies have been interpreted to mean that monkeys cannot engage in 'imitation learning' or novel imitation, research employing a cognitive imitation paradigm—where rhesus monkeys had to copy novel serial rules pertaining to the order of pictures, independently of copying specific motor responses—has provided convincing evidence of novel imitation in monkeys. Rather than suggesting that monkeys are poor imitators, these results suggest that monkeys can learn novel cognitive rules but not novel motor rules, possibly because such skills require derived neural specializations mediating the planning and coordination of fine and gross motor movements. If true, such evidence represents an important discontinuity between the imitation skills of monkeys and apes with significant implications for human cognitive evolution.*

Keywords - *Social learning, observation learning, imitation, cultural learning, primates, monkeys, apes, humans.*

Introduction

The answer to the question, "do monkeys imitate?" depends very much on how "imitation" is defined. As with all complex questions phrased so simply, the answer inevitably depends on a confluence of factors including how one defines imitation, how one operationalizes this definition and finally, what evidence counts as an exemplar of the concept. For instance, many have come to the conclusion that monkeys cannot imitate. This conclusion is based on a variety of studies that required monkeys to operate tools in a specific manner. In all cases, researchers have argued that any social learning evidenced by monkeys is best explained by learning mechanisms other than imitation learning (Adams-Curtis, 1987; Beck, 1976; Fragazy & Visalberghi, 2004; Visalberghi & Fragaszy, 1990; 2002; Whiten & Ham, 1992). But lest you think that monkeys are the only primates believed to be unable to imitate, note that doubt has been cast on the imitation skills of virtually all primate species tested to date. This doubt is perhaps best captured in the titles of well-known publications, which have asked, 'Do apes ape?' (Whiten A *et al.*, 2004), 'Do monkeys ape?' (Visalberghi & Fragaszy, 1990; 2002), and even, 'Do humans ape or do apes human?' (Horowitz, 2003). It's a curious (albeit somewhat depressing) fact that despite more than a century of research,

answers to these questions remain controversial and disagreement abounds among imitation experts. The problem stems, in part, from the question itself, which rests on a tangled and complicated concept, imitation.

Various efforts have tried to ameliorate this problem by proving a historical context for the term 'imitation' (e.g., Galef, 1988; Mitchell, 1987). Others have offered detailed definitions of common terms used in the social learning literature (e.g., Zentall, 1996; 2007). Still others have proposed new concepts and alternate social learning mechanisms to assuage the problem (Byrne & Russon, 1998; Subiaul *et al.* 2004; Tomasello, 1990; Whiten & Custance, 1996; Whiten *et al.*, 2004). Others have provided a theoretical framework explaining the mechanisms underlying social learning (e.g., Bargh & Chartrand, 1999; Byrne & Russon, 1998; Carpenter & Call, 2002; Heyes, 2004; Metlzoff & Moore, 1977; 1988; Mitchell, 1987; Tomasello & Call, 1997; Whiten & Ham, 1992). Yet, the success of these efforts is uncertain. Arguably, many of these ideas and terms have led to greater confusion and disparate usage of what should be standard terminology. But, this by no means is a new complaint. At the beginning of the 20th century, Morgan (1900) expressed the same frustration. He wrote, "In the face of such apparently diverse usage it is necessary to show within what limits and with what qualifications the word [imitation] may profitably here be used to individuate a factor in social evolution" (p 180). Given these problems, it seems reasonable to begin a review of the primate faculty for imitation with a conceptual framework that narrowly defines this faculty's features in order to provide the reader with the tools to judge for themselves the imitation skills of monkeys and other animals.

Dissecting the imitation faculty

First and foremost it is a mistake to think of imitation as one unitary concept or skill that organisms either have or lack entirely. Rather, the imitation faculty is like other vertical cognitive faculties (Fodor, 1983), such as language, that are modular, specialized and consist of multiple components with discrete functions. In this conceptualization, the imitation faculty represents a specialized psychological mechanism involved in the copying of responses in specific 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 super-ordinate and sub-ordinate imitation mechanisms associated with the processing of specific types of stimuli (e.g., novel, familiar, auditory, motor, social, etc.). The super-ordinate imitation mechanisms include, (a) 'familiar imitation,' or the copying of familiar rules or responses and (b) 'novel imitation,' or the copying of novel rules or responses; often referred to as 'imitation learning,' which is distinguished from 'familiar imitation' in that it requires observation 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 a novel behavior(s) and the copying of behaviors that already exists in an individual's repertoire (Byrne & Russon, 1998; Heyes, 2001; Visalberghi & Fragaszy, 2002). However, these investigators have tended to argue that these skills are not related and consequently have tended to give these skills different names, which imply that they exist outside of a dedicated cognitive faculty for imitation. In this framework, both skills are brought together and form part of the same cognitive faculty that mediates the ability to flexibly copy rules or responses, imitation. Moreover, subsumed within those two broad functional concepts are domain-specific sub-ordinate mechanisms of imitation involved in the copying of different types of information (motor, auditory, cognitive) with unique computational demands. These different subordiante imitation mechanisms grant individuals the ability to flexibly copy specific rules or responses. That is, the behavioral rule that is copied is both deliberate and replicable; not a result of

happenstance or trial and error learning. In this definition, the term 'rule' is broadly defined as a response involving more than two steps (with a clear beginning, middle and end) that are hierarchically organized and structured 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 mechanism that in association with rapid trial-and-error learning may represent an ancestral learning mechanism that predates (and may have co-evolved) with the imitation faculty. The same is true of narrow species-specific skills such as copying mate preferences that while impressive, learning does not extend beyond a very narrow and specific context (i.e., mating) and stimuli (i.e., females).

Like all psychological faculties, the imitation faculty is adapted to solve a number of problems common among social animals. Some of these problems include: (a) the problem of learning dominance relationships, where individuals can minimize injury by inferring from observational learning who is likely to be dominant/submissive, (b) the diet problem; learning what is edible and what is not or what to eat when, (c) the problem of alliances and cooperation, where individuals can minimize the risks of bad alliances by inferring from observation who is a reliable/unreliable partner, (d) the problem of extractive foraging, where individuals can learn from others how to process or acquire protected food products, (e) the problem of social conventions, where individuals use others' behaviors to guide where and when they should display species-typical behaviors. And there are certainly others. In each instance, specialized mechanisms in the imitation faculty in coordination with other cognitive faculties grant individuals the flexibility to make rapid inferences about the dispositions of others or the causal structure of actions, bypassing the costs associated with trial and error learning, which in some instances may be lethal (e.g., the diet problem). Some of these instances require 'imitation learning' or novel imitation (when knowledge is first acquired and reproduce), but others only require the copying of species-typical behaviors—familiar imitation (e.g., social conventions)—where previously learned behaviors (either by imitation or trial and error) are appropriately and adaptively displayed. Below is an outline of the characteristics of this most significant of mental faculties.

Super-ordinate mechanisms of imitation: Novel imitation

Part of the confusion in the imitation literature is that 'imitation' has been largely conceptualized as 'novel imitation' or the imitation of novel behaviors. For example, in 1898, Thorndike defined imitation as "learning to do an act from seeing it done" (p. 79). Nearly a half-century later, Thorpe defined imitation more narrowly and in purely behavioral terms: "copying a novel or otherwise improbable act" (p. 122). These definitions are often viewed as synonymous, but they are quite different. One core difference between these two definitions is the requirement that individuals *copy* another's behavior. Copying is, arguably, the essence of imitation. After all, what is imitation if it is not copying something? Yet, Thorndike's definition does not mention or imply copying but rather observational learning. The distinction between observational learning and imitation is an important one. It is possible to learn something from another, yet not overtly express the acquired knowledge; for example, learning what *not* to do. In such instances, one can learn from a model without imitating the model. Thorpe's definition, unlike Thorndike's, stresses both (observational) learning and copying. Learning is implied in the criteria because what is copied is 'novel' rather than something that already exists in the observer's behavioral or cognitive repertoire. Despite a number of qualifications and revisions (e.g., Galef, 1988; Tomasello & Call, 1997; Whiten & Ham, 1992), Thorndike (1898; 1911) and Thorpe's (1956) definition of imitation remain influential because of their simplicity and the ease with which they lend themselves to experimentation. Nevertheless, these definitions, which conceptualize imitation as the copying

of specific and novel motor responses, have largely ignored an equally important function of the imitation faculty, familiar imitation.

Super-ordinate mechanisms of imitation: Familiar imitation

Familiar imitation involves the ability to flexibly and adaptively copy common or recognizable rules/responses that exist within an individual's behavioral or cognitive repertoire. In the motor domain, everyday actions fall into two distinct and conceptually significant categories: transparent versus opaque. Transparent responses are those responses that are immediately available to the senses such as transitive actions that involve reaching for and interacting with objects and, as a result, may be executed via a visual-visual match (i.e., my hand on an object looks like your hand on an object). However, opaque responses cannot be executed in the same fashion, as they are not available to the senses in the same way as transparent actions. Consider the act of imitating someone scratching their head. What you perceive when you see someone scratch their head is very different from what you perceive when you scratch your own head. The phenomenological experiences are very different. This problem of translating a visual experience into a corresponding proprioceptive response has been termed the "correspondence problem" (Dautenhahn & Nehaniv, 2002).

While to some, the distinction between 'novel' and 'familiar' imitation may be obvious, there is significant debate as to what should count as a 'novel' response. Does 'novel' imply an entirely new behavior? By the most strict of standards this would exclude all species-typical behaviors; a constraint that significantly limits research questions. One way around such a constraint is to require animals to execute a series of familiar behaviors in arrangements that are never (or rarely) observed. This technique—of stringing familiar actions in an arbitrary sequence—has been employed by a number of animal researchers (apes: Whiten, 1998; birds: Nguyen *et al.*, 2005; monkeys: Caldwell & Whiten, 2002) and represents one way of

operationalizing 'novelty' in imitation research. Another technique has been to use a tool in novel problem-solving tasks (e.g., Visalberghi & Fragaszy, 1989, 1990, 1995). Perhaps these studies, more than any other, represent the most strict standards of novelty, as subjects must often learn how to handle the tool and then learn how use the tool *in relation to* another object. But there are other ways to operationalize 'novelty' without using tools or specific motor responses. Subiaul and colleagues (2004), for instance, developed a cognitive imitation paradigm, where subjects had to copy novel serial rules independently of copying novel motor actions. All of these tasks require that subjects learn something new in order to be reinforced, and exclude the possibility that subjects already know how to execute the target response.

Others have tried to operationalize 'novelty' using single actions on objects (e.g., Bugnyar & Huber, 1997; Voekl & Huber, 2000; 2007). Here, the rationale is that while a behavior such as mouthing is species-typical, mouthing an object in order to open it is novel. The problem is that animals often explore objects using their mouths and certainly use their mouths on objects associated with food. So, while a particular behavior directed toward a specific object may be unique, the actual behavior is not. In this regard, it's more likely that familiar imitation of the familiar action (e.g., mouthing) rather than novel imitation is the primary mechanism underlying the behavioral response in single-action paradigms. Such paradigms also make it difficult to distinguish between various mechanisms of the imitation faculty and the products of perceptual and motivational mechanisms in which, for example, an animal's interaction with an object may direct an observer's attention to that object (stimulus enhancement) or a part of that object (local enhancement), motivating the observer to interact with it (social enhancement). In such instances, these two individual's responses may be very similar, yet the similarities are likely to be the products of stimulus and social enhancement as well as rapid trial-and-error learning, rather than by any mechanisms of the imitation faculty.

Sub-ordinate mechanisms of imitation: Cognitive, motor & vocal imitation

In addition to distinguishing between familiar and novel imitation, it is important to distinguish between various sub-ordinate mechanisms that form part of the imitation faculty. These domain-specific imitation mechanisms mediate the copying of different classes of stimuli, for example, auditory, motor, and cognitive stimuli and are referred as: vocal imitation (the imitation of vocal/auditory responses), motor imitation (the imitation of motor actions), and cognitive imitation (the imitation of cognitive rules, including rules governing serial order, social conventions and spatial relationships, for example). The distinction between super-ordinate mechanisms of imitation (e.g., novel v. familiar) and sub-ordinate mechanisms of imitation (e.g., vocal, motor and cognitive) are important because it allows researchers to specify what type of imitation individual organisms are capable of. For example, an individual may be able to reproduce *familiar* vocal rules (e.g., words), but may not be able to copy *novel* vocal rules (e.g., novel words) as is the case in autism (Williams et al., 2004). Moreover, individuals may be able to copy novel *cognitive* rules (e.g., serial order), but not novel *motor* rules (e.g., specific action sequences) as appears to be the case in monkeys (Subiaul et al., 2004). The literature summarized below uses this framework in an effort to clearly identify the imitation skills of monkeys. But, certainly, 'monkeys' are not a monolithic group and are more diverse in morphology, social organization and ecological range than apes. However, because it is impossible to test all monkey species in a systematic fashion, most imitation studies with monkeys—and those discussed here—have included only a few species of New World monkeys (marmosets and capuchin monkeys) as well as a few species of Old World monkeys (baboons and macaques).

Finally, it's worth noting that this framework does not necessarily replace familiar terms that have become an integral part of the social learning literature such as emulation, where individuals copy the outcomes or 'affordances' of actions or goal emulation, where individuals copy the 'indended' action of others using idiosyncratic means. Rather, it questions the logic that terms such as emulation are alternatives to imitation. Here, I advance the contrarian's view that terms such as emulation and goal emulation describe the imitation of different types of rules or responses; specifically, copying rules—novel or familiar—about environmental affordances or goals, respectively.

Early methods and experimentation on novel imitation in monkeys

'Observation cage method'

No individual researcher has had a greater impact on contemporary comparative research than Edward L. Thorndike. For better or worse, his research and critique of imitation have been similarly influential (Thorndike, 1898; 1911). Thorndike (1898; 1911) was amongst the first to stress that behavioral similarities could be achieved by many different learning mechanisms. He was also the first to develop an experimental paradigm to test novel imitation. His paradigm emphasized two measures: (a) the speed of behavior acquisition and (b) fidelity in copying the target behavior (Thorndike, 1898). Though Thorndike and others noted that the second measure (fidelity of copying) was somewhat subjective, the former was not. He reasoned that if subjects were truly using imitation to learn from the actions of an experienced model (who had been over-trained in the solution to a given problem or task) then, surely, the subject that had been exposed to the model would discover the solution to the problem faster than those who had not been exposed to a model. Studies with chickens, cats, dogs and monkeys failed to satisfy this criterion. That is, there was no difference between the performance of animals with a model and those without. In Hall's (1963) review of imitation methodologies, he refers to Thorndike's (1898) paradigm as "the observation cage-method" where a naive observer is exposed to an experienced model or "demonstrator" solving

a given problem. In this paradigm, the model is removed from the cage, following an observation/ demostration period, and replaced with a naive observer who is then presented with the same problem. Mills (1899), Haggerty (1909) and later Warden and Jackson (1935) immediately identified the shortcomings of this design. These authors noted that the disruption of moving the naive observer from one cage to another introduced a significant distraction, confounding negative results with increased anxiety, distraction, and task ambiguity.

'Single cage method'

The next major effort to rigorously test imitation in monkeys (8 capuchins, 3 rhesus macaques) was carried out by Haggerty (1909) who developed the "single cage method" (Hall, 1963). In this new experimental design, both the naive observer and the model were in the same cage and had access to the same problem. Haggerty devised eight different problems, each varying in degree of difficulty. All involved manipulating various levers and pulling certain springs that were not always in sight. In one case, a sheet of paper covered the solution to the task. Haggerty reported that his design controlled for the disruption of moving the observer and allowed for an evaluation of degrees of success. These various degrees of imitative success were coded as, "immediate," "partial," or complete "failure." This classification placed a greater emphasis on the outcome of the actions and less on the means by which the subject arrived at the outcome. Hence any matching response made by the monkeys in these studies may have been the result of rapid trial and error learning or imitation. Zuckerman (1932), for example, pointed out that the success of Haggerty's monkeys was probably due more to perseverance than to an actual ability to copy the model. Kempf (1916), Zuckerman (1932) and Hall (1963), among other critics of Haggerty, pointed out that it was impossible to measure precisely *what* the student learned from the model. Zuckerman suggested that Haggerty's monkeys could have learned to solve the tasks by a combination of factors akin to what is

presently called stimulus/local enhancement, social facilitation and trial-and-error learning. Another possibility was that monkeys arrived at the solution to the various problems by emulation learning or even by imitation. But, unfortunately, there were no controls to rule out these alternative explanations. The "single-cage method" was consequently abandoned in response to these criticisms.

'Duplicate cage method'

A third imitation paradigm, which Hall (1963) named "the duplicate cage method," was introduced by Warden and Jackson (1935) and later developed by Warden and colleagues (1940). This design involved two identical testing chambers placed side-by-side. Each chamber was equipped with identical machinery in the exact same location (i.e., objects to be pulled, turned or twisted were in a fixed position). As with other paradigms, naive animals ('students') were given the opportunity to observe an experienced model. Following this period of observation, students were allowed to respond without being moved from their cage. The goal was to correct the shortcomings of past imitation researchers such as Haggerty (1909) and Thorndike (1898; 1911). Specifically, Warden and colleagues were interested in what they called "intelligent" imitation (or novel imitation). To test this type of imitation five variables were viewed as necessary: (1) the task must be novel and sufficiently complex, (2) the response must appear immediately after observing the model, (3) practice must be excluded by the experimental conditions, (4) the act of the imitator must be substantially identical with that of the model's, and (5) a sufficient number of instances must occur, under varied conditions, to eliminate behavior-matching by happenstance.

Warden and Jackson's (1935) task involved (a) pulling down a chain to obtain a reward, (b) opening a door, (c) operating a simple latch and then opening a door, and (d) operating two latches and then opening a door. These tasks were intended to vary in degrees of difficulty, the last two being more difficult than the first

two. It is also important to note that the last two have an A→B element, and while reducing the possibility of behavior matching due to stimulus enhancement, it does not entirely exclude the possibility of local enhancement because the target objects were in a fixed position in both chambers and so it's possible that after responding to one item correctly (perhaps with the aide of stimulus enhancement) the subject may have interacted with the last item by default. The procedure used was as follows: (1) a naive monkey would be exposed to an experienced monkey. After a given observational period, the naive monkey was presented with the same problem in his own cage. Performance was coded in varying degrees of success ranging from "immediate imitation" to "absolute failure." Monkeys were evaluated on whether or not they copied the precise methods employed by the demonstrator (mechanism) and the speed with which they acquired this behavior (outcome). The monkeys' imitation performance on the very first testing session (using Warden & Jackson's criteria) ranged from 29% (Task 1) to 50% (Task 4). The failure rate ranged from 36% (Task 1) to 43% (Task 4). Because these monkeys' performance was not compared to a baseline condition it's impossible to know whether performance was driven by social facilitation, for example. Moreover, because the items were in a fixed position, local enhancement cannot be ruled out in the cases where monkeys appeared to reproduce the motor responses of the model. Many of these short-comings were corrected by later researchers who introduced novel experimental paradigms, but in doing so, introduced new confounds that resulted in new interpretational challenges (see below).

Experimental evidence from 1970 to Present

Novel motor imitation

Starting in the early 1970s, Beck (1972, 1973, 1976) published various studies exploring the imitative abilities of baboons and macaques. All of these studies involved the use of a tool (L-shaped and rake-like) to obtain out-of-reach food. As macaques and baboons (and, in fact, virtually all monkeys) do not habitually use tools in the wild, learning how to operate a tool to procure reinforcement represents an test of novel motor imitation. Beck used a Single-Cage Method (Hall, 1963) to test his subjects. This method was hampered by many of the same interpretational confounds present in Haggerty (1909). For instance, whereas social facilitation may explain the few examples of motor imitation recorded by Beck (1976) in one study, social inhibition likely explains the lack of motor imitation (Beck, 1973). The failure of monkeys to learn in this second novel motor imitation task was replicated by Chamove (1974), who reported similar results with rhesus macaques.

Adams-Curtis and Fragaszy (1995) developed a new task that involved the use of a mechanical puzzle to test the imitative abilities of capuchin monkeys. The use of a mechanical puzzle box represents another means of testing novel motor imitation. These researchers allowed their subjects to interact with a protected object after observing an expert model interact with the same project. Adams-Curtis and colleagues (1987; 1995) reported that while naïve capuchins appeared interested in the task and were attracted to various aspects of the puzzle (i.e., stimulus enhancement), subjects neither discovered the solution nor performed the model's sequence of actions while engaged in the task.

Visalberghi and Fragaszy (1990; 1995; 1996) have been credited for testing the full range of capuchin's imitative abilities (Tomasello and Call, 1997). These authors devised a tool-using/tool-making task, which tests specific modes of utilizing a given tool(s) in a given context. Perhaps their most well-known paradigm is the 'trap tube' task (Fig. 1). Tasks such as the trap tube exclude entirely the possibility of any familiar imitation by virtue of both the novelty of the problem and the fact that in some experiments the tool, while familiar, had to be composed (or decomposed) in a specific and novel fashion in order to be operational. In the course of nearly half a dozen studies, Visalberghi and Fragaszy's results corroborated the

conclusions of Adam-Curtis and colleagues (1987; 1995). That is, while subjects were motivated to interact with the tool and the experimental task (i.e., stimulus and social enhancement), they were either uninterested or unable to replicate the precise means used by a model to solve the problem or even how to use the tool, itself. From this, Visalberghi and Fragaszy (2002) have concluded that monkeys likely learn from individual trial and error and/or stimulus/local enhancement rather than from 'true' imitation.

Caldwell & Whiten (2004), in another novel motor imitation paradigm, presented common marmosets with a version of an "artificial fruit", a mechanical puzzle box that was originally developed for the purposes of testing the imitation learning skills of chimpanzees (Whiten *et al.*, 1996)). The apparatus used by Caldwell and Whiten (2004) was smaller and had only a single defense; a handle that had to be removed to release a lid in order to obtain the food reward enclosed. Caldwell & Whiten (2004) report results that are very similar to those reported for capuchin monkeys by Adams-Curtis, Visalberghi, Fragaszy and colleagues. In effect, the marmosets that saw a full demonstration interacted with the apparatus more and were more likely to make
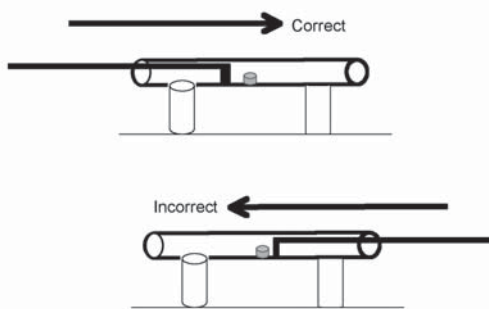

Fig. 1 - Schematic of the Trap-Tube Task. In this task, a reward is placed in the center of the tube either to the right or the left of a 'trap' (a hole from which the reward cannot be retrieved). In order to retrieve the reward, subjects must insert a tool that fits in the tube and push the reward away from the trap.

contact with the relevant parts of the apparatus (i.e., stimulus enhancement) than control monkeys who either saw a partial demonstration (i.e., a monkey eating next to an open apparatus) or those that saw no demonstration.

There are, of course, a number of different reasons why monkeys may have failed to demonstrate learning in these novel motor imitation paradigms. In some instances (e.g., Beck, 1976), learning may have been inhibited by the presence of a dominant conspecific (Fragaszy & Visalberghi, 1989; Visalberghi & Fragaszy, 1990), in other instances (e.g., Visalberghi and Fragaszy, 1995; 1996), learning may have been limited by sometimes onerous motor confounds. The latter is a significant concern given that monkeys do not habitually use tools in the wild, perhaps with the single exception of capuchin monkeys (Perry & Mason, 2004). These limitations have lead to the development of paradigms that attempt to assess different facets of the imitation faculty in monkeys: (a) the two-action paradigm (Dawson & Foss, 1965) and (b) the cognitive imitation paradigm (Subiaul *et al.*, 2004; 2007a); each will be discussed in turn.

Familiar motor imitation: two-action tasks

The concern over motor confounds and a limited motor repertoire has led to the use of a bidirectional (Dawson & Foss, 1965) or two-action imitation procedure (Akins & Zentall, 1996). In these paradigms, reinforcement results from the use of two (or more) possible actions (for example, pushing versus pulling a door to retrieve a reward). The assumption of such paradigms is that if individuals are sensitive to the actions of others and are capable of copying specific motor movements, they should be more prone to copy the model's technique than an alternative technique, which is also associated with reinforcement. In fact, many animals— from rats to various species of birds—have been shown to copy the model's motor response (for a review see Zentall, 2007). However, because the target actions are all familiar to the observers and present in their behavioral repertoire, there is no motor learning *per se*. However, because in some

instances individuals are learning how to apply a familiar rule in a novel context, such behaviors may be achieved by the coordinated activities of a novel cognitive imitation mechanism (see below) and a familiar motor imitation mechanism.

Two-action or bidirectional procedures markedly differs from those described above where individuals must learn a novel operational rule. Rather, these procedures tests subjects' ability to copy a specific, but familiar motor response in a purposeful and replicable fashion. As a result, these two-action and bidirectional procedures represent a measure of *familiar* motor imitation, not *novel* motor imitation.

Bugnyar & Huber (1997) were among the first to use this paradigm in a monkey species, the common marmoset. In this paradigm, monkeys observed a model use one of two familiar actions to open a door—pulling or pushing—and retrieve food hidden behind it. Although there were two possible means of opening the door, only one method was demonstrated ('pulling'). The control group did not see any type of interaction with the box, hence there was no 'enhancement' control. Given these limitations, Bugnyar & Huber reported that during the first phase of the study, two of the five monkeys showed a preference for the modeled 'pull' technique. But, in subsequent testing sessions these monkeys settled upon the alternate 'push' technique, perhaps because it was less motorically complex. In a follow-up experiment by Voelkl & Huber (2000) subjects had to open a film canister using either the mouth or the hand. There were three groups: (a) full-demonstration (mouth or hand opening), (b) no demonstration and (c) olfactory control (no demonstration, but presented with the canisters opened by mouth). Voelkl & Huber (2000) report that, of the six subjects that observed a conspecific using the mouth opening technique, four used the same technique, whereas, none of the subjects that saw the hand opening technique used the mouth technique. These results are intriguing, but complicated by the fact that the first session of testing included 15 trials (first trial performance is not reported) and, in those 15 trials, only two

monkeys (WI and SQ) used the mouth opening technique consistently. The other monkeys were either as likely (MO) or more likely to use the hand opening technique. This contrasts with monkeys that saw the hand technique who used the same technique as the model 100% of the time. This pattern of performance is inconsistent with familiar motor imitation as defined above. If monkeys are capable of familiar motor imitation, then performance in the mouth opening group should resemble performance in the hand opening group and should not be restricted to just one type of action. The fact that it does not, suggests that these monkeys are biased to use a particular type of motor response or that individual responses are mediated by motivational and attentional mechanism that lie outside the imitation faculty.

In a third experiment, Voelkl and Huber (2007) focused on the mouth opening technique and, using detailed motion analysis, evaluated whether observers and non-observers copied not only the global action, but the specific movement patterns associated with the mouth opening technique. Using a discriminant function analysis, the authors report that the overall movement patterns of observers were more like those of the demonstrators than the movement patterns of the non-observers. They argue that because the movement path to successful opening is rather broad, any similarities cannot be explained by functional constraints alone. However, Voelkl and Huber's (2007) results would be more compelling if individuals could reliably copy movement patterns other than a single species-typical action (i.e., mouthing).

Nevertheless, there is at least one other study that suggests that monkeys are capable of familiar motor imitation. Research by Fragaszy and colleagues (2001, 2002 as cited by Fragaszy & Visalberghi, 2004) is consistent with the conclusion of Voelkl and Huber (2007). In a series of studies, Fragaszy and colleagues devised a two-action task where juvenile capuchin monkeys living in two captive groups could obtain juice in one of two ways: (a) by putting a finger into an opening and turning a wheel that provided juice or (b) by pushing down a lever in order to get a

burst of juice. Both of these actions are familiar to animals, as such they represent examples of familiar motor imitation. Fragaszy *et al.* (2001; 2002 as cited by Fragaszy & Visalberghi, 2004) report that none of the juveniles solved the problem or learned a specific technique. However, when a different group of immature capuchin monkeys were allowed to watch adult capuchin models, there was some evidence of familiar imitation. Importantly, the authors note that observers tended to adopt the solution style of the adults in their groups. However, because these studies are unpublished it is difficult to evaluate the exact methods used. One potential problem is that the actions used by the models may have been opaque (i.e., inserting a finger in an opening may have occluded the view of an observer) and thus limited motor imitation performance.

Nevertheless, the results reported by Voelkl and colleagues and those reported by Fragaszy, Visalberghi and their associates are perhaps the best evidence that monkeys despite their poor performance in novel motor imitation tasks (such as those that require the use of tool), are sensitive to specific movement patterns and are capable of copying familiar motor actions. But certainly, more research is needed before we can confidently state that monkeys are capable of familiar motor imitation or are incapable of novel motor imitation.

Familiar motor imitation: oral-facial imitation

Marmosets' ability to match opaque facial and head movements (i.e., Voelkl & Huber, 2007) parallels reports on human infants copying oral-facial expressions such as mouth openings and tongue protrusions (Meltzoff & Moore, 1977; 1983; 1989). It has long been believed that the ability to match oral-facial expression represented a human cognitive specialization (Meltzoff, 1988; 1999) associated with higher-order cognitive abilities (Meltzoff & Moore, 1977; Meltzoff, 1988; 2002). However, the uniqueness of this ability has been put in doubt by reports showing that chimpanzees (Myowa-Yamakoshi & Matsuzawa, 2004) and rhesus monkeys (Ferrari *et al.*, 2006) are also sensitive to such stimuli and copy these expressions in a pattern similar to that present in humans.

However, researchers have cast doubt on the notion that matching oral-facial responses is best characterized as imitation (as defined here or elsewhere). First, an extensive review of the literature revealed that only tongue protrusions are matched by human infants (Anisfeld, 1991; 1996; Anisfeld *et al.*, 2001). Second, and perhaps most surprisingly, a number of studies have demonstrated that a moving pen (Jacobson, 1979), blinking light(s) (Jones, 1996) and music (Jones, 2006) are all as likely to elicit tongue protrusions in human neonates, as is watching a model display the same behavior. However, the study by Ferrari and colleagues on neonatal imitation in macaques is unique in that the experimental design included a non-social control (a spinning disk) in addition to the typical social stimuli in such experiments (i.e., mouth opening, tongue protrusions, etc.). Ferrari and colleagues reported that lipsmacking and tongue protrusions occurred significantly more often in response to displays of those same actions. However, lipsmacking occurred the most often in response to different types of stimuli, much like tongue protrusions in human infants (Jones, 1996). Ferrari *et al.* (2006), noting the amount of inter-individual variation and the sensitivity to specific oral-facial movements (e.g., mouth openings and tongue protrusions) in both human and monkey neonatal imitation, pointedly caution that "the capacity to respond to the model may not reflect a general imitative skill but rather a sensorimotor sensitivity turned to specific facial gestures" (p. 1506). At this point it's impossible to say with any certainty whether these results are mediated by a mechanism independent of the imitation faculty or whether they simply reflect the output an imitation faculty that is not yet mature.

Taken together, the research reviewed above suggests that the motor imitation skills of monkeys are significantly limited. The preliminary conclusion is certainly more true for novel motor imitation than for familiar motor imitation; at least as measured by the two-action procedure(s). This begs the question of whether or not monkeys suffer from a novel imitation deficit in general (Ferrari *et al.*, 2006;

Visalberghi & Fragaszy, 2004) or whether monkeys specifically lack the mechanism for novel motor imitation. In order to answer that question, however, a test must isolate the copying of novel motor rules from the copying of non-motor (cognitive) rules.

Novel cognitive imitation: copying serial rules

Although much has been written about motor imitation as well as vocal imitation in mammals (for reviews see Janik & Slater, 2000; Zentall, 2006), little has been written about the imitation of non-motor, non-vocal rules. Subiaul (2004) and colleagues (2004; 2007; 2007a, 2007b) were the first to demonstrate that the copying of cognitive—serial—rules can be isolated from the copying of motor rules. The studies conducted on novel cognitive imitation were analogous to learning someone's password at an automated teller machine (ATM) after looking over that person's shoulder and later entering that password on the key pad. Because the observer already knows how to enter numbers on the keypad, no motor learning is necessary. (In some respects, the actual paradigm that was used

was more difficult because unlike the numbers in a key pad, the items on the screen changed spatial position from trial to trial; see Fig. 2). Nevertheless, the ATM example illustrates the two different rules that individuals might learn from such an event. 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 principal difference is the type of rule: spatial/motor versus cognitive/representational that is learned and subsequently copied by the observer.

In one experiment (Subiaul *et al.*, 2004), two rhesus macaques were given the opportunity to execute serial chains (Fig. 2) 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
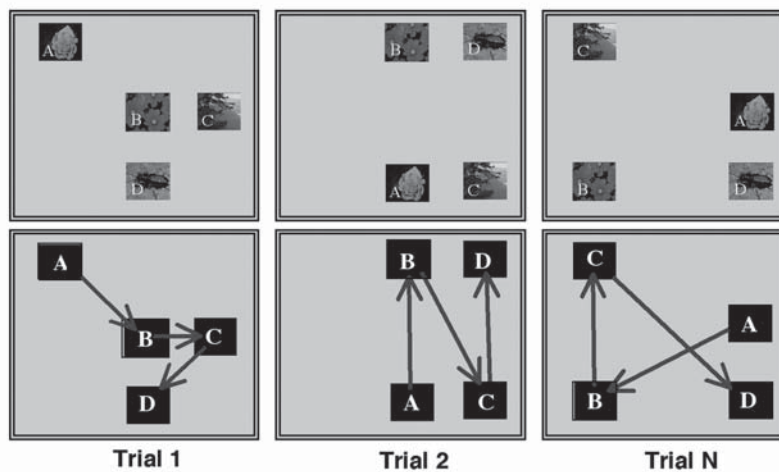

Fig. 2 - Simultaneous Chaining Task. (Top panel) Arbitrary pictures comprise list items, which are displayed concurrently throughout each trial on a touch-sensitive video monitor. (Bottom pannel) Each item's position is varied randomly from trial to trial. The subject's task is to respond to each item in a particular order, regardless of its spatial position. Variation of spatial position prevents subjects from performing the required sequence as a fixed–motor pattern or as a discrete set of responses to specific external spatial cues, such as the choice points of a maze.

chamber (social-learning condition). This paradigm corresponds with Warden & Jackson's (1935) duplicate cage method. Figure 3 shows two monkeys during the 'Observation Phase' of the social-learning 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 where 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 where 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 condition would be the result of social facilitation (Zajonc, 1976) rather than novel imitation. Yet, the rate of learning in the social-facilitation and the baseline condition did not statistically differ.

In all three conditions, computer feedback was available to students. However, in the social-learning condition (Experiment 1) the student could have learned the ordinal position of individual picture items from computer feedback alone, rather than from the actions of the model. 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 is often referred to in the literature as the 'Ghost Control.' After 20 trials, the student was tested on the same list. As was done in the previous experiments,
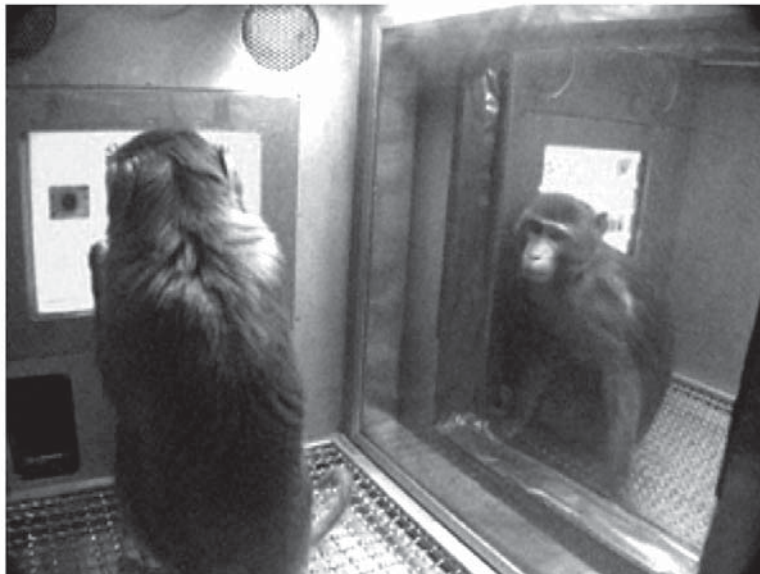

Fig. 3 - Cognitive Imitation Paradigm. During an 'Observation' phase, a 'student' monkey (right) was given the opportunity to learn the order of novel picture items from he 'expert' monkey (left) immediately before being tested on the order of those same items.

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 human children and individuals with autism showed that children learned in the ghost control (Subiaul *et al.*, 2007b); a result that has been replicated in numerous motor imitation studies with children (Huang & Charman, 2005; Thompson & Russel, 2004) but not other primates, including apes, who have failed to learn in this control condition (Hopper *et al.*, 2007; Tennie *et al.*, 2006).

What might account for the differences between monkeys and other animals and human participants' performance in the Ghost Condition? One hypothesis is that the difference may rest on the propensity of human subjects (but not non-human animals) to generate cognitive rules about agency, goal-directedness and/or intentionality to aid imitation in the ghost control. This potentially unique human ability has been reported in human infants, who attribute intentionality and/or goal-directedness to a ball that jumps over a barrier and navigates around obstacles (Csibra, 2003). Yet, no comparable evidence exists for monkeys (Cheney & Seyfarth, 1990; but see Hauser, 1998 for one possible exception) or other animals. In sum, the fact that monkeys are capable of flexibly copying novel cognitive rules suggests that monkeys lack a mechanism for novel motor imitation, specifically, rather than a general novel imitation mechanism. In other words, the fact that monkeys can copy novel cognitive rules from a model demonstrates that monkeys are capable of certain types of novel imitation. Additionally, given that some evidence exists for novel motor imitation in apes but similar evidence is absent in monkeys indicates 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.*, 2002; Mercader *et al.*, 2007).

Novel cognitive imitation: copying food preferences

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; costs which are too high if not impossible to manage without a social learning mechanism such as familiar imitation or novel cognitive imitation. But novel cognitive imitation may also be critical in foraging problems, particularly those that involve 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 have 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 while they are moderately neophobic of new foods, captive capuchins sit near each other during feeding and closely attend to what others are eating (de Waal, 1997**;** Visalberghi & Fragaszy, 2004). Capuchins are also very tolerant; allowing conspecifics to take small bits of food they have dropped (Visalberghi & Fragaszy, 2004). Given these characteristics, it seems that their behavior and motivation are optimal for novel cognitive imitation. Visalberghi & Fragaszy (2004) reason that there are at least three mechanisms by which individuals could learn and copy novel food preferences. These mechanisms range from (i) a general (arousal/motivational) mechanism that increases feeding without regard to particular food items, to (ii) a more subtle mechanism where subjects are attracted to novel items in general (e.g., neophilia), to (iii) cognitive imitation, where individuals acquire a dietary rule(s) pertaining to the palatability of particular foods.

Visalberghi & Fragaszy (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 Visalberghi & Fragaszy, 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; Visalberghi & Adessi, 2000). For example, Adessi & Visalberghi (2001) presented capuchins with novel food items (consisting of different food products that were mashed and differentially colored) in three different conditions: (i) alone, (ii) in the presence of non-eating group members and (iii) 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. While these results provide important insights into the feeding behavior of capuchin monkeys, they are not designed as social learning experiments *per se* as subjects are not provided with a choice, for example, between a 'palatable' and a 'non-palatable' food item. However, Visalberghi & Fragaszy (2004) cite unpublished data (i.e., Adessi & Visalberghi, 2002) that suggests that even when provided with a such choice, capuchin monkeys do not show a preference for the 'palatable' food. Moreover, 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, where subjects discovered the palatability of the food item by happenstance (Visalberghi & Adessi, 2001).

In contrast to capuchins, cotton-top tamarins living in a family group avoided palatable food (tuna) that was experimentally manipulated to be unpalatable after observing a conspecific reject the food (Snowdon & Boe, 2003). In three groups of tamarins, the aversion for the unpalatable food was long-lasting. The avoidance and disgust

reactions toward tuna was still present after 10 months. These results provide some evidence of vicarious learning. But, given the tamarins were presented with either a palatable or unpalatable food choice, it's possible that mechanisms that lie outside of the imitation faculty could have mediated the avoidance response. An ideal study on cognitive imitation for novel food preferences would have a 'student' see a model eat different types of novel food items that are entirely unknown to the student and whose palatability vary along a continuum. The dependent variable would then be whether the student's response(s) (i.e., latency to approach and expressions of disgust/avoidance) prior to tasting the foods in a forced choice test, for example, are consistent with the responses of the model. To my knowledge no such study has been published, but such studies would clarify whether the mechanism(s) mediating food preferences are consistent with the operations of the imitation faculty or some other independent mechanism associated with approach/avoidance responses.

Imitation in the brain: mirror neurons and resonance mechanisms

Given the performance of monkeys in motor imitation tasks, it may come as a surprise to many that studies on the macaque brain have led to important insights into the neurobiology of motor imitation. In a now famous series of studies that initially sought to understand the neural mechanisms of goal-directed actions (Rizzolatti *et al.*, 1988), Rizzolatti and colleagues (di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996) stumbled upon a class of neurons in the inferior frontal lobe (F5) that became active (fired) both when the monkey executed a specific action such as grasping a peanut and when they observed someone else execute that same action (i.e., grasping a peanut), hence, the name: "mirror neuron." But mirror neurons do not act in a vacuum. Research has demonstrated that F5 is part of a network with a number of neural regions that appear to be important for

motor imitation. For example, Perrett, Harries, Bevan and colleagues (1989) have demonstrated that neurons in the superior temporal sulcus (STS), which encodes biological motion and goal-directed actions, project to mirror neurons in F5. STS and F5 neurons project to area PF in the rostral part of the inferior parietal lobule that has been associated with action observation. A fraction of these neurons respond to the observation of actions executed by others and another group of neurons in this region have mirror properties, much like mirror neurons in F5. According to Rizzolatti (2005) the STS-F5-PF circuit in the macaque brain provides multiple descriptions of specific actions with identical meaning (e.g., grasping), 'concentrating' the different visual descriptions of the same action on a select group of neurons on the one hand and 'labeling' them with motor meaning on the other. Rizzolatti (2005) and colleagues believe that through this mechanism, actions are understood and by extension, provide the means by which they can be imitated. Based on a number of studies, Rizzolatti claims that "the mirror neuron system plays a central role in the imitation of actions that are already in the motor repertoire of the individual" (71); that is, familiar imitation. It is hypothesized that this feat is achieved by matching an observed action with motor responses stored in the premotor cortex, resulting in a fast and efficient response to the observed action.

The presence of such a mirror neuron system in the monkey brain, is consistent with the conclusions of Voelkl and Huber (2007) who argue that monkeys are capable of matching familiar motor actions (i.e., familiar motor imitation). Perhaps most importantly, research into the neurobiology of imitation has also provided some insights into why monkeys may be capable of familiar motor imitation but not novel motor imitation. Rizzolatti (2005) argues that the motor and sensory computations that the monkey mirror neuron circuit can make are constrained relative to that of the human mirror neuron circuit. In particular, Rizzolatti (2005) notes that the monkey mirror neuron circuit appears to be insensitive to intransitive actions

(i.e., actions executed in the absence of objects that are real or imagined, as in pantomime) and so may be unable to generate sensory codes for them. This feature of the monkey mirror neuron system contrasts with this same system's well-documented ability to encode transitive actions (i.e., actions directed toward specific objects), where the meaning of an action is defined in relation to an interaction with a specific object. No such meaning can be derived from intransitive actions as they are entirely abstract and 'objects' or 'goals' must be imagined as they are not visible.

The relative poverty of the monkey mirror neuron system contrasts with research with human subjects using transcranial magnetic stimulation (TMS), which suggests that the human mirror neuron system is capable of storing rich representations of intransitive actions. From this, Rizzolatti (2005) concludes that, "Without the storage of intransitive actions to complement basic object-related actions and precise copies of actions, the capacity of the monkey system to imitate the behaviors of others should be rather limited" (74). Research into the neurobiology of imitation has shed new light on an old question and furthered our understanding of what comprises the imitation faculty and how this faculty may be represented in the brain. The work by Rizzolatti and colleagues has also provided us with important clues as to what characterizes the monkey imitation faculty and what distinguishes it from the human imitation faculty. In particular, the work by Rizzolatti and colleagues is consistent with the behavioral literature which shows that when monkeys must copy familiar actions directed to objects (c.f., Voelkel & Huber, 2007) or when copying familiar facial expressions like lip-smacking (Ferrari *et al.*, 2006), they are more likely to succeed than when they are tasked with copying novel actions governed by rules pertaining to the relation between actions *and* objects (i.e., intransitive actions); a feature of novel motor imitation paradigms (e.g., Visalberghi and colleagues, 1990; 1995). The work by Subiaul and colleagues (2004; 2007a) is consistent with this conclusion, demonstrating

that the limiting factor for monkeys is motor in nature, because despite the inability to copy novel motor responses, macaques appear capable of copying novel cognitive rules. However, note that in Subiaul *et al*'s paradigm, the actions executed by the monkeys were familiar.

Do monkeys have 'traditions'?

The existence of complex, population-specific behavioral traditions in the wild certainly suggests social learning, if not specific functions of an imitation faculty. But, unfortunately, there are many limitations to studying imitation learning in the wild. The most obvious limitation is that in field settings when an animal copies the actions of another, it's impossible to distinguish whether such copying represents an instance of familiar or novel imitation as it's impossible to know with any certainty whether the behavior was acquired by trial and error and is now being copied by familiar imitation or whether the behavior was copied *de novo*, which would correspond with an instance of novel imitation. Another problem is that in field settings it's impossible to evaluate whether imitative responses (familiar or novel) are flexible and adaptive or whether they are mediated by attentional or motivational mechanisms (i.e., stimulus/local enhancement). Nevertheless, extensive behavioral traditions that are characterized by population-specific and complex behaviors that seem difficult if not impossible for multiple individuals to discover through individual innovation or happenstance may represent a unique piece of evidence in support of an imitation faculty in primates in general and monkeys in particular. Below, two potential examples of 'traditions' in monkeys are reviewed and critiqued.

'Proto-culture' in Japanese macaques

Kawai (1965) and colleagues were the first to suggest that monkeys could create and sustain traditions, which they called 'proto-culture.' The behavior in question was sweet potato washing (SPW) which spread within a population of Japanese macaques. Sweet potato washing is a behavior that involves taking a piece of food, in this case a piece of sweet potato, to a body of water and washing off the sand by placing the food object in the water. Kawai described monkeys dipping the potato in water by holding it in one hand and then removing the sand by brushing the potato with the other hand (Kawai, 1965). Sweet potato washing originated with a 1.5 year old macaque name Imo. According to Kawai (1965), the "behavior spread to others gradually, and by 1956 eleven monkeys acquired it" (3). Learning was initially biased in favor of females and younger members of the troop. However, by 1963 males and females were equally represented among the sweet-potato-washers (20 females, 17 males).

Kawai (1965) and colleagues also documented the spread of another behavior, wheat washing (WW) in Japanese macaques. WW resulted from researchers dropping wheat grains on the beach sand where monkeys would scoop-up a handful of sand mixed with wheat grains and then drop it in a nearby pool of water where the wheat would float while the sand dropped to the bottom of the pool. This allowed the monkeys to easily grab the floating grains of wheat. As with SPW, more females than males were represented in the WW sample. Like SPW, WW was characterized by an age-specific trend. Specifically, younger individuals were, again, more likely to be WW than older individuals. In fact, no one past the age of 12 was seen engaged in WW. Kawai (1965) does point out that whereas SPW was a characteristic feature of individuals who were 1 and 2 years old, WW was predominantly found in individuals that were 4 and 5 years old. This suggested to him that SPW might be a less complex task to master than WW.

Critiques of Japanese Monkey 'Proto-Culture'

Critiques of Kuwai's (1965) work have centered on the nature of the learning and the rate of transmission. With regard to the nature of learning, Tomasello and Call (1997) first note that washing food is much more common in nonhuman primates than was previously thought. They point out that potato washing has been witnessed

independently in four other troops of human-provisioned macaques. This suggests that various individuals had learned the behavior on their own (i.e., via individual learning). These critics go on to argue that experimental evidence has shown that when other primate species in captivity are provided with sandy food, they learn quite rapidly to process the food in bowls of water (Visalberghi and Fragaszy, 1990). Yet, interestingly, this was not the case in Koshima. Even though all animals were provisioned on the same beach, the behavior did not independently erupt in multiple individuals.

Galef (1992) has critiqued the work on the basis of the speed of transmission. According to Galef (1992), the mean and median time it took for the behavior to spread to most group members was approximately two years. Tomasello and Call (1997) like Galef (1992) argue that, "this would not seem consistent with a process of imitation, which is typically thought of as a rapid process" (277). Moreover, they point out that as the number of SPW increased, the rate of transmission remained constant. In sum, Tomasello and Call (1997) explain SPW (and other cases of social learning among Japanese macaques) as follows:

"There is an individual 'inventor' who did not learn by any form of social learning. Other individuals were then exposed to the appropriate learning conditions at different times, with those more closely related to the inventor being exposed first. They then learned individually as well, likely facilitated by processes of stimulus enhancement in which their engagement with the wheat or rocks was stimulated by the engagement of the inventor. As in the other cases, individuals in closest proximity to the inventor and other practitioners would be in a better position to see and be attracted to the objects with which they were interacting" (278).

Anthropologists have similarly been critical of the notion of animal culture (i.e., Holloway, 1969; Kitahara-Frisch, 1991). Whereas, Holloway (1969; 1981) pointed to the symbolic aspects of culture, Kitahara-Frisch (1991) focused on the characteristics of cultural transmission.

In a critique of the Japanese monkey culture, Kitahara-Frisch (1991), for example, notes that four characteristics are generally present in definitions of "culture." These include: (1) the notion of culture as a comprehensive and organized whole, (2) a mode of social behaviors, (3) behavior that is non-genetically transmitted across generations and (4) an expression of a body of common understandings, such as are manifest in consciously transmitted rules. Kitahara-Frisch (1991) acknowledges that some of these features are present (for example 2 and 3) but not all. Some of these criticism and definitions of culture, however, may be regarded as too anthropocentric and invalid for making between-species comparisons. A similar criticism had been leveled toward Tyler's (1871) famous definition of culture, which he famously stated was "…that complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society." Among the most important (but rarely cited) features of culture were articulated by Kroeber (1928) nearly a century ago. Kroeber identified eight features: (i) innovation, (ii) dissemination, (iii) standardization, (iv) durability, (v) diffusion, (vi) tradition, (g) species-valid, and (h) transcendent. Other features have since been added. Tomasello (1999), for example, has added the feature of 'accumulation,' where particular behavioral patterns evolve and build upon pre-existing behavioral patterns. Galef (1992) has added 'imitation,' arguing that culture consists of traditions that are transmitted by novel motor imitation, specifically. And, Whiten and van Schaik (2007) have added 'variability,' arguing that culture is characterized by multiple traditions (at least two or more) in multiple domains (e.g., social, ecological). Table 1 defines these different components of 'culture' and their distribution in humans, non-human (NH) apes and monkeys (specifically, capuchin monkeys). Using this criteria it's clear that Japanese macaques lack many of the critical features of 'culture.' Perhaps most critically, Japanese macaque 'proto-culture' fails to meet the criteria of 'species-valid' and 'transcendence' (Refer to Table 1).

'Traditions' in Capuchins

A number of field studies with wild capuchin monkeys have identified patterned behaviors that appear to be common to certain groups but not others. Panger and colleagues (2002) for instance have identified various food-processing techniques that varied across 3 different sites. The behaviors they describe include: (a) rubbing food products against hard substrates or (b) pounding them (using rocks or sticks) to break them open, (c) using a fulcrum to apply pressure on a food product, (d) taping an object with fingertips, usually in a rhythmic fashion, and (e) wrapping an object in a leaf and then rubbing the wrapped product against a substrate ('left wrapping'). Panger *et al.* (2002) report that of the 61 food species that were compared, 20 were processed using a different technique. Additionally the techniques used were not homogenous across sites. There was geographic variation in the technique used to process identical species of food. Specifically, Panger and colleagues highlight three behaviors: fulcrum use, leaf-wrapping and a third behavior 'army anting,' which involves monkeys following a column of foraging ants and capturing insect or animal prey that are flushed out by the swarming ants. These behaviors, they note, are present in some sites but not others and their distribution has no obvious ecological correlate. However, leaf-wraping, may represent an example of a clumped 'idiosyncratic behavior' that resembles a specific group 'tradition' but is not. In one site, Loma Barbudal, the individuals that were observed displaying this behavior were peripheral and had very few opportunities to learn tool-use behaviors from other group members. Thus, it's likely, this behavior may have been 'discovered' through trail and error learning.

Another compelling piece of evidence indicative of 'traditions' has been reported by Perry

Tab. 1. Components of 'Culture.' Below is a list of the characteristics of culture proposed by different authors and their distribution in humans, non-human (NH) apes and monkeys (specifically, capuchin monkeys).

COMPONETS ON CULTURE	HUMANS	NH APES	MONKEY
INNOVATION: *New behavioral pattern is invented**	+	+	+
DISSEMINATION: *Transmitted from individual to individual**	+	+	+
DURABILITY: *Pattern persists beyond demonstrator's presence**	+	+	-
DIFFUSION:*Pattern spreads across groups**	+	+	+
TRADITION:*Pattern endures across generations**	+	+	-
STANDARDIZATION: *Pattern is consisted and stylized**	+	+	~
SPECIES-VALID: *Not an artifact of human influence**	+	+	+
TRANSCENDENT: *Not determined by biophysical enviroment**	+	+	+
ACCUMULATION: *Traditions build over time***	+	-	-
IMITATION: *Ability to copy novel motor responses‡*	+	+	-
VARIABILITY: *Two or more patterned behaviours in more than one domain§*	+	+	+
CONFORMITY: *Preference for groups' standard(s)˙*	+	+	-

* Criteria from Krober (1928), ** Tommasello & Call (1997), ‡ Galef (1992),
§ Whiten & van SchaILk (2007), ˙ Heinrich & McElreath (2007).
Key: (+) present; (-) absent; (~) unknown or debatable

and colleagues (2003). Perry and her associates describe five different social conventions in four large study sites (Santa Rosa, Lomas Barbudal, Palo Verde, Curu). By their very nature, such conventions appear, on the surface, to be entirely arbitrary and independent of ecological variables. Thus avoiding many of the criticism leveled against the Kawai (1963) observations of potato and wheat washing behaviors of Japanese Macaques. The conventions in question include: (a) hand sniffing, (b) sucking, (c) finger game, (d) hair game, (e) toy game. As can be seen in Table 2, one group—Abby's Group—frequently exhibits all of the conventions in question, while a second group "Cuajiniquil" frequently exhibits two of the five behaviors. According to Whiten and van Schaik (2007) the distribution of these social conventions meet their criteria for 'tradition' whereas those of the Japanese macaques do not because it meets their criteria of variability (see Table 1). However, note that these behaviors lack a number of features present in both chimpanzee and human cultures, including: durability, tradition and imitation (see Table 1). Durability and tradition are absent because some of the described conventions among capuchin monkeys disappeared when the innovator disappeared. These features of monkey 'culture' may explain why such patterned behaviors are extremely rare in monkeys and, where present, lack the number and variation that has been documented in apes.

Tab. 2. Five different 'traditions' described by Perry et al. (2003) in four different wild capuchin groups. Although there might be some behavioral overlap in some of these traditions (e.g., 'games') not that the distribution of each is unique.

BEHAVIOURS	SANTA ROSA (Cuajiniquil)	LOMAS BARBUDAL (Abby's Group)	PALO VERDE (Station Group)	CURU (Better's Group)
HAND SNIFFING *Monkeys insert their finger in another monkey's nose or cups their hands over their mouth or nose*	+	+	+	-
SUCKING *Sucking another monkey's fingers, toes, ears or tails for a significant amount of time*	+	+	⌣	⌣
FINGER GAME *A monkey inserts their finger in another monkey's mouth who clamps down on their finger, preventing them from removing their finger*	?	+	-	-
HAIR GAME *Monkeys take turn bitting tufts of hair from each other's bodies in a playful fashion*	?	+	-	-
TOY GAME *Monkeys take turn taking things out of each others mouths (sticks, leaves, etc.)*	-	+	-	+

Key: (+) behaviour is common; (~) behaviour is extremely rare; (-) behaviour not seen after more than 250 hours; (?) insufficient data or inadequate data

The characteristics of traditions in the wild as well as their respective function point to selection pressures acting on individuals as well as on networks of individuals (particularly kin) creating a baldiwinian effect between the need for certain traditions and the cognitive mechanism(s) that maintain them. Although field studies make it impossible to distinguish between novel and familiar imitation and in many instances it's impossible to separate attentional and motivational mechanisms, it's likely that at least in the case described by Perry and colleagues (2003), such conventions likely represent examples of familiar imitation. The same may be true for the examples described by Panger and her associates (2002).

The evolution of the imitation faculty

Any contemplation of the evolution of the imitation faculty must begin with the question 'What is imitation for?' How might having a simple imitation faculty consisting of only familiar imitation, for example, be adaptive? How might it increase fitness? First and foremost, familiar imitation solves the problem of where and when to execute species-typical behaviors (e.g., social conventions in capuchin monkeys). In contrast, novel imitation solves the problem of copying new and, perhaps, rare behavioral rules or responses at a low cost. However, in each both cases, imitation (familiar and novel) reduces the costs (e.g., time, energy) associated with trial-and-error. When viewed this way, familiar imitation minimizes the need to learn *where or when* to execute familiar responses, in the case of novel imitation, it minimizes learning *how* and*, perhaps *why* to do a novel response. As many have noted, these problems are particularly acute in environments that are constantly changing. That environment may be social, it may be physical or it may be both. The more flux, the greater the need to quickly adapt to the new situation and the greater the selection pressures favoring an imitation faculty. This view

has been supported by various mathematical models which have, in effect, demonstrated that the evolution of the imitation faculty is linked to life in ever-changing environments (Boyd & Richardson, 1986; Henrich & McElreath, 2003). An evaluation of animals such as birds and primates who live in variable social and physical environments, suggests that these animals possess social learning skills consistent with at least a basic imitation faculty (Reader & Laland, 2002; Lefebvre *et al.*, 1998). Interestingly, Reader and Laland (2002) have reported that among primates, brain size correlates most significantly with social learning, but also with innovation and tool-use. But innovation may represent an important problem-solving adaptation that co-evolved with the imitation faculty. Consistent with this view is the fact that in their analysis, social learning, innovation and tool use are all strongly inter-correlated (Reader & Laland, 2002). Similar data exists for birds (Lefebvre, *et al.* 1996; Lefebvre, *et al.*, 1998), providing evidence of convergent evolutionary processes.

The research summarized above shows that new and old world monkeys, like apes and humans, possess a faculty of imitation. That is, a psychological faculty that translates incoming sensory information into a matching response. However, macaques, capuchins and marmosets appear capable of only familiar motor imitation and rhesus monkeys have evidenced novel cognitive imitation. But these same monkey species appear incapable of novel motor imitation. This feature of the monkey imitation faculty contrasts with that of chimpanzees, orangutans and gorillas (as well as humans) who are capable of at least certain types of novel motor imitation (Byrne 2005; Whiten *et al.*, 2004). From this it follows that novel motor imitation is likely to be a derived feature and a characteristic of the hominoid imitation faculty; one that is perhaps intricately linked with tool-use. In this view, the more dependent an organism is on technology or motor learning for subsistence, the more sophisticated and versatile the imitation faculty. The main reason being that the use of technology—tools—requires specialized sensorimotor, inferential and, perhaps,

problem-solving (or innovation) mechanisms working in a coordinated fashion to selectively attend to and encode certain types of information that produces a template that serves as the basis for a matching response. Such pressures should be stronger among apes than monkeys because while monkeys have specialized dentition and digestive systems, apes have somewhat generalized dental anatomy and, with the exception of gorillas, lack specialized digestive systems (Ankel-Simons, 2000). These anatomical differences mean that whereas monkeys are able to enjoy a relatively diverse diet, apes do not have the same luxury. In monkeys, diets range from non-ripe fruits and mature leaves to insects, small animals and gum. Ape anatomy, however, limits dietary options to a narrow range of foods that consist mostly of mature, non-fibrous fruits with high sugar and calorie content (Maier, 1984). As a consequence of these dietary limitations, the great apes occupy a fairly narrow range of ecological habitats, being largely restricted to tropical and woodland forests (Potts, 1998; 2004). Contrast the narrow ecological range of chimpanzees and orangutans to that of macaques that have made a home in the arid lands of Africa as well as the snowy hillside of Japan.

These ecological, morphological and dietary pressures that, among primates, are mostly unique to the great apes, placed a premium on novel behavioral, cognitive, and life history strategies that are critical to fitness (Potts, 2004) and presumably served as a compensatory mechanism for morphological limitations. One such behavioral strategy used to broaden the apes diet is the systematic pursuit of prey in groups— or 'hunting'—(Watts & Mitani, 2002), another has been extractive foraging using tools (Goodall, 1986; Whiten *et al.*, 1999). Yet another, might have been the fission-fussion social organization of chimpanzees and bonobos. Both of these behavioral innovations—hunting and tool-use— likely favored an elaboration of the imitation faculty, in particular, the evolution of a robust novel imitation mechanism that was functionally integrated with other domain-specific imitation mechanisms (e.g., motor and cognitive imitation). Certainly, the novel motor imitation skills of apes

are less robust than those known to be present in children as young as 2.5 years of age (Herrman *et al.*, 2007). These more derived novel motor imitation skills likely date to the first members of the genus *Homo,* where the need and dependence on stone-tool technology and other methods of subsistence including hunting and gathering placed increasing pressures on various mechanisms of the imitation faculty. Some of these elaborations may have included functional connections with other domain-specific mechanisms mediating, theory of mind, agency-attribution, and certain attentional and memory systems.

Nevertheless, given the ecological circumstances of non-human great apes, an imitation faculty capable of novel motor imitation would immediately increase the fitness of chimpanzees, for example, as it would have provided individuals with the skills to effectively steal the technical knowledge of conspecifics and immediately use that knowledge to supplement their diets. Given the importance of such a skill, it should then be no surprise that apes have elaborate tool-traditions (Whiten et al., 1999) which afford the means to develop and maintain these skills across generations ('tradition') and outside the innovator's presence ('durability'). Yet, note that traditions as they exist in chimpanzees and orangutans are mostly absent in monkeys. And where they exist, as appears to be the case in capuchin monkeys, they comprise of just 2 or 3 behaviors (Boinski et al., 2003; Panger et al., 2002; Perry et al., 2003) which lack the diversity and complexity that characterized chimpanzee and orangutan behavioral traditions (Table 1). These differences may rest on the fact at least in captivity, chimpanzee traditions are mediated by motor imitation coupled by a strong tendency to always use the group's preferred technique; 'conformity' (Whiten et al., 2005). No comparable evidence exists for capuchin monkeys, or any other monkey species. Again, perhaps the discontinuity between cultures in monkeys and apes is not surprising, given that monkeys', as a group, are characterized by numerous anatomical specializations that are specifically adapted to their niche, which in no

small measure grants them the ability to exploit a wide range of diets and habitats without tools or the need for sophisticated traditions.

Given the evidence that capuchin, marmoset and rhesus monkeys as well as chimpanzees, orangutans and gorillas share a familiar imitation mechanism, familiar imitation is likely to be the most basic and ancestral feature of the imitation faculty, and the feature that is likely to be present in all animals that possess a faculty of imitation. The models proposed by Boyd & Richardson (1986) and Henrich & McElreath (2003) explain this facet of the imitation faculty best. While it's possible for an animal to possess an imitation faculty that can copy only familiar responses (familiar imitation), it's difficult to imagine an imitation faculty capable of novel imitation, yet incapable of familiar imitation. From this it follows that the evolution of a derived imitation faculty that includes the ability to copy novel responses is premised on mechanisms that mediate familiar imitation. Some of the neurobiological evidence reviewed above provides some insights into how the elaboration of the STS-F5-PS circuit in the macaque brain, for example, can make at least novel motor imitation possible via the representation of intransitive actions (Rizzolatti, 2005). However, logically, novel motor imitation is premised on novel cognitive imitation. The former seems difficult (if not impossible) without first having the ability to copy novel cognitive rules. But what selection pressures might have driven the elaboration of this faculty? One possibility is the need to develop and acquire more effective extractive foraging techniques; specifically, techniques that require the use of tools.

The data summarized above provides compelling evidence that monkeys possess a faculty of imitation. This imitation faculty appears to consist of the ability to copy familiar motor actions (i.e., familiar motor imitation) as well as novel cognitive rules (i.e., novel cognitive imitation). These skills, afford monkeys the ability to appropriately copy the (familiar) actions of their conspecifics; a skill likely to be a specific adaptation to the pressures of group living, such as pressures associated with managing social hierarchies and group feeding. From this it follows that familiar imitation should be common in most social species where the ability to adaptively copy the familiar behaviors of conspecifics during synchronized activities like foraging, feeding and territory defense would afford important fitness benefits; reviews of social learning in a variety of animals suggests that this is the case (see Zentall, 2006). Novel imitation should be common in species with generalized anatomies and where technical (or specialized motor) knowledge is critical for survival. Thus, in this view, the elaboration of a critical social cognition skill—imitation—was the product not of social factors but physical factors associated with knowledge of tools, motor actions and spatial relations.

Conclusions

There is no simple answer to the question 'Do monkeys ape'. In fact, there is no simple answer to the question 'Do humans ape.' The main reason being that imitation is not a unitary skill. Here, imitation has been conceptualized as a multifaceted psychological faculty whose function is to adaptively and flexibly copy rules or responses expressed by others. This faculty has two general functions: the ability to copy familiar skills and the ability to copy novel skills as well as domain-specific functions that correspond with the the ability to copy different types of stimuli: motor, vocal and cognitive. Given the behavioral and neurobiological evidence, it's been proposed that the ability to copy familiar responses represents the primitive state of this faculty. The ability to copy novel responses represents a more derived state of the same faculty.

Monkeys appear capable of copying familiar motor rules as evidenced by studies demonstrating that marmosets use the same opening technique as a model to open a sealed can, for example (Voelkl & Huber, 2007). Macaques also possess the ability to copy familiar facial expressions such as lip-smacking and mouth opening. However, monkeys have not evidenced novel motor

imitation. This result is in contrast to apes, who have been shown to differentially copy novel or arbitrary motor actions (Horner & Whiten, 2005; Myowa-Yamakoshi & Matsuzawa, 1999; Whiten, 1998). Yet, despite monkeys' inability to copy novel motor responses, they are capable of copying novel cognitive (non-motor) rules (Subiaul, *et al.*, 2004); a result which demonstrates that while monkeys may be incapable of novel motor imitation, they are capable of novel cognitive imitation or imitation learning.

In sum, while novel motor imitation represents a highly advanced cognitive skill that may be unique to the great apes perhaps due to dietary pressures favoring tool-use in apes (but not in monkeys), familiar imitation represents a more general, yet indispensable skill for social animals who must conform to the vagaries of sometimes strict social hierarchies and coordinated group activities such as feeding and territory defense. These pressures common in social animals should favor a basic imitation faculty whose primary skill is to adaptively copy familiar rules and responses expressed by conspecifics. Such a skill in response to social pressures is not significantly different from the folk saying among humans that compels us to engage in familiar imitation, 'When in Rome, do as the Romans do."

Acknowledgements

Info on the web

http://www.subiaul.com

Cognitive imitation; imitation learning in children and monkeys

http://www.emory.edu/LIVING_LINKS/

Living Links (Emory University, Yerkes National Primate Research Center): Comparative psychology, great apes and monkeys

http://www.cognitiveevolutiongroup.org/

Cognitive Evolution Group (University of Louisiana): Cognitive evolution, comparative research on great apes and human children

http://primatelit.library.wisc.edu/

PrimateLit (University of Wisconsin, Madison): Bibliographic database of primate research

References

Adams-Curtis L. 1987. Social context of manipulative behavior in *Cebus apella*. *Am. J. Primatol.,* 12: 325.

Adams-Curtis L. & Fragaszy D.M. 1995. Influence of a skilled model on the behavior of conspecific observers in tufted capuchin monkeys (*Cebus apella*). *Am. J. Primatol.,* 37: 65-71.

Addessi E. & Visalberghi E. 2001. Social facilitation of eating novel food in tufted capuchins (*Cebus apella*): Input provided by group members and responses affected in the observer. *Anim. Cogn.*, 4: 297-303.

Akins C.K. & Zentall T. 1996. Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *J.Comp. Psychol.*,

110: 316-20.

Anisfeld M. 1991. Neonatal imitation: Review. *Dev. Rev.,* 11: 60-97.

Anisfeld M. 1996. Only tongue protrusion modeling is matched by neonates. *Dev. Rev.* 16: 149-161.

Anisfeld M., Turkewitz G., Rose S.A., Rosenberg .FR., Sheiber F.J., Couturier-Fagan D.A., Ger J.S. & Sommer I. 2001. No compelling evidence that newborns imitate oral gestures. *Infancy,* 2: 111-122.

Ankel-Simons F. 2000. *Primate Anatomy: An introduction.* Academic Press, London.

Bargh J.A. & Chartrand T.L. 1999 The unbearable automaticity of being. *Am. Psychol.,* 54: 462-479.

Beck B.B. 1972. Tool use in captive hamadryas baboons. *Primates,* 13: 277-95.

Beck B.B. 1973. Observation learning of tool use by captive Guinea baboons (*Papio papio*). *Am. J. Phys.l Anthropol.,* 38: 579-82.

Beck B.B. 1976. Tool use by captive pigtailed macaques. *Primates,* 17.

Boinski S., Quatrone R.P., Sughrue K., Selvaggi L., Henry M., Stickler C.M. & Rose L.M. 2003 Do brown capuchins socially learn foraging skills? In D. Fragaszy & S. Perry (eds.): *The Biology of Traditions*, pp. 365-390. Cambridge University Press, Cambridge.

Boyd R. & Richerson, P.J. 1996. Why culture is common but cultural evolution is rare. *Proceedings of the British Academy,* 88: 73-93.

Boyd R. & Richardson P.J. 1985. *Culture and the evolutionary process.* Chicago University Press, Chicago.

Brosnan S.F., Earley R.L. & Dugatkin L.E. 2003. Observational learning and predator inspection in guppies (*Poecilia retuculata*). *Ethology,* 109: 823-833.

Bugnyar T. & Huber L, 1997. Push or Pull: an experimental study on imitation in marmosets. *Anim. Behav.,* 54: 817-831.

Byrne R.W. & Russon A.E. 1998. Learning by Imitation: a hierarchical approach. *Behav. Brain Sci.,* 21: 667-721.

Caldwell C.A. & Whiten A. 2002. Evolutionary perspectives on imitation: is a comparative

psychology of social learning possible? *Anim. Cogn.,* 5: 193-208.

Carpenter M., Call J. & Tomasello M. 2002. Understanding "Prior Intentions" Enables Two-Year Olds to Imitatively Learn A Complex Task. *Child Dev.,* 73: 1431-1441.

Chamove A.S. 1974. Failure to find rhesus observational learning. *J. Behav. Sci.,* 2: 39-41.

Cheney D.L. & Seyfarth R.M. 1990. *How Monkeys See The World.* University of Chicago Press, Chicago.

Csibra G. 2003. Teleological and referential understanding of action in infancy. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.,* 29: 447-58.

Dautenhahn K. & Nehaniv C. 2002. *Imitation in animals and artifacts.* MIT Press, Cambridge.

Dawson B.V. & Foss B.M. 1965. Observational learning in budgigars. *Anim. Behav.,* 13: 470-4.

Di Pellegrino G., Fadiga L., Fogassi L., Gallese V. & Rizzolatti G. 1992 Understanding motor events: a neurophysiological study. *Exp. Brain Res.,* 91: 176-180.

Ferrari P.F., Visalberghi E., Paukner A., Fogassi L., Ruggiero A. & Suomi S.J. 2006. Neonatal imitation in Rhesus Macaques. *Plos Biol.,* 4: 1501-1508.

Fodor J. 1983. *The Modularity of Mind.* MIT Press, Cambridge.

Fragaszy D. & Visalberghi E. 2004. Socially biased learning in monkeys. *Learn. Behav.,* 32: 24-35.

Galdikas B.M.F. 1982. Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *J. Hum. Evol.,* 10: 19-33.

Galef B.G., Jr. 1988. Imitation in Animals: History, definition, and interpretation of data from the psychological laboratory. In Z. Galef (ed.): *Social Learning: Psychological and Biological Perspectives*, pp. 3-28. Lawrence Erlbaum, New Jersey.

Galef B.G., Jr. 1988. Imitation in Animals: History, definition, and interpretation of data from the psychological laboratory. In Z. Galef (ed.): *Social Learning: Psychological*

and Biological Perspectives, pp. 3-28. Lawrence Erlbaum, New Jersey.

Galef B.G., Jr. 1992. The question of animal culture. *Hum. Nat., 3*: 157-178.

Haggerty M.E. 1909. Imitation in Monkeys. *Comparative Neurology and Psychology, 19*: 337-441.

Hall K.R.L. 1963. Observational Learning in Monkeys and Apes. *Br. J. Psychol., 54*: 201-226.

Hauser M.D. 1992. Costs of deception: cheaters are punished in rhesus monkeys. *Proc. Natl. Acad. Sci.* U.S.A., 89: 12137-9.

Hauser M.D. 1998. Expectations about object motion and destination: experiments with a non-human primate. *Dev. Sci., 1*: 31-38.

Henrich J. & McElreath R. 2003. The evolution of cultural evolution. *Evol. Anthropol., 12*: 123-135.

Heinrich, J. & McElreath, R. 2007. Dual-inheritance theory: the evolution of human cultural capacities and cultural evolution. In R. I. M. Dunbar & L. Barrett (Eds.): The *Oxford Handbook of Evolutionary Psychology*. Oxford University Press: Oxford.

Herrmann E., Call J., Hernandez-Lloreda M.V., Hare B. & Tomasello M. 2007 Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science, 317*: 1360-1366.

Heyes C. 2001. Causes and Consequences of Imitation. *Trends Cogn. Sci., 5*: 253-261.

Heyes C.M. 2004. Imitation by association. In S Hurley & N Chater (Eds): *Perspectives on Imitation*. MIT Press, Cambridge.

Holloway R.L. 1969/1991 Culture: A Human Domain. *Curr. Anthropol., 10*: 395-412.

Hopper L.M., Spiteri A., Lambeth S., Schapira S., Horner V. & Whiten A. 2007 Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim. Behav., 73*: 1021-1032.

Horowitz A.C. 2003 Do humans ape? Or do apes human? Imitation and intention in humans (Homo sapiens) and other animals. *J. Comp. Psychol., 117*: 325-36.

Huang C. & Charman T. 2005. Gradations of emulation learning in infants' imitation of actions on objects. *J. Exp. Child Psychol., 92*: 276-302.

Jacobson S. 1979. Matching behavior in the young infants. *Child Dev., 30*: 425-430.

Janik V.M. & Slater P.J.B. 2000. The different roles of social learning in vocal communication. *Anim. Behav., 60*: 1-11.

Jones S.S. 1996. Imitation or exploration? Young infants' matching of adults' oral gestures. *Child Dev., 67*: 1952-1969.

Jones S.S. 2006. Exploration or imitation? The effect of music on 4-week-old infants' tongue protrusions. *Infant Behav. Dev., 29*: 126-130.

Kanner L. 1943. Autistic disturbances of affective contact. *Nerv. Child*, 2: 217-50.

Kawamura S. 1959. The process of sub-culture propagation among Japanese macaques. *Primates, 2*: 43-60.

Kempf E.J. 1916. Two methods of subjective learning in the monkey Macacus rhesus. *J. Anim. Behav., 6*: 256-265.

Kitahara-Frisch J. 1991. *Culture and Primatology: East and West*. State University of New York Press, New York.

Krober, A. L. (1928). Sub-human cultural beginnings. *Quaterly Review of Biology*, 3, 325-342.

Lefebvre L., Gaxiola A., Dawson S., Timmermans S., Rozsa L. & Kabai P. 1998. Feeding innovations and forebrain size in Australasian birds. *Behaviour, 135*: 1077-1097.

Lefebvre L., Whittle P., Lascaris E. & Finkelstein A. 1996. Feeding innovations and forebrain size in birds. *Anim. Behav., 53*: 549-560.

Maier W. 1984. Tooth morphology and dietary specialization. Plenum Press, New York.

Meltzoff A.N. 1988. The Human Infant as Homo Imitans. In Z. Galef (ed.): *Social Learning: A Psychological and Biological Perspective*. Lawrence Erlbaum Assoc., Publishers, Hillside.

Meltzoff A.N. 1999. Origins of Theory of Mind, Cognition and Communication. *J. Commun. Disord., 32*: 251-269.

Meltzoff A.N. 2002. Building blocks for a developmental theory of imitation. In

Melzoff & Prinz (eds.): *The Imitative Mind: Development, Evolution, and Brain Bases*. Cambridge University Press, Cambridge.

Meltzoff A.N. & Moore K.M. 1977. Imitation of Facial and Manual Gestures by Human Neonates. *Science,* 198: 75-78.

Meltzoff A.N. & Moore K.M. 1989. Imitation in Newborn Infants: Exploring the Range of Gestures Imitated and the Underlying Mechanisms. *Dev. Psychol.,* 25: 954-962.

Meltzoff A.N. & Moore M. 1983. Newborn infants imitate adult facial gestures. *Child Dev.,* 54: 702-9.

Mercader J., Barton H., Gillespie J., Harris J., Kuhn S., Tyler R. & Boesch C. 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc. Natl. Acad. Sci. US.A.,* 104: 3043-8.

Mercader J., Panger M. & Boesch C. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science,* 296: 1452-5.

Mills W. 1899. The nature of animal intelligence and the methods of investigating it. *Psychol. Rev.,* 6: 262-274.

Mitchell R.W. 1987. A comparative-developmental approach to understanding imitation. In P.P.G. Bateson & P.H. Klopfer (eds.): *Perspectives in ethology*, pp. 183-215. Plenum, New York.

Mitchell R.W. 1987. A comparative-developmental approach to understanding imitation. In P.P.G. Bateson & P.H. Klopfer (eds.): *Perspectives in Ethology*, pp. 183-215. Plenum, New York.

Morgan C.L. 1900. *Animal Behavior*. Arnold, London.

Myowa-Yamakoshi M., Tomonaga M., Tanaka M., Matsuzawa T. 2004 Imitation in neonatal chimpanzees (*Pan troglodytes*). *Dev. Sci.,* 7: 437-442.

Myowa-Yamakoshi M. & Matsuzawa T. 1999. Factors influencing imitation in manipulatory actions in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.,* 113: 128-136.

Nguyen N.H., Klein E.D. & Zentall T.R. 2005. Imitation of two-action sequences by pigeons. *Psychon. Bull. Rev.,* 12: 514-518.

Panger M., Perry S., Rose L.M., Gros-Louis J., Vogel E., Mackinnon K.C. & Baker M. 2002. Cross-Site Differences in Foraging Behavior of White-Faced Capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.,* 119: 52-66.

Perrett D.I., Harries M.H., Bevan R., Thomas S., Benson P.J., Mistlin A.J., Chitty A.J., Hietanen J.K. & Ortega J.E. 1989. Frameworks of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.,* 146.

Perry S., Panger M., Rose L.M., Baker M., Gros-Louis J., Jack K., Mackinnon K.C., Manson J., Fedigan L. & Pyle K. 2003. Traditions in wild white-faced capuchin monkeys. In D. Fragaszy & S. Perry (eds.): *The Biology of Traditions*, pp. 391-425. Cambridge University Press, Cambridge.

Potts R. 1998. Environmental hypotheses of hominin evolution. *Am. J. Phys. Anthropol. Suppl.,* 27: 93-136.

Potts R. 2004. Paleoenvironmental basis of cognitive evolution in great apes. *Am. J. Primatol.,* 62: 209-28.

Reader S.M. & Laland K.N. 2002. Social Intelligence, Innovation, and Enhanced Brain Size in Primates. *Proc. Natl. Acad. Sci. U.S.A.,* 99: 4436-4441.

Rizzolatti G. 2005. *The mirror neuron system and imitation*. MIT Press, Cambridge.

Rizzolatti G., Camarda R., Fogassi L., Gentilucci M., Luppino G. & Matelli M. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp. Brain Res.,* 71: 491-507.

Rizzolatti G., Fadiga L., Gallese V. & Fogassi L. 1996. Action recognition in the premotor cortex. *Brain,* 119: 593-609.

Snowdon C. & Boe C. 2003. Social communication about unpalatable foods in tamarins (*Saguinus oedipus*). *J. Comp. Psychol.,* 117: 142-148.

Subiaul F., Cantlon J., Holloway R. & Terrace H. 2004. Cognitive Imitation in Rhesus Macaques. *Science,* 305: 407-410.

Subiaul F., Lurie H., Romansky K., Klein T., Holmes D. & Terrace H.S. 2007b. Cognitive imitation in typically-developing 3- and 4-year

olds and individuals with autism. *Cog. Dev.,* 22: 230-43.

Subiaul F., Romansky K., Cantlon J., Klein T. & Terrace H. 2007a Cognitive imitation in 2-year old human children (*Homo sapiens*): A comparison with rhesus monkeys (*Macaca mulatta*). *Anim. Cogn.,* Epub ahead of print.

Tennie C., Call J. & Tomasello M. 2006. Push or pull: emulation versus imitation in great apes an human children. *Ethology,* 112: 1159-1169.

Thompson D. & Russell J. 2004. The ghost condition: imitation versus emulation in young children's observational learning. *Dev. Psychol.,* 40: 882-9.

Thorndike E.L. 1898. Animal intelligence: An experimental study of the associative processes in animals. *Psychol. Rev. Monogr. Suppl.*, 2: 8.

Thorndike E.L. 1911. *Animal Intelligence*. Macmillan, New York, NY.

Thorpe W.H. 1956. *Learning and Instinct in Animals*. Methuen, London, UK.

Tomasello M. 1990. Cultural Transmission in the Tool Use and Communicatory Signaling of Chimpanzees? In P. Gibson (ed.): *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*, pp. 274-311. Cambridge University Press, Cambridge.

Tomasello M. & Call J. 1997. *Primate Cognition*. Oxford University Press, New York.

Visalberghi E. & Fragaszy D. 1990. Do monkeys ape? In S. Hurley & N. Chater (Eds): *Perspectives on Imitation*. MIT Press, Cambridge.

Visalberghi E. & Fragaszy D. 2002 Do monkeys ape? Ten Years Later. In K. Dautenhahn & C. Nehaniv (eds.): *Imitation in animals and artifacts*, pp. 471-479. MIT Press, Cambridge.

Visalberghi E. & Fragaszy D.M. 1995 The behaviour of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. *Anim. Behav.,* 49: 1089-1095.

Visalberghi E. & Fragaszy D.M. 1996. Pedagogy and imitation in monkeys: ye, no, or maybe? In D. Olson & N. Torrence (eds.): *Handbook of education and human development*, pp. 277-301. Blackwell, London.

Visalberghi E. & Trinca L. 1989. Tool Use in Capachin Monkeys: Distinguishing Between Performing and Understanding. *Primates,* 30: 511-521.

Voelkl B. & Huber L. 2000. True imitation in marmosets. *Anim. Behav.,* 60: 195-202.

Voelkl B. & Huber L. 2007. Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS ONE*, 2 (7): e611.

Warden C.J., Fjeld H.A. & Koch A.M. 1940. Imitative Behavior in Cebus and Rhesus Monkeys. *J. Genet. Psychol.,* 56: 311-322.

Warden C.J. & Jackson T.A. 1935. Imitative behavior in the Rhesus monkey. *Pedagogical Seminar,* 46: 103-125.

Watts D. & Mitani J.C. 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.,* 23: 1-28.

Whiten A. 1998. Imitation of the Sequential Structure of Actions by Chimpanzees (Pan troglodytes). *J. Comp. Psychol.,* 112: 270-281.

Whiten A. & Custance D.M. 1996. Studies of Imitation in Chimpanzees and Children. In C.M. Heyes & B.G. Galef (eds.): *Social Learning in Animals: The Roots of Culture.* , pp. 291-318. Academic Press, San Diego.

Whiten A., Custance D.M., Gomez J.C., Teixidor P. & Bard K.A. 1996. Imitative Learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.,* 110: 3-14.

Whiten A. & Ham R. 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Adv. Study Behav.*, 21: 239-83.

Whiten A., Horner V., Litchfield C. & Marshall-Pescini S. 2004. How do apes ape? *Learn. Behav.,* 32: 36-52.

Whiten A. & van Schaik C.P. 2007. The evolution of animal 'cultures' and social intelligence. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.,* 362: 603-620.

Williams, J. H. G., Whiten, A. & Singh, T. 2004. A systematic review of action imitation in autism spectrum disorders. *J. of Autism &*

Developmental Disorders, 34: 285-299.

Zajonc R.B. 1965. Social Facilitation. *Science,* 149: 106-109.

Zentall T. 1996. An Analysis of Imitative Learning in Animals. In H Galef (ed.): *Social Learning in Animals: The roots of culture*, pp. 221-243. Academic Press, San Diego.

Zentall T. 2006. Imitation: Definitions, evidence, and mechanisms. *Anim. Cogn.,* 9: 335-367.

Zentall T. 2007. Temporal discrimination learning by pigeons. *Behav. Processes,* 74: 286-292.

Zuckerman S. 1932. *The social life of monkeys and apes.* Kegan Paul, London.

Emiliano Bruner, Associate Editor