SOCIAL LEARNING IN MOTHER-REARED AND “ENCULTURATED” CAPUCHIN MONKEYS (*CEBUS APELLA*)

Tamar Fredman

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Table of Contents

Declarations

I, Tamar Fredman, hereby certify that this thesis, which is approximately 59,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree

Date …………………………. Signature of Candidate……………………………….

I was admitted as a candidate for a degree of Doctor of Philosophy the higher study for which this is a record was carried out in the years between 1998 and 2008.

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Acknowledgments

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Abstract

This thesis explores social learning in mother-reared and “enculturated” capuchin monkeys *(Cebus apella).* At the outset a framework for understanding the social influence on learning is discussed, followed by a review of the social and cognitive abilities of capuchin monkeys, establishing the rationale for studying social learning in this species.

Studies of wild capuchins suggest an important role for social learning but experiments with captive subjects have generally failed to support this. Some potential reasons for the lack of evidence in experimental settings are given.

An example of using the two - method design to test social learning in acquiring behaviour by enculturated subjects is addressed. The results are related to findings with other species tested with a similar apparatus. Before testing mother-reared monkeys, an observational study of the object manipulation and tool-use repertoire of the subjects was carried out in order to facilitate the design of suitable social learning tasks for these monkeys.

The first empirical study in Chapter 6 reports results of experiments with the enculturated and mother-reared capuchin monkeys employing the two -action method together with a third control group. The enculturated monkeys exhibited high fidelity copying that included the specific tool use technique witnessed while opening the foraging box. Mother-reared monkeys exhibited fidelity at a lower level, tending only to re-create the results the model had achieved.

The second empirical study in Chapter 7 tested whether capuchin monkeys could show cumulative cultural learning manifested in the ability to switch from an established mode of manipulating a dipping box to a complex yet more advantageous one. Both populations were able to do so. The enculturated monkeys, as in the previous study, showed higher fidelity copying of the model.

The last experiment was a preliminary study employing the “do as I do” method which was carried out with four of the enculturated monkeys. It provides suggestive evidence for at least one monkey's understanding of the task.

The results of the studies are discussed in relation to previous experimental research as well as to data from capuchin monkeys in nature. The possible role of enculturation in social learning ability is considered.

Prologue

> The typical Israeli way of washing floors, known as the "sponja", uses a bucket full of water mixed with washing liquid and a T shaped stick which has a piece of rubber on the bottom . A rag is first soaked in the bucket and then folded round the rubber end of the stick. After washing the floor the rubber end is then used to wipe up the remaining water. When Rusty, a male capuchin monkey, was about five years old I saw him do just this while I was washing the floors in the house. He soaked the rag in water, put it on the rubber part of the stick (although he did not actually rap the rag around the stick) and holding this long stick with his two hands pushed it along the floor. He has enjoyed doing this ever since. Was he imitating?

It has been almost twenty years now since my first encounter with capuchin monkeys, which was followed by my living with a small group of these monkeys for more than five years. Living with capuchin monkeys, and not always being the alpha in the group, demanded that I was alert at all times, trying to understand what was going on in their minds and how they saw the world we lived in. I seemed to be juggling between the emotional way I perceived them, being at times anthropomorphic towards them, but at the same time trying to view them and their behaviour through a primatologist's eye, hoping to see them for what they truly were.

During these years, I did not always have the time to stop and think about each of the fascinating behaviours I was witnessing, taking it for granted that monkeys would "pick up" behaviours they saw around them. Throughout history, man has accepted without question the notion that it is in a monkey's nature to imitate. This is so rooted in our belief systems that in many languages the word "to imitate" is connected to the word monkey (Visalberghi & Fragaszy, 1990a). This is true as well as in Hebrew and is captured in the popular saying "Kof acharey ben-adam" - "Monkey after man" – that describes a person copying someone else. This reflects the common notion that monkeys imitate and do so for the pleasure of imitating. "It is proverbial that monkeys carry the principle of imitation... they are animals that imitate for the mere sake of imitating" (Romanes, 1884 p.477). Yet, although "my" capuchins seemed to pick up many behaviours which were happening in the house, many more behaviours were not copied. Why was that so?

Social animals are continually communicating with each other through different modes of communication; visual, acoustic, chemical and so on. Some animals are finely tuned to receive some of these transmitted signals, sometimes in ways that other animals cannot. For example, pygmy marmosets *(Cebuella pygmaea)* may emit high pitch tones which other primates and animals cannot perceive (Snowdon & Hodun, 1981). However, when information is transmitted socially, what kind of tuning is required? As opposed to overt communication, social information does not necessarily require intention (conscious or not) on the part of the transmitter. It is the "responsibility" of the observer to make use of the information or part of it. Which part of my actions and behaviour were the monkeys tuned to? Were they paying attention to every fine movement? To the end result? Which situations were more influential and which components of the behaviours were totally neglected? These and many more questions are far from being new and have intrigued researchers for decades, during which time they have tried to define the social influence on behaviour in many ways. This thesis seeks to find some of the answers.

Chapter 1

IDENTIFYING SOCIAL LEARNING AND IMITATION

In this chapter I present a framework to study social learning and imitation. I discuss three different levels of social influence on the behaviour of an observer according to the information s/he utilizes from the model's actions. I also address related issues regarding the motivation for social learning, the significance of the type of action observed and relevant characteristics of the model and the observer.

Two general frameworks guide the current quest for understanding social learning. The first, depicted in Figure 1.1, looks at the general context in which social learning occurs, and takes into account factors such as the type of action observed and the characteristics of the model and the observer. The second, shown in Table 1.1, is a more detailed analysis of one of the components described in the first framework; namely, the type of information the observer derives from the model's action. This is divided into three general levels. Table 1.1 presents some of the different terms used for describing this social influence. Several points should be made before proceeding:

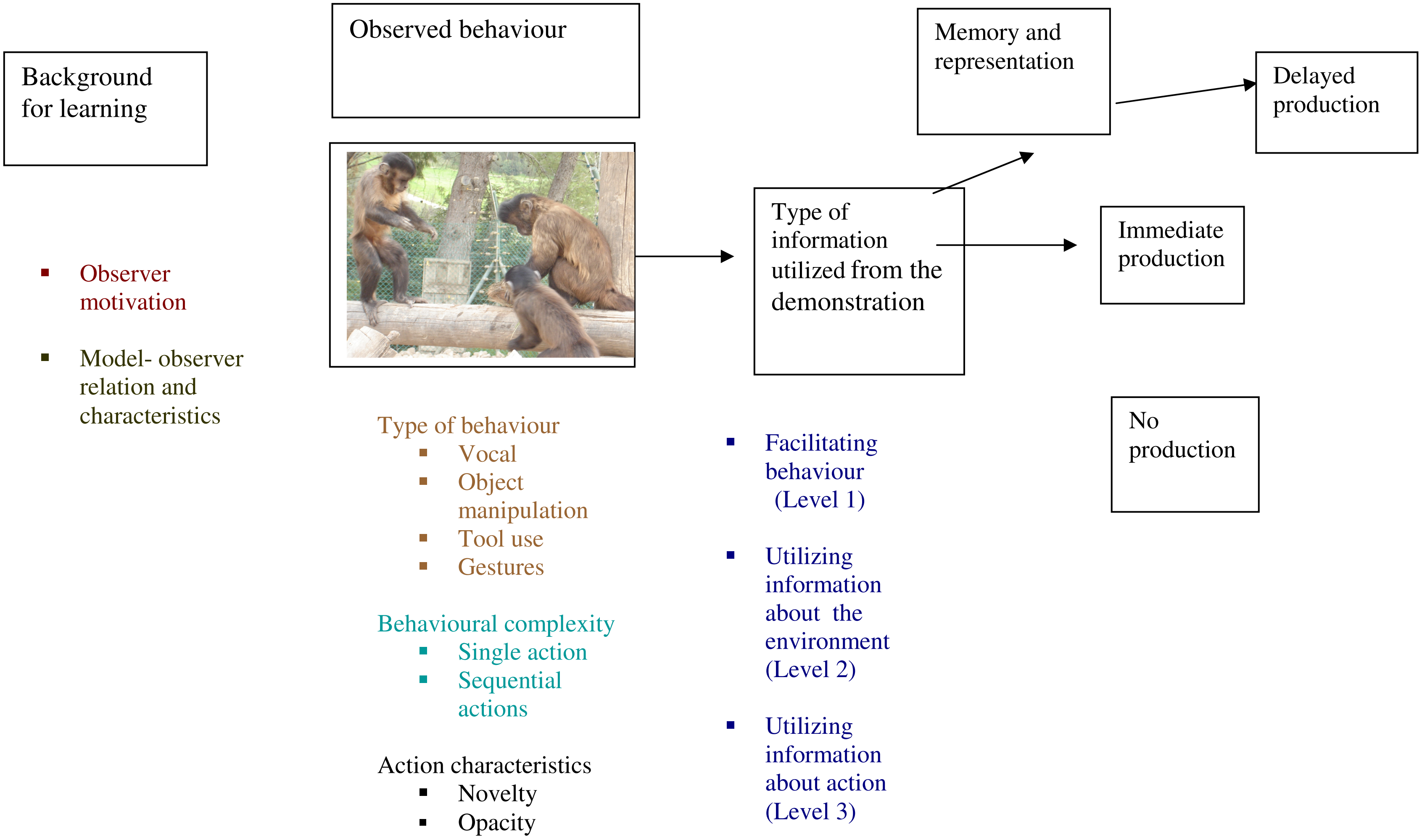
A. I use the word "level" and not "types", as it is accepted by most authors that there is a qualitative difference between the three levels in terms of the cognitive demand (however see e.g. Heyes, 1994; Zentall, 1996). I return to this issue later on in depth.

B. One of the problems in integrating the history of social learning research is the vast number of terms and definitions used in the literature. Table 1.1 summarizes the most important terms. However it should be borne in mind that the terminologies come from different fields and eras, which makes it very difficult to compare them in a systematic and hierarchical way (Heyes, 1994).

C. It has been acknowledged that different levels of influence may result in the same behaviour by the observer (e.g. Thorpe, 1956; Galef, 1988, 1992; Whiten & Ham 1992); thus, it is often difficult to conclude what information was actually used to produce the behaviour. It is also worthwhile remembering that in any given situation the observer may be utilizing information on different levels in concert, as the levels are not mutually exclusive.

Table 1.1 Levels of social influence on behaviour. Terms used in the literature to describe social learning.

Level 1	**Level 2**			**Level 3**	
Facilitating a behaviour	**Learning about the environment**			**Learning about behaviour**	
	Learning about locus	**Learning about stimuli**	**Learning about results**	**Learning about Action**	**Learning about Action+ Intention**
Contagious Behaviour (Thorpe, 1956). **Response Facilitation** (Byrne, 1994). **Mimesis** (Armstrong, 1951).	**Local enhancement** (Thorpe, 1956). **Matched dependent learning** (Miller & Dollard, 1941).	**Stimulus enhancement** (Spence, 1937). **Emulation** (Call & Tomasello, 1994). **Observational conditioning** (Cook *et al*. 1985). **Valence transformation** (Hogan, 1988).	**Goal emulation** (Wood, 1989). **Object movement re- enactment** (Custance *et al*. 1999).	**Impersonation** (Tomasello, 1990) **Copying** (Galef, 1988) **Mimicry** (Tomasello, 1996)	**Imitation** (Thorndike, 1898) **Reflective imitation** (Morgan, 1900) **True imitation** (Thorpe, 1956) **Observational learning** (Hall, 1963)



Background for learning

- Observer motivation
- Model- observer relation and characteristics

Observed behaviour

Type of behaviour
  - Vocal
  - Object manipulation
  - Tool use
  - Gestures

Behavioural complexity
  - Single action
  - Sequential actions

Action characteristics
  - Novelty
  - Opacity

Type of information utilized from the demonstration

- Facilitating behaviour (Level 1)
- Utilizing information about the environment (Level 2)
- Utilizing information about action (Level 3)

Memory and representation

Delayed production

Immediate production

No production

Figure 1.1 The social context of learning including: the background for learning, the properties of the action observed, the type of information utilized from the observation, and its production.

Level 1: Socially facilitating behaviour

Before starting to examine what capuchin monkeys are able to learn from each other or from humans I shall briefly consider the level of social influence on behaviour which will not be dealt with further in this thesis, and referred to as Level 1 in Table 1.1. The mere presence of a conspecific can alter the motivational state of an animal and may facilitate or retard behaviour (Zentall & Levine, 1972; Levine & Zentall, 1974). The term s*ocial facilitation* has been used in many different ways (see Level 1, Table 1.1). Zajonc (1965) first used it to describe **“**a motivational facilitation of performing a behavioural act already in the individual’s repertoire (whether acquired phylogenetically or ontogenetically) through experiencing another individual behaving similarly” (see also Clayton, 1978). On the other hand, Thorpe (1956) suggested that social facilitation only enhances innate stereotyped behaviour patterns. He labelled such learning *contagious behaviour.* This behaviour is released involuntarily (Zentall, 1996). Examples are adult humans yawning after seeing another yawning (Provine, 1989) and flight responses in various animals (Galef, 1988). Byrne (1994) uses the term *response facilitation* to describe a wider range of contagious behaviour: “the presence of a conspecific performing an act (often one resulting in reward) increasing the probability of an animal which sees it doing the same” (p. 236). It differs from contagion by the fact that the responses may be voluntary as well as involuntary. Such social influences on the behaviour of an observer may seem to be based on simple mechanisms, but response facilitation has not been widely documented in animals, and thus might be a more demanding process than described by Byrne (Byrne, 1994). I shall return to this question later.

Social influence is powerful enough to result in cultural transmission of behaviours when accompanied by other mechanisms such as associative learning (Noble & Todd, 1999) as animals, which behave contagiously as a response to other animals responding to stimulus X, may eventually associate stimulus X with that behaviour and respond to it directly themselves.

However learning *something new* from a demonstration is the basic component which differentiates social learning from social influence and this will now be discussed.

Social learning

Throughout the history of social learning research, authors have tried to classify different types of social learning in terms of what has been learned. Drawing on the vast literature of definitions and classifications (e.g. Byrne & Russon, 1988; Call, 1999; Fragaszy & Perry, 2003; Galef 1988; Heyes, 1994; Miklosi, 1999; Mitchell, 1987; Nicol, 1995; Whiten & Ham, 1992; Tomasello *et al*. 1987; Visalberghi & Fragaszy, 1990a), I describe two main levels of information use by an observer in a social context (see Table 1)**.**

Level 2. Using information about stimuli - Learning something new about the environment.

Level 3. Using information from the action - Learning something new about a potential behaviour or action.

Unlike social facilitation discussed earlier, in which the presence of the model merely facilitates behaviour already in the observer's repertoire, in levels 2 and 3 the observer makes use of information to learn something new.

Level 2. Using stimulus information to learn about the environment

Local enhancement (Thorpe, 1956) and stimulus enhancement (Spence, 1937) have been used to describe how an organism is attracted to some salient feature in the environment after viewing a conspecific interacting with it. As a result, the organism tends to approach or contact it or a similar stimulus. The observer then may perform acts which are already in its repertoire and which are therefore usually very similar to the behaviour of other members of its species. In both stimulus and local enhancement, the observer learns about the stimuli and not about the behaviour itself or the intentions behind it. When simple objects and actions are involved, stimulus enhancement can result in very rapid learning, which highly resembles the action viewed and may mistakenly be considered as imitation.

This mechanism is very powerful and plays a major role in many socially transmitted behaviours. Its ecological importance can be seen in the way different species acquire knowledge of which plants and food items are edible and where to find them (Whiten, 1989). This has been shown in birds (e.g. Mason & Reidinger, 1981, 1982; Fisher & Hinde, 1949). Stimulus enhancement has also been found to be the basis of mate choice behaviour in fish (Dugatkin, 1996 for guppies).

It can be important for an animal to see the end result of the action and incorporate this in its representation. Palameta & Lefebvre (1985) showed how learning through stimulus enhancement occurred only when the observer bird saw the model succeed in gaining food. This, to my knowledge, has not yet been tested in primates.

Learning about the rewarding or aversive aspect of the stimulus is known as *observational conditioning* (Cook et al. 1985; Whiten & Ham, 1992), in which an observer may learn to approach an object or avoid it after seeing the reaction of a conspecific towards the object (e.g. red winged black birds, Mason & Reidinger, 1981, 1982). When the observer itself is rewarded at the same time as the model is rewarded, learning is strengthened (e.g. bar pressing behaviour in rats: Del Russo, 1971).

Mineka & Cook (1988) showed how naive Rhesus monkeys learned to fear snakes (but not arbitrary objects) through the observation of the behaviour of other monkeys. The observer must be exposed to both in order to be conditioned to fear.

Matched dependent behaviour (Miller & Dollard, 1941) is yet another process suggested for the way a subject may learn socially about the environment. In this case a learner uses the model's behaviour as a discriminative cue for emitting a response. For example, rats may learn to solve a maze by following a leader rat (Church, 1957). However, once the model no longer responds or is absent, the learner stops responding as well. For the behaviour to become part of the learner's repertoire a transfer must be made to a control by an external cue independent of the model**.**

However, Zentall (1996) noted that both observational conditioning and matched dependent behaviours are examples of simple conditioning processes. The first is an example of classical conditioning in which the model's behaviour (the UR) becomes associated with the stimuli (CS) to bring about a similar response in the observer (CR). Matched dependent behaviour is a special case of operant conditioning.

Watching a model interact with a stimulus may provide more information than merely "approach or avoid". An observer may learn about more specific properties of the stimulus, as described in *emulation*. Emulation has been given different meanings in the social learning literature. Tomasello *et al.* (1987) first used the term emulation to describe the increase in the salience of a tool as well as learning its properties and its affordance (Gibson, 1979) and realising its function as a tool. Byrne (2002) also described this form of learning as “stimulus enhancement of an object in the specific context of an action.” Tomasello (1990) argued that many of the elaborate tool use behaviours of wild chimpanzees could be learned through emulation rather than imitation.

A related concept, which focuses on the movement of the object and not the actual behaviour of the model, is *object movement re-enactment* (Custance, Whiten & Fredman, 1999) in which the observer attends to how an object moves in space and not to the precise movement used by the model to move the object. A similar focus is found in the term *object centred social learning* (Custance *et al.* 2001).

Further information, which can be derived from the environment, is about the end state of the behaviour, as described in the term *goal emulation* (Wood, 1989; Tomasello, 1990; Whiten & Ham, 1992). In this usage, emulation describes focusing on the end results of the model’s behaviour. The way the observer reaches these results is based on previous knowledge and/or trial and error learning. Here again the observer may act towards the results in a similar way to the action of the model, or in a totally different manner.

What, then, is the importance of the model on this level of social learning if what the observer is learning is only connected to the stimulus and not to the model’s actions? Would an animal learn, for instance, about the “cracking” properties of a stone falling by chance on a hard shelled fruit just as much as watching a conspecific use the stone? Does the model give extra strength to the learning process? Fragaszy & Perry, (2003) conclude that

> “The trajectory of action and perception through time is different in social versus non-social conditions. This could arise through increased salience of experiences that occur in presence of others… Social partners generate particular experiences: they are animate, active agents and they produce behaviours that are particularly salient to conspecifics…Social context constitutes a means of focusing behaviour more effectively or differently than would have occurred in an asocial context” (pp. 9-10).

Heyes *et al.* (1994) suggested a “ghost” study to test the importance of the model for learning to take place. In their study, a joystick was operated automatically without the intervention of the model. The rats in that experiment showed a bias toward moving the joystick in the direction they had observed only when it was moved by a conspecific and not automatically. Fawcett and colleagues (Fawcett *et al.* 2002) tested European starlings (*Sturnus vulgaris*) in a “ghost” experiment in which the demonstrator attended closely to the stimuli but did not operate it. The results showed that the action of the model was crucial for social learning to take place. Results for chimpanzees have not been conclusive. Tennie *et al* (2006) found that chimpanzees, but not children, acted in the same way regardless of whether they had watched the model act or the "ghost" condition. By contrast, Hopper *et al.* (2007) found that chimpanzees had benefited more from watching a conspecific act than a "ghost" demonstration.

Thompson & Russell (2004), on the other hand, found that 14-26 month old children were just as likely to learn in the ghost situation as when a human model was involved.

Level 3. Using information about actions or behaviour

Imitation in its different definitions (e.g. Thorndike, 1898; Spence 1937, Mitchell, 1987; Lefebvre & Palameta, 1988; Visalberghi & Fragaszy, 1990a) focuses on the way the observer makes use of information from the actual *action* of the model.

In this thesis I will use the definition proposed by Mitchell (1987), with additions by Visalberghi & Fragaszy (1990a) and Whiten & Ham (1992), as a working definition. An action may be considered imitative when the following criteria are fulfilled:

1. Something C (the copy) is produced by an organism.
2. C is similar to M (the model).
3. Observation of C is necessary for the production of M (above baseline levels of C occurring spontaneously).
4. C is designed to be similar to M.
5. C must be novel at least in some aspects (Whiten & Ham 1992) or not already organized in that precise way in the organism's repertoire (Visalberghi & Fragaszy, 1990a).

The requirements of each of these criteria are discussed below.

1. **Production of observed behaviour**

A potential limitation of this stipulation is that a behaviour may be learned but not performed immediately. An observer may implement what s/he learned only later, in suitable conditions. Such delayed imitation has been considered by some authors to be more advanced than immediate imitation (Bandura, 1969). Piaget (1945) used the term *deferred imitation* and claimed it required remembering the action, representing it and performing it without the model's presence. According to Meltzoff, the ability for deferred imitation is important as a social tool and has been shown from nine months of age, when infants produce an observed act after 24 hours. Older children at the age of 14 months can even re-enact motor actions after a week (Meltzoff, 1988a b, c).

Dorrance & Zentall (2001) found that quails showed a significant tendency to reproduce the same behaviour they observed even after a delay of half an hour between observation and production. Zentall (2005) thus claims that in infants below the age of nine months, the inability for deferred imitation may reflect "sensory and especially motor limitations rather than an inability to imitate" (p. 191). Enculturated chimpanzees and orang-utans have also demonstrated deferred imitation (Bering *et al*. 2000; Bjorklund *et al*. 2000).

2. Similarity between observed behaviour and its production

How can one tell if the observer has learned the behaviour s/he observed? An act may be recognized as imitative even if the replication is only "in outline" or if it only involves one or two of several features, which could potentially be copied. Such features could include, for example, the shape of movement, its speed or laterality (Whiten & Ham, 1992).

Even when an action has been represented in the observer's mind its production may take some practice in order to reproduce it faithfully (Bernstein, 1996). The social context for performance is important as well. Caldwell (2002) found that subordinate olive baboons performed poorly when in the presence of dominant individuals.

3. The necessity of observation for producing the copy

This criterion is important in order to preclude the possibility that the subject is merely producing a well known behaviour in its repertoire, which would imply social influence of the kind found in Level 1 and Level 2. It also stresses the need to eliminate explanation of trial and error learning. This will further be dealt with in Chapter 2 while discussing empirical data from social learning studies in primates.

4. **Intention to imitate**

This condition is the most problematic to apply to the study of imitation with subjects without language, especially as regards free observation and anecdotal reports, since it is almost impossible to infer the intention to imitate merely from the behaviour of an animal. An example of such a problematic interpretation can be found in Breuggeman (1973), who described a young female rhesus monkey that carried a coconut shell the exact way her mother carried her infant, and suggested that the young monkey was intending to imitate her mother.

This type of example highlights the need for an experimental paradigm designed to pinpoint intentionality to imitate directly. One key feature which should be included in such a paradigm is *persistence*. Persistence is one of the criteria put forward by Bates *et al.* (1979) to identify intentional communication in infants. It would be worthwhile to test this operationally with non-human primates in a social learning context.

5. **Novelty**

As early as 1937, Spence argued that imitation through observation can only be considered to have taken place in the case of novel behaviour. He claimed that the behaviour observed must be novel, sufficiently complex, and that the observer has not had an opportunity to practice the behaviour.

Want & Harris (2002) attempted to broaden the range for novelty, and suggested that the task should be novel in terms of action, affordance and goal (p. 6).

More flexible definitions allow the action to be either novel or an "… *improbable* act or utterance, or some act for which there is clearly no instinctive tendency" (Thorpe, 1956 pp. 122) or not part of the animal's repertoire (Clayton, 1978).

Others claim that a "novel" behaviour does not necessarily have to be *totally* novel. It is sufficient for part of the behaviour to be novel; for example acting in a familiar way in a new location or on novel stimuli (Zentall, 2001), or a new combination of activities (Watson, 1914).

Novelty is an elusive concept, since any action an animal is able to perform has most likely been performed in some sense in its past (Mikolski, 1999; Whiten & Custance, 1996). Laland & Bateson (2001) suggest more lenient criteria and claim that novelty can be considered even when the behaviour is common but used in an "unfamiliar context" (p. 210). Thus, even when acts already in the observer's repertoire are combined with each other or with an environmental interface, this can still be seen as imitation (Heyes & Ray 2000; Whiten & Custance, 1996).

What is the minimum component for novelty? Is changing the orientation towards a stimulus as a result of observation enough to be considered novelty? Heyes (1995) claims it is. Others (e.g. Byrne & Tomasello, 1995) do not see this as sufficient.

One operational way to achieve novelty in experimental investigations is by using arbitrary acts, which are not necessary for solving the task used in the experiment; another may be by using uncommon gestures.

Mechanisms underlying imitation

Why is imitation so scarce in the animal literature? What makes it so difficult to achieve? Two suggestions have been put forward by researchers to explain the complexity of imitation:

1. There is need for high cognitive computation abilities in order to transform visual information into the matching motor acts (Bruner, 1972; Whiten & Ham, 1992; Heyes, 1993).
2. There is need for mental abilities to represent the intention of the model as it is manifested in his/her behaviour (Piaget 1945).

I shall now elaborate on these suggestions and discuss the necessity of such mechanism for imitation.

Imitation: the complexity of kinesthetic–visual matching

In order to reproduce an action, the imitator has to transform visual input into action using kinesthetic and/or proprioceptive stimulation as feedback (Mitchell, 1994). This is an especially demanding variety of visual-tactile cross-modal performance (Heyes, 1993) especially when the imitator cannot see his own action, thus not having visual feedback for his acts (e.g. when imitating facial expressions or using body parts which cannot be seen).

Heyes & Ray (2000) rank all actions on a continuum of perceptual opacity, starting from the most opaque actions to the most perceptible behaviours. The less opaque behaviours are easier to replicate (Zentall, 2001), such as vocal sounds in which the observer has to match his own sounds that sound (almost) the same as a memorized template of the sound he heard. In the same vein, actions on stimuli, which are more visible than body gestures, should be easier to imitate. However, even when movements can be seen, there is still need for a transformation from how the behaviour looks on the model to how it feels when acted by the observer, since additional factors may be involved such as when observer and model are standing opposite to each other and a transformation of the actions has to be made.

Such visual - kinesthetic matching is also the basis for mirror self -recognition, in which the subject can translate visual information into haptic information and understand that what s/he sees in the mirror is similar to what s/he feels (e.g. Guillaume 1926/1971; Parker, 1991; Mitchell, 1992). Mirror self- recognition has only been found in humans, great apes and perhaps dolphins (Gallup, 1970, 1985; Lewis & Brooks-Gunn, 1979; Anderson, 1984a, b, Patterson & Cohn, 1994; Marten & Psarakos, 1994) and mainly these species have been shown to imitate (Mitchell, 1987; Visalberghi & Fragaszy, 1990a; Whiten & Ham, 1992). It was thought at one time that rats could challenge this assumption as Heyes (1993) claimed to have shown imitation in this species yet rats do not evidence mirror self -recognition. However, further studies showed that the rats in Heyes's (1993) experiment were not imitating but rather responding according to the odour on the rod they were moving (Mitchell, Heyes & Gardner, 1999). Studies with birds (e.g. pigeons Zentall, Sutton & Sherburne, 1996; quails Akins & Zentall, 1996; starlings Campbell *et al.* 1999) have also claimed to show imitation without demonstrating self-recognition, thus posing a problem for the theory (although Epstein *et al.* (1981) showed that through training pigeons could be brought to recognize dots on their body by using a mirror, but later experiments failed to replicate these results, Thompson & Contie, 1994). *Callithricidae* are another exception: it has been claimed (Bugnyar & Huber, 1997; Voelkl & Huber, 2000) that marmosets can imitate, and it has been found that a related species, cotton top tamarins, demonstrate mirror self-recognition (Hauser *et al.* 1995). However, this evidence is problematic. Some researchers characterized two of the tamarins' actions toward a mirror as looking at their body parts, which are not visible without a mirror, or wiping off a mark near their face while looking in the mirror (Hauser *et al.* 1995). However, there was no baseline for this behaviour before placing the mirror, thus alternative interpretations are possible (Anderson & Gallup, 1997). Similarly, some potential evidence for action imitation in marmosets (Bugnyar & Huber, 1997) may result from visual-visual matching and/or chance similarities in handedness between the observer and the demonstrator (see Mitchell, 2002), but the evidence is still suggestive.

Support for the assumption of a connection between imitation and self-recognition comes from studies dealing with autistic children, who have difficulties in imitation as well as in mirror self- recognition (Mitchell, 1997). Child development studies suggest that there is a synchrony between the development of self-recognition and generalized bodily imitation (Nielsen, 2001; Baudonnière *et al*. 2002).

A breakthrough as to how visual information may be transformed into action comes from neuroscience where the study of mirror neurons in monkeys suggests that a direct mapping may exist between movements a primate sees and movements performed, in that the same neurons fire when observing an action in a conspecific and when performing the action (Gallese & Goldman, 1998). However, these finding are still not enough to explain how the visual-tactile transformation actually occurs.

Imitation - the ability to represent the intention of the model

Several authors have suggested that for imitation it is not enough for an observer to be able to behave in a way topographically similar to the behaviour he or she observed. More than that is needed for imitation to be feasible. Piaget (1945) suggested that the basis for imitation lies in the ability to take the perspective of the other; to treat others as intentional beings, thus giving their actions extra meaning. This has been echoed also in the primate social-learning literature by Tomasello and colleagues (Tomasello & Call, 1997; Call & Tomasello, 1995; Tomasello *et al*. 1993).

These authors, as well as Povinelli and colleagues (e.g. Povinelli *et al*. 1996), first claimed that no non-human primate could take the perspective of the other or understand its intentions. However, in the last few years more data have been accumulated shedding new light on how primates, and particularly chimpanzees, understand the mental states of the other (Tomasello, Call & Hare, 2003). It was found that at least in competitive situations, chimpanzees can take into account what a conspecific can and cannot see, and represent their intentions (Call *et al*. 2004). Capuchin monkeys also showed a preference to take food, which was hidden from the dominant monkeys. However, the subordinate capuchin did not preferentially approach the hidden food first when given a head start (just like the chimpanzees in Karin-D'Arcy & Povinelli, 2002), suggesting that the capuchins were predicting the dominant's behaviour based on gaze and movement cues but did not appreciate their perspective (Hare *et al*. 2003).

Fidelity of Imitation

Different behaviours may fit the definition of imitation presented above but still show different degrees of resemblance to the model's action. It has been suggested that imitation may best be seen as a continuum of behaviours reflecting the degree of fidelity of copying the model's action (a function also of the information utilized from the model's action) (see Table 1.1).

When only information about the topography of the action is used, such imitation is referred to as *copying* (Galef, 1988), *impersonation* (Tomasello, *et al.* 1993) or *mimicking* (Tomasello, 1996). There are only few valid examples for such imitation; one example comes from Hayes & Hayes (1952), who raised a common chimpanzee named Viki in their home. After intensive training, Viki was able to imitate different actions shown to her after the spoken command "Do this". Taylor & Saayman (1973) described bottlenose dolphins' impersonation of some behaviours of humans and a sea-lion all of which were foreign to the dolphins' natural repertoire.

When information is used about the action and goal of a behaviour – this is referred to as *true imitation* (Thorpe 1956). An example of the difference between imitation and mimicking can be found in Call & Tomasello's (1995) study in which a human-raised orang-utan was trained to mimic different body movements. When the same ape was presented with a goal-orientated tool use problem, he was not able to solve the problem through observation. The authors therefore concluded that this orang-utan was able to mimic but not imitate.

Is Level 3 of social learning more adaptive than Level 2? This might not always be so. First, technically speaking, it is not always easy to differentiate between the two and thus Whiten (2000) suggests "we should be thinking of an imitation/ emulation continuum, rather than a neat dichotomy" (p. 483), since this continuum may be governed by fidelity based on different parameters of the model's action the observer pays attention to and makes use of.

Second, it is not always the case that imitating rather than emulating is the more intelligent, beneficial choice. In some situations, emulation would actually be the better choice. For example, when the mechanism of a behaviour with a tool may not be understood or visible, imitation may be the best choice, whereas when the mechanism can be understood, emulation may be more useful. Thus, emulation may result in more flexible knowledge than imitation (Want & Harris, 2002). The same conclusion was reached by Huber (2002): "We conclude that emulation learning is a very intelligent and creative learning process that, in some circumstances, is a more adaptive strategy than imitative learning" (p. 1).

Although emulation has been used as a "null hypothesis" for detecting imitation in great apes, the ability of non-human apes to emulate has been doubted (Byrne, 2002; Byrne & Russon, 1998).

However, Horner & Whiten (2005) found that when the causal information which was available to a subject was manipulated, chimpanzees showed both emulation and imitation, whereas 3-4 year old children imitated regardless of the causal information they had, thus demonstrating the strong tendency of humans to imitate.

In order to complete the theoretical discussion of social learning, I now return to Figure 1.1., which describes the social learning context, to address additional several points.

1. Background for learning

For learning to take place, there is a need for a facilitating background that includes

a. Motivation – physiological and social, as well as
b. Supportive social conditions – the model and the observer's characteristics.

Motivation

Motivation is important for any type of learning to take place. As in individual learning, physiological states such as hunger, thirst and fear may facilitate or retard social learning.

The importance of reward for social learning has been stressed by several authors (Bandura, 1986; Bruner, 1972; Yando *et al.* 1978) and has been shown in birds (e.g. pigeons, Palameta & Lefebvre, 1985; Japanese quails, Dorrance & Zentall, 2001) and rats (e.g. Heyes *et al.* 1993), as well as in primates (e.g. chimpanzees were able to learn arbitrary gestures through rewards: Custance *et al.* 1995). In some cases, however, the reward had an interfering effect. Whiten (1998b) suggested that seeing the food reward through the Plexiglas of an 'artificial fruit' interfered with the learning of the observer, because less attention was paid to the model's actions.

Social motivation may also play an important role (Tomasello, Savage Rumbaugh & Kruger, 1993), and the social reward in these cases can have a considerable effect. This may be manifested by receiving attention from a caretaker, as in infant mimicry (Myowa-Yamakoshi *et al.* 2004). Matsuzawa *et al.* (2001) and de Waal (2001) claim that in non-human primates as in humans, performing socially-learned behaviours may be strengthened by the need to conform to salient performers.

Model and observer’s characteristics

Learning socially may be more advantageous than individual learning “…when the observer is not proficient, when opportunities for practice are limited, when the costs of errors are high, and when learning by individual experience would slow the process” (Visalberghi & Fragaszy, 1990a, p. 247). Laland & Kendal (2003) add that learning socially is beneficial when competition for resources is high.

However, although learning from the other can in some situations be beneficial, animals do not learn completely indiscriminately. In a social context, the relationship between model and observer, as well as their properties, may play a role in facilitating learning.

Social tolerance between the observer and demonstrator can be crucial for learning to take place (Coussi-Korbel & Fragaszy, 1995; Russon & Galdikas, 1995). Van Schaik has described how social tolerance is important for transmitting technological traditions in apes (van Schaik, 2003; van Schaik *et al.* 1999). Rank and gender of the learner and model can be important in determining the level of tolerance the observer can receive from the model.

Since learning demands attention, memory and perhaps reasoning, the observer has to be mature enough to display the required abilities (Custance *et al.* 1995). On the other hand, field studies have shown that young monkeys are more likely to learn “new tricks”, as young animals are also usually more tolerated around adults and thus have better opportunities to observe and learn (Perry & Manson, 2003). Thus, there may be an optimal time window in the life of an animal, which better facilitates social learning.

Although it can be important that the model acts competently, studies have shown that viewing an unskilful model can result in better learning (e.g. Vanayan *et* *al*. 1985 for pigeons; Templeton, 1998 for starlings). This may be due to the emphasis on response–reinforcement contingencies.

Recently, capuchin monkeys have been seen to make use of conspecifics' mistakes in order to learn how to open a box (Kuroshima, 2008). But young chimpanzees, as well as 3-4 year old children, did not benefit from seeing others' mistakes while learning a difficult trap-tube task (Horner & Whiten, 2007).

2. Type of behaviour observed

As described in Figure 1.1, the type and complexity of the action observed may play a significant role in the process of social learning.

Action versus a sequence of actions

The behaviour observed may be a single action or a sequence of actions. Is there a difference in socially learning a sequence of actions rather than a single action?

Byrne (Byrne, 1995; Byrne & Russon, 1998) dealt with this question and suggested a *program level of imitation*, in which a sequence of action is learnt, but the actions building the sequence may not be a perfect copy and can be learnt through trial and error. Thus, the observer copies "... the structural organization of a complex process (including the sequence of stages, subroutine structure, and bimanual co - ordination) by observation of the behaviour of another individual, while furnishing the exact details of actions by individual learning" (Byrne & Russon, 1998, p. 676) or by other social processes, such as emulation. In this sense imitation is one part of the cognitive mechanisms that deal with hierarchical representations of behaviour.

Byrne found support for this assumption in the way wild mountain gorillas (*gorilla gorilla beringei*) learn complex leaf eating techniques. Hundreds of hours of focal observations of these apes gathering and preparing plant food have shown that these gorillas use complex techniques, which are divided into different levels. But the general structure of the leaf gathering process is highly standardized, although there are individual variations in the more detailed movements (Byrne & Byrne, 1991, 1993). The inherent improbability of such complex sequences being achieved through individual learning has been used to claim that gorillas imitate at the 'program-level' (Byrne, 1994; Byrne & Russon, 1998).

The idea that behaviour is hierarchically organized (Lashley, 1951) implies that, in principle, imitation can be used at any level of the hierarchy and, depending at what level it is used, we should find different patterns of behaviour.

In order to copy the logical structure of a behaviour there is no need to understand the intentions of the model. It does, however, put a burden on memory span and requires understanding that the sub-goal order is important.

Nevertheless, even when a sequence of behaviours is learned socially, it may not be achieved by imitation after all, and just like action learning, could be learned by emulation (Whiten, 1996; Byrne, 1995).

To conclude

The social context has a complex multilevel influence on the acquisition of behaviour by an individual. Inference of the process underlying a behaviour just from observing its production is not possible. There is a need to take into account the different factors described in this chapter when addressing potential cases of social learning in animals, such as those which will be described in the next chapter.

Chapter 2

DO “CEBUS SEE CEBUS DO”?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My eyesight was getting worse, but thanks to my new glasses, I can play "Monkey see, Monkey do" again...

In this chapter I shall portray the characteristics of *Cebus* monkeys, which make them good candidates for studying social learning and imitation. I will then proceed to describe the evidence from the field which suggest the existence of social learning in this species and discuss these finding as related to traditions and culture. Next, I will review what laboratory experiments can tell us about the mechanisms underlying social learning in capuchin monkeys. Last, I will deal with the issue of enculturation and its influence on the ability to imitate, as some of the subjects used in this thesis can be regarded as enculturated capuchin monkeys.

I . Capuchin monkeys - what makes them potential social learners?

Rusty, an adult *Cebus apella* living in the Israeli Primate Sanctuary, loves to make "mud cakes". He fills a small bucket with earth then takes it to the tap to add water. While kneading the "dough" he sometimes adds more water or a handful of earth until the texture is satisfactory. Eventually, he turns the bucket upside down to take out the cake.

Such complex behaviour has prompted human interest in *Cebus* and has often raised the question of whether such behaviour is acquired socially or learned individually by each monkey. These small South American monkeys acquired their name “capuchin” from the brown hair on the top of their head, which resembles the "capuche", the hood worn by Franciscan monks. *Cebus* are widely spread in South

America from Honduras to Argentina, with *Cebus apella* being the most widespread species, ranging from Colombia to Argentina (Kinzey, 1997).

1. Tool use

Capuchin monkeys' varied diet, which includes plants and prey, together with their highly manipulative foraging strategies (Izawa, 1979), have enabled them to live in a variety of habitats (Robinson & Janson, 1987) as well as survive in a habitat where fruit is relatively scarce (Fernaneds, 1991; Hernandez-Camacho & Cooper, 1976). It is in such situations that we would expect to find capuchins employing their tool use skills to find food. A recent report, which strengthens this claim, comes from Moura & Lee (2004), who describe how capuchin monkeys in Brazil use stones as spades to dig up tubers as well as hammers to crack open nuts. Nut-cracking behaviour is seen mainly in areas where the monkeys are more terrestrial, perhaps because in order to do this action efficiently, suitable hard objects are needed to serve as a hammer and an anvil.

Cebus' complex foraging ability, as seen in tool use behaviour, may be partially explained by their large brain in relation to their body size (Jerison, 1973; Stephan *et al.* 1988). McGrew (1993) argued that primates feeding on animal protein were more likely to use tools. However, the fact that capuchin monkeys have often been seen feeding on meat, but more rarely use tools in their natural environment, puts this theory in some doubt (Fragaszy *et al.* 2004).

Capuchin tool use in captivity has been characterized by its flexibility: monkeys can use one type of tool for different purposes as well as using different tools for a specific purpose (Visalberghi, 1993a). A vivid example of the creative tool use of capuchin monkeys is found in Warden, Koch & Fjeld (1940), who describe one of their subjects using tools to rake in hard- to- reach food items. On one occasion the monkey even used an albino rat for this purpose. Parker & Gibson (1977) claim that capuchin monkeys show an intelligent tool using ability characteristic of the fifth sub-stage of the sensorimotor period (Piaget, 1952) (See Chapter 4 of this thesis for a more detailed descriptions of capuchin monkeys' tool use repertoire).

2. *Cebus* cognition

2a. Cognitive basis of tool use behaviour

Object manipulation and object-object relations are possible due to the development of cognitive abilities (Vauclair, 1984). Yet, the question may be asked as to what *Cebus* monkeys understand about the relation between the tool and the task. Do they have a mental representation of the task? This has great relevance to the study of social learning in this species, as it taps the question of which information a capuchin can make use of while observing a model. More specifically, can they utilize information based on the causal relation between the action of the model and the tools the model uses? Most studies claim that capuchin monkeys learn how to use tools through trial and error (Anderson, 1990; Visalberghi, 1987). Others, e.g. Parker & Poti (1990), conclude that *Cebus* monkeys are capable of perceiving means-end relations as manifested in their success in using a stick as a rake.

Tool choice

Choosing the right tool for a task could indicate that these monkeys have a representation of the task and an understanding of its components. However, studies have not been conclusive on the ability of *Cebus* monkeys to choose a tool correctly. Several authors report result of experiments in which their subjects showed a definite preference towards choosing the right tool for the task (Anderson & Henneman, 1994; Antinucci & Visalberghi, 1986; Chevalier-Skolnikoff, 1989; Westergaard & Fragaszy; 1987a; Westergaard & Suomi 1993a), e.g. choosing a stone as a hammer more often than a wooden block or plastic container.

The use of a 'tool set'- two or more different tools used one after the other to obtain a goal (Brewer & McGrew, 1990) - can also indicate an understanding of which tool is more suitable for which purpose. Several studies have described capuchin monkeys using tool sets (Anderson & Henneman,1994; Westergaard & Suomi, 1993a; Westergaard *et al.* 1997), e.g. using a stone to crack open a nut and then a stick as a probing tool to extract the inner meat.

Capuchin monkeys in nature have been seen to descend to the ground and carry palm seeds to a suitable anvil in order to crack them open (Fragaszy *et al.* in Fragaszy *et al.* 2004; Jalles-Filho *et al.* 2001; Ottoni & Mannu, 2001; Oxford, 2003). This carrying behaviour may also imply that the monkeys understand the necessary requirements for successful nut cracking.

Visalberghi (1990) argues that, as opposed to apes, capuchin monkeys are not able to understand the requirements of a problem. Visalberghi and colleagues have shown, through analyzing the type of mistakes the monkeys made when trying to solve a probing task with a stick in a series of experiments, that the capuchin monkeys in their studies were unable to choose the right tool for the task (Visalberghi & Trinca, 1989). Their results indicate that *Cebus* tool use behaviour may be successful without demanding understanding of all its physical properties such as the shape or size of tool, or the effect of a well-shaped trap (Visalberghi & Limongelli, 1994).

A later experiment by Fujita *et al.* (2003) strengthens the claim that capuchin monkeys have only a basic understanding of causality, similar to that found in cotton-top tamarins in a similar study using an apparatus with traps (Hauser, 1997)**.**

2b. Non tool–use tasks

Testing capuchin monkeys on tasks not relying on tool use has shown that on several tests of learning abilities capuchins do not always score higher than other primates (see Anderson, 1996 for examples). However in tasks relying on sensorimotor intelligence, capuchins (like great apes) surpass other monkeys; this has been shown, for example, for the object concept (Schino *et al.* 1990; Mathieu *et al.* 1976) and causality problems (Natale, 1989).

3. Social structure and behaviour

Not only outstanding tool use ability characterizes this species. Capuchin monkeys differ from other platyrrhine primates in their social structure and behaviour, which is said to resemble Old World cercopithecine monkeys.

Cebus apella live in groups composed of 7-30 monkeys. One male and one female usually dominate the group (Welker, 1992) and the alpha female is dominant over all members of the group except the alpha male. There are strong relationships among males in the group in captivity (Fragaszy *et al*. 2004, p. 213) and low rates of aggression have been noted between males in wild groups (e.g. Izawa, 1980; van Schaik & van Noordwijk, 1989). Kinship and friendship relations are stable over years, starting even from infancy, and mothers and their offspring maintain strong ties even when they grow up (Welker, 1992; personal unpublished data). Capuchins are very attentive to conspecifics' behaviour (Fragaszy & Adams-Curtis, 1987).

Youngsters are attentive to older monkeys, while the adults are tolerant of the infants and youngsters (Fragaszy & Adams-Curtis 1991; Ottoni & Mannu, 2001).

Some researchers argue that social problems "are the driving force behind primate cognitive sophistication" (Byrne & Whiten, 1988; de Waal, 1989). In this domain as well, there is evidence of complex *Cebus* behaviour. Mendres & de Waal (2000) found that pairs of capuchin monkeys showed some aspects of cooperation on food-retrieving tasks such as glancing at each other in a similar way *Cebus apella* monkeys glance to recruit help in agonistic situations (Freese & Oppenheimer, 1981). These findings contrast with the results reported by Chalmeau *et al.* (1997) and Visalberghi *et al.* (2000), who did not find such cooperation in their subjects. This may be a result of the different type of tasks used in these studies (Mendres & de Waal, 2000). Such basic cooperation may be related to a high level of social tolerance, not only towards young members of the group but also to other adults, as has been shown also in the acceptance of food sharing. Other studies have documented food sharing and tool exchange, again somewhat resembling observations of chimpanzees (de Waal *et al.* 1993; Savage Rumbaugh *et al.* 1978; Westergaard & Suomi, 1996 cited in Westergaard *et al.* 1997).

Conclusions

The background for studying social learning in *Cebus* has been set out in this section. Social learning requires the exploitation of other's expertise. In order for this to happen, the social structure of the group must facilitate close probing into conspecifics' behaviour or even their minds. Capuchin monkeys are very social and tolerant, rendering social observation of a conspecific at work possible. Reader (2003) found a correlation between executive brain size, innovation, tool use and social learning, factors which are applicable to capuchin monkeys, as described above. Can they, then, learn to use tools as well as other behaviours, through observation? Bearing this in mind I shall next discuss existing data on the ability of capuchin monkeys to learn in this way in nature as well as in laboratory experiments.

II. Evidence for social learning in capuchin monkeys

a. Field studies - Do capuchin communities have cultures?

The debate over primate culture has gained momentum in recent years with descriptions of distinct behaviours of different populations of wild chimpanzees (Whiten *et al.* 1999), orang-utans (van Schaik, 2003) and capuchins (Ottoni & Mannu, 2001; Panger *et al.* 2002; Perry *et al.* 2003; Perry & Manson, 2003).

Not all authors are happy to use the word "culture" in the context of non human animals and prefer to reserve this term to describe human culture, stressing its complex aggregate of art, rules, fashions, customs, technology and so on, mediated by language, teaching and imitation. Further, human culture is based on a ratchet effect, in which new traditions are built on older ones and the modifications of behaviours accumulate over time (Galef, 1992; Levinson, 2006; Tomasello, 1990, 1994; Tomasello *et al.* 1993).

Thus, terms such as "protoculture" and "preculture" (e.g. Count, 1973; Kawai, 1965) were used in the past to differentiate between human and non-human culture. In current days, the term "tradition" is often preferred to describe a behaviour found in one group of animals but not in another, which has been transmitted socially and not caused by genetic or environmental variability between groups (Heyes, 1993). Such behaviour must also be persistent over generations or at least long- lasting (Nishida, 1987; Perry & Manson, 2003).

This definition of tradition does not say much about the mechanism of the social transmission, recognizing that several mechanisms, alone or together, can sustain a tradition.

Such social information can be transmitted in two directions (Laland, Richerson, & Boyd 1993): horizontal transmission between monkeys of the same age group, and vertical transmission, from older to younger monkeys, typically parents to offspring. This latter path, according to Laland *et al*., results in stable traditions.

Whiten (in press) and Whiten & van Schaik (2007) support a less strict account of culture and suggests that the term culture can be attributed to non-human animals if they exhibit multiple traditions found in different domains of their life.

Identifying traditions and culture

The difficulty of collecting all the relevant data in nature imposes constraints on the possibility of determining whether a behaviour has been socially transmitted, or is merely a result of ecological and or genetic factors. Several theoreticians have proposed ways to overcome this problem.

a. Longitudinal observations of a population. This may require more luck than careful planning. Sapolsky (2006) was lucky to witness a change in social behaviour in the level of aggression in a troop of olive baboons that took place after the death of the high ranking aggressive males and continued after the original males had left and been replaced by others. Such a change could only be transmitted socially.

It is not considered to be ethically appropriate to intervene in the life of groups in nature, to relocate monkeys from one group to the other to see whether they bring their traditions to their new group or conform to new ones. The closest possibility is to bring in an unknown food item to a group, as was done by Matsuzawa with chimpanzees (Matsuzawa, 1996).

However, as Tomasello claims "it is clear that simple observation of animals in their natural habitats is not sufficient to determine the ways in which various behaviours may be acquired and transmitted" (1990 p. 282); see also Galef (1976, 1982, 1988).

b. Group contrast model of traditions or "regional contrast" or "methods of eliminations". These are different terms for an approach claiming that finding different behaviours in two groups of the same species, which are genetically similar and living in similar ecological environments, may imply that the behaviours were transmitted socially among the group members. This approach does not necessarily prove social learning but does eliminate other influences. It is used mainly in primatology where "subjects are too long lived to adopt an ontogenetic, or process, approach" (McGrew, 1998).

This approach has been criticized on several grounds:

1. It does not identify false negatives (although ecological and genetic factors may differ, social factors may still be involved) and false positives (perhaps other, asocial factors are involved) (Fragaszy & Perry, 2003).
2. It is very difficult to prove identical environments and identical genetics (Fragaszy & Perry, 2003).

3. Genetics may play a larger role than first thought as some of the identified behaviours for chimpanzees and orang-utans have been found in different subspecies (Laland & Janik, 2006).

Therefore, Fragaszy & Perry (2003) claim it is only possible to say that social factors *aided* the behaviour.

c. The Cue Reliability Approach - CRA (Dewar, 2003). Animals may be using social and non-social cues to make decisions. Therefore, it is possible to state that a behaviour has been transmitted socially only if we can show that non-social, reliable cues were not available and that the social cue reliability was higher than the reliability threshold for that individual. The CRA is a highly theoretical proposal and implementing it is very problematic. As Dewar herself mentions, it is not always obvious what the are variables in the decision making problem facing the animals. "Some researchers have shown that animals do not always exploit environmental and social cues in ways that seem consistent with optimality models, e.g. Fragaszy & Visalberghi, 1996" (Dewar, 2003 p. 140).

The CRA is restricted to behaviours that have an adaptive consequence. It is also not useful in situations where it is not possible to estimate the reliability threshold for the animal.

Nevertheless, this theory may predict when a behaviour will be learnt socially, taking into account factors such as age, sex, rank, etc.

In what follows I shall review the data available regarding behaviours in monkey societies in the wild, which have been interpreted as traditions, through the prism of three questions.

1. Does the behaviour fit the definition of tradition stated above?
2. Is it possible to determine the social mechanism involved in the transmission of the behaviour?
3. Does the specific society of monkeys have other traditions to qualify them as having culture?

Tradition in monkey societies

As early as 1952, Imanishi suggested that many groups of primates have their own culture. By this, he meant behaviours acquired through social learning. As a result, Imanishi and his Japanese colleagues began intensive research on Japanese macaques (*Macaca fuscata*) (1952, 1957a, 1957b, 1960), resulting in one of the classic descriptions of tradition in non-human animals.

On Koshima Island, a young female macaque, Imo, began washing sweet potatoes in water instead of just cleaning the sand off them with her hands, as the rest of the troop did. In subsequent years this behaviour spread to other members of the troop.

It was first proposed (Kawamura, 1954, cited in Itani & Nishimura, 1973) that imitation was the mechanism through which the behaviour spread. The potato-washing behaviour was thought to be strong evidence for the assumption that traditions are transmitted through imitation. This was inferred from the fact that with time the number of monkeys showing this behaviour increased.

However, with the development of social learning research and theorizing, many questions have been raised and other explanations have been put forward:

1. The importance of social cues for the spread of the washing behaviour was questioned since it was found that macaques as well as capuchin monkeys spontaneously wash food without a need for social learning (Visalberghi & Fragaszy, 1990b). When water and sandy fruits are available, capuchins and crab-eating macaque start washing objects in a few hours. Furthermore, Visalberghi (1994) found that seeing a model wash fruit (termed live information) does not increase the likelihood of learning the behaviour more than when seeing a piece of fruit in the water (still information). However, although imitation is not necessary for the acquisition of this behaviour, the presence of food washers was important for its spread because it made the conditions suitable for learning by familiarizing the monkeys with water and making the clean food remains accessible.
2. Learning could have developed individually, because when provisioning the monkeys with potatoes, food was thrown in or near water, encouraging the monkeys to perform this behaviour (Green, 1975 cited in Tomasello & Call, 1997). Further, washing potatoes might simply have been a generalization of cleaning and brushing sand off food items seen in this group (Tomasello & Call, 1997).
3. The fact that the behaviour spread to kin and play-mates was first thought to be a proof of imitation. However, stimulus enhancement too can explain the direction of spread from Imo to her relatives and friends. This seems logical since in macaque species, relatives and peers spend time together and thus have suitable opportunities and situations for learning from each other. In the same way, youngsters who were

next to their washing mothers could have learnt this behaviour not necessarily through imitation but by individual learning using the cues the mothers had left around – such as finding potatoes in the water (Galef, 1992; Matsuzawa, 2003; Whiten & Ham, 1992).

4. A further problem in attributing the learning to imitation is the slow rate of the spread of the behaviour (Galef, 1992). If imitation was the underlying cognitive mechanism for learning this behaviour, it should have been a much faster process, as each monkey that mastered the new behaviour could at once serve as an additional model. (Galef, 1990; Boyd & Richerson, 1985). But this did not happen and the rate of new learners decreased over the years.

Laland & Kendal (2003) argue that such expectations for a high rate of spread do not take into consideration individual differences in learning, which could also be expected in social learning. Social learning as well may show different learning curves, which are due to individual characteristics such as age, gender, social rank, and competition for resources (Laland *et al.* 1996, Lefebvre & Giraldeau, 1996), as well as the differences in relevance of a particular behaviour to different members of the group and group size (Huffman & Hirata, 2003).

I have described at length the different angles from which this behaviour has been analyzed as it is a good example of how a phenomenon should be approached and all possible explanations exploited. The study of the Koshima Japanese macaque had an enormous impact on the notion of traditions. Since then, many more behaviours have been observed as traditions in Japanese macaques, such as wheat cleaning through a behaviour known as "placer mining" in which the monkeys throw a handful of wheat and sand into the water and gather the clean wheat that floats to the surface, fish eating (Watanabe, 1989), hot spring bathing (Suzuki, 1965), candy eating (Itani, 1965), as well as pool making.

All these traditions have adaptive functions, which may explain why they have been sustained, although the explanation of perhaps being individually learned could also be warranted. However, other behaviours observed in these monkeys, such as stone handling (Huffman, 1984) and grooming techniques (Tanaka, 1995), have no apparent adaptive function, but still spread in provisioned groups. Tanaka (1998) concluded that only imitative processes could explain how the changes in grooming technique were adopted by kin. For a description of many more of the traditions of the Japanese macaque see McGrew (1998).

I now return to the three questions enumerated at the beginning of this section and recast them in terms of the Japanese macaque:

a. Do the behaviours of the Japanese macaque qualify as traditions? These behaviours fit the different requirements even though some behaviours could have theoretically been learned individually.

b. What mechanism underlies the behaviours? It is not possible to determine this from the data.

c. Is it culture? As the traditions of Japanese macaque are so rich and embodied in so many different domains in the macaque life, the answer to this question is in the affirmative.

Japanese macaques have been studied intensely for years and this is perhaps why most information about traditions in monkeys has been found in this species. It is logical to presume that at least some other species of macaque monkeys would show traditions too, considering that they share many similar properties of social organization (see Table 2.1 for a summary of suggested traditions in populations of monkeys in nature).

Table 2.1 Behaviours observed in populations of monkeys in nature claimed to be examples of tradition. This table does not include research with the Japanese macaque and capuchin monkeys which are dealt with separately.

Species	**Reference**	**Behaviour**	**Path Of Diffusion**	**Limitation**	**Is It A Tradition?**
Macaca fascicularis	Wheatley (1988)	Food washing, rubbing and peeling	Un known	1,3	Not sufficient information
	Chiang, (1967)	Opening oysters with stones, washing food	Un known	1	Not sufficient information
Papio ursinus	Camberfort (1981	Knowledge about location of new food items	All learnt from one juvenile	2,3	+
Papio anubis	Strum (1975)	Specific hunting method and meat sharing		1	Not sufficient information
Cercopithecus aethiops	Camberfort (1981)	Knowledge about location of new food items	Several, not much attention to conspecifics	2,3	+ Less convincing than with baboons
	Hauser (1988)	Acacia pod dipping	among adults, mother to offspring,	1,3	Not sufficient information

1. No research done on neighbouring groups - needed to eliminate ecological factors.
2. McGrew (1992) added the criterion of "naturalness" to the six criteria already proposed by McGrew & Tutin (1978) as an operational definition of culture. By 'naturalness', McGrew means that the behaviour is not affected by direct human influence (the other criteria are innovation, dissemination, standardization, durability, tradition, non-subsistence).
3. No information about the duration of this behaviour was obtained for the group.

It is very difficult to know how many useful behaviours are not socially transmitted in the wild. For example, an adaptive behaviour of rubbing spines off caterpillars in squirrel monkeys (*Saimiri oerstedii*) did not spread in the group (Boinski & Fragaszy, 1989). Kummer & Goodall, (1985) concluded that “of the many [innovative] behaviours observed, only a few will be passed on to other individuals, and seldom will they spread through the whole troop” (p.213). It is just as interesting a question to find out why such behaviours are not transmitted socially to other members of the group, as which behaviours are transmitted.

It is evident from Table 2.1. how little research has been carried out in nature to examine traditions in monkey populations (except for the Japanese macaque studies). The accumulation of information about capuchin traditions in nature, which I discuss now, is therefore impressive and should serve as a framework for studying traditions in other species of monkeys as well.

Traditions in capuchin monkeys

In La Macarena national park, Colombia, the brown capuchins (*Cebus apella*) employ complex techniques of exploiting palm nuts (*Astocaryum chambira)* according to the ripeness of the palm (Izawa & Mizuno 1977; at Raleighvallen, Izawa 1979; Struhsaker & Leland, 1977). The monkeys penetrate the nut with their canines and drink the juice through the hole they have made, then they pound the nut on guadua bamboo and eat the coco, which comes out of it.

Other complex foraging techniques have been shown in other sites as well (e.g. Izawa 1978, 1979 catching frogs and termites). Boinski *et al*. (2003) claim that “In many respects the manipulative abilities are ... comparable to those described for wild chimpanzees. Only the young show different inefficiencies in this behaviour, the older show persistence and very aimed smooth actions” (p. 367).

Nishida (1987) suggested that this very sophisticated food processing behaviour of capuchin monkeys might be a result of cultural learning. “*Cebus* monkeys, for example, can obtain important nutrients (palm nuts, frogs and insects) that could not easily be obtained without apparently cultural knowledge and techniques” (Nishida, 1987, p. 465).

Yet in order to make such an assumption there is a need to compare behaviours with other groups of capuchin monkeys facing the same challenging food items and see the techniques these monkeys use. Furthermore, there is a need to observe the way infants and youngsters acquire these food-processing techniques.

This challenge was taken up by Chapman & Fedigan (1990), Panger *et al.* (2002), Boinski *et al.* (2003) Perry *et al.* (2003) and Rose *et al.* (2003), who compared different behaviours in different groups of capuchin monkeys.

Table 2.2 summarizes behaviours considered to be traditions in capuchin monkeys. Such behaviours include food processing techniques, predator avoidance, hunting techniques and social conventions

Panger *et al.* (2002) carried out the first systematic comparison of food processing behaviours in white-faced capuchins (*Cebus capucinus*) found in three long-term study sites, which were similar ecologically. They listed the food items processed in the different sites and then assessed whether there was a difference in the processing methods. Six techniques, which seemed to differ, were later more thoroughly examined. In addition, the authors calculated the correlation between proximity scores and individuals who displayed the same techniques, finding statistically higher scores for such dyads than other dyads in the group. Just as with findings of ape cultures, some foraging techniques were found at one site but not at another. On a small scale these results resemble the findings on traditions in chimpanzees (Whiten *et al.* 1999). The resemblances between the two taxa maybe due to "[similar] extractive foraging, dexterous manipulation, tolerant gregariousness, long life-history variables, large brain size relative to body size, and/or an omnivorous diet" (Panger *et al.* 2002, p. 62).

Panger *et al.* did not try to determine what social learning mechanism was responsible for the differences found, as this was not possible to infer from the data available.

Table 2.2 Behaviours regarded as tradition in wild populations of *Cebus capucinus* [1, 2,5,6,7] and *Cebus apella*[3,4]

Domain	Behaviour Reference	Groups	Ecological Explanation?	Duration	Individual Learning?	Direction Of Spread
Food processing techniques	Pounding or scrubbing of 16 different food species [1]	10	Ruled out	?		?
	Different ratio of fruit to insect to meat in diet [2]	3	Ruled out		Cannot be ruled out	
	Leaf wrapping, fulcrum use, ant following [1]	3	Ruled out	?		?
	Substrate use Tool use [3]	4	Needs further exploring			
	Rocks as hammers [4]	1	Ruled out	?	No	?
Hunting behaviour	Neck bite to kill Squirrels [5+6]	1	Ruled out	1 year		?
Predator avoidance	Behaviour towards Indigo snakes [6]	1	Ruled out	1 year		?
Social conventions	Hand sniffing [7]	5	Ruled out	7 years	No	Among adults
	Appendage sucking[7]	3	Ruled out	6 month	No	?
	Finger-in-mouth game[7]	1	Ruled out	10 years	No	Immature to adult kin; among adults
	Hair game[7]	1	Ruled out	10 years	No	Immature to adult kin; among adults
	Toy game[7]	2	Ruled out	9 years	No	Among adults; adult to young
Other	Grooming of spider monkeys[7]	2	Ruled out	4 years	Cannot be ruled out	?

1= Panger *et al.* 2002 2= Chapman & Fedigan, 1990 3= Boinski *et al.* 2003 4= Ottoni & Mannu, 2001 5= Perry *et al.* 2003, 6= Rose *et al.* 2003 7 = Perry *et al.* 2003

Boinski *et al.* (2003) tested two categories, substrate use and tool use, in order to assess whether these behaviours could be described as a tradition. They found that there was hardly any variation between the skilful monkeys' actions. The authors are confident that this behaviour can be called “tradition”. They describe a life cycle in which young capuchins are tolerated by adults while they process fruits through tool or object use. Once they have matured and move to the periphery they have to find new ways to process less available foods and when they later get a position in the centre they can in turn act as models for the young (Boinski relies on the notion that good foragers have a higher status as adults and thus these inventors will find their way to the centre). However, to identify tradition, further studies of other sites still need to be done, in order to test whether the different techniques used for different husked fruits cannot solely be ascribed to the different fruits' morphology, or the abundance of the fruit.

From their results, Panger *et al.* (2000) and Boinski *et al.* (2003) were unable to determine the mechanism underlying the transmission of the behaviours they observed. The most they could say at this stage is that "Social facilitation may be important in sustaining the traditions of substrate use among brown capuchins at Raleighvallen" (Boinski *et al.* 2003 p. 380).

Hunting behaviour and predator avoidance behaviour were also seen to differ between sites even though the same predators were present in the different sites.

Perry *et al.* (2003) found that the capuchin monkeys spent a long time mobbing snakes and emitting alarm calls, even after they no longer presented a danger. The authors suggested this may be a way the adults teach the juveniles. The adults spent more time engaging in this behaviour than needed to help the juveniles learn. This is only anecdotal and more data are needed. Nevertheless, teaching is an important factor in the cultural transmission of behaviour in humans and thus collecting information about ways in which monkeys actively enable learning of others is important to our understanding of how behaviours spread in primate groups.

Social influences on behaviour are even more convincing in the case of social conventions, since, unlike tool use behaviours, where monkeys can find used tools and learn the behaviour by themselves, social conventions cannot be discovered individually. There are relatively few studies in the literature dealing with diffusion of social conventions in primates, which is odd as one might expect to find more in this domain given that primates live in complex societies. Studies on chimpanzees, which have dealt with this subject, describe behaviours such as scratching, hand clasp grooming, and leaf grooming (Boesch 1996; McGrew & Tutin 1978; Whiten *et al.* 1999).

Perry and colleagues studied social conventions in white-faced capuchin monkeys and found behaviours such as hand sniffing, sucking partner’s body parts and different social games (Perry *et al.* 2003). They defined social conventions as “dyadic social behaviours of a communicative nature that are shared among members of particular social network” (Perry *et al* .2003, p. 397). Why should monkeys take part in such seemingly bizarre behaviours, especially as they seem very uncomfortable? Perry *et al.* claim that these behaviours may serve different functions but they all have some elements in common: they are seen between dyads, separated from the group, performing the behaviours in a very relaxed way, sometimes for a very long time (an hour or more) and as mentioned above, can be uncomfortable and even dangerous, e.g. poking a finger into the side of the eye of a conspecific.

These behaviours may be a way of testing the strength of bonds between dyads (Zahavi, 1977). Their importance, as a ritual, is not the action itself but more the cooperation, the joint intense focus on the behaviour, which emphasizes to the partners that they can rely on each other (Perry *et al*. 2003). Perry *et al*. suggest that these conventions are transmitted through ontogenetic ritualization. “In ontogenetic ritualization a communicatory signal is created by two individuals shaping one another's behaviour in repeated instances of a social interaction” (Boesch & Tomasello, 1998).

Whiten (2002) suggests that behaviours such as those seen in these social conventions may be based on imitation, as the monkey that is to reciprocate to a gesture, such as hand sniffing or body parts sucking, has to acquire the “idea” to do so from the partner.

The careful analysis of data carried out by the authors above authorizes the claim that most of the behaviours qualify as traditions. The rich array of traditions described for capuchin monkeys does qualify it as culture.

The findings, however, cannot explain what social mechanism is involved in the spread of these traditions. In fact, the specific mechanism is irrelevant to determining whether capuchin monkeys have traditions or not. However, some claim it is important if we want to ascribe culture to them: “…individual learning supplemented by emulation learning and ritualization, are sufficient to create and maintain their species typical cultural activities but they are not sufficient to create human-like cultural activities displaying the ratchet effect and cumulative cultural evolution” (Tomasello, 1999 p. 36).

Nevertheless, understanding what kind of social learning mechanism a species is capable of using may help to explain what kind of behaviours can or cannot be transmitted socially and what level of fidelity we might expect to find. This is where controlled laboratory experiments are important. They may help identify what type of behaviours can be learnt socially, in what situations and which mechanism(s) are at work. However, this is still far from reconstructing what really goes on in natural settings (Huffman & Hirata, 2003).

b. Empirical evidence of social learning in capuchin monkeys

Early experiments with monkeys tended to disconfirm the notion that monkeys can imitate. The few, which did claim to find positive evidence, were criticized on methodological grounds, mainly for their lack of suitable controls to rule out other learning process, such as stimulus enhancement (see Table 2.3 for a summary of these experiments).

Table 2.3 Early laboratory experiments on social learning in capuchin monkeys and some other monkey species. N= number of subjects in the experiment. H=human model; M= monkey model; IL= individual learning; SE= stimulus enhancement, E=emulation; I=imitation; DI=deferred imitation,

Reference	Control	N	Task	Model	Author's Conclusions.	Critique
Romanes (1883)	No	2	Puzzle box		IL	
Thorndike (1901)	No	3	Puzzle box & Free play	H+M	IL	need more subjects
Watson (1908)	No	2 +other species	Tool use & Puzzle box	H+M	IL	
Watson (1908)	No	2	Free play	H+M	Circular behavior	
Hobhouse (1901)	No	2		M	I + E	
Kinnaman (1902)		1 rhesus	Puzzle box		I	SE
Haggerty (1909)		8+ other species	Puzzle box	M	I + DI	Over training =IL, No control for SE
Warden et al. (1940)	No		Puzzle box	M	I	SE

Later, a developmental approach was taken up and research on imitation in primates made use of the Piagetian scheme of sensorimotor development using test settings employed with children (Piaget, 1952). Parker (1977) observed the behaviour of an infant stump-tailed macaque (*Macaca arctoides*) and concluded that the monkey "displayed no purposeful matching of his behaviour patterns to those of other animals, nor did he come to imitate behaviour patterns outside his repertoire as human infants do" (Parker, 1977 p. 65). Chevalier-Skolnikoff (1977) tested capuchin monkeys and claimed that the imitative ability of these monkeys was at stage 5 or 6 of imitation in the sensorimotor series. For example, one monkey, after watching a conspecific bang two objects together, immediately picked up two objects and banged them together, too. However, the behaviours the author mentions are very common capuchin behaviours; thus there is no way to prove that imitation was taking place and not individual independent actions.

Critics of using Piaget's framework provide evidence that Piaget underestimated the capacities of infants to imitate. Meltzoff and his colleagues claim that the basic ability to imitate facial expressions, such as mouth opening, is present already at birth, establishing an altogether different timetable for the development of infant imitative development than suggested by Piaget (Meltzoff & Moore, 1999). Humans seem to be so predisposed to imitating that the term Homo *imitans* applies (Meltzoff 1988d). Thus, there is an innate human ability for visual kinesthetic transformation. However, results show that infant chimpanzees also imitate tongue protrusion and mouth opening (Myowa-Yamakoshi *et al.* 2004). Similar results have recently been found in infant rhesus macaques (Ferrari *et al.* 2006). At the age of three days, these infants were able to imitate lip smacking, tongue protrusion, and mouth opening, after seeing a model. This period of neonate imitation in rhesus is much shorter than the one found in humans and chimpanzees, yet it still could be an important tool for communication between mother and infant as in chimpanzees and humans (Meltzoff & Moore, 1994).

Experiments attempting to elicit this behaviour in infant capuchin have not been successful (Visalberghi & Fragaszy, 2002). This might be connected to the fact that *Cebus* infants are carried on the mother's back from birth whereas macaque as well as chimpanzee infants are at first carried on the mother's ventrum and thus have face-to-face contact with their infant.

One of the problems with this line of testing imitation is that no controls are employed. Further, researchers have found that capuchin monkeys do better in other sensorimotor series, such as achieving stage 6 on the object concept scale (Schino *et al.* 1990). Thus, "imitation must be studied in its own right, not as an element in a larger coordinated program of cognitive development" (Visalberghi & Fragaszy, 1990a pp. 252).

It was only with the very detailed experimentation of Visalberghi, Fragaszy and colleagues that brick after brick was built towards a better understanding of *Cebus* cognition and social learning in particular. More solid information about social learning processes was collected. Some of these studies were planned directly to assess social influence on learning. Others were part of a battery of studies dealing with tool use capacity and therefore often lacked suitable controls, as they were not planned to answer social learning questions. However, they do have importance in raising new questions and providing results, which are of interest to this field. For example, tool use experiments in capuchin monkeys showed that not all monkeys in a group learnt to use a specific tool (e.g. Visalberghi, 1987; Westergaard & Fragaszy, 1987a). Such findings then triggered experimentation aiming to discover why these monkeys were not using tools and how, if at all, they could benefit from observing tool-using conspecifics.

I shall discuss these experiments, as well as the few others carried out with capuchin monkeys by other researchers, and will compare them, when possible, to what is known about other primates' social learning in similar conditions and experimental settings. Comparisons with other species of primates that live in similar as well as different social and ecological environments, but tested on similar procedures, may help to better understand the nature of the results found in capuchin monkeys (constraints on such comparison are discussed by Caldwell & Whiten, 2002).

1. Social learning of food choice

Social learning of food choice, as well as predator avoidance, has been considered by many (e.g. Kummer, 1971; Nishida, 1987) as suitable domains for testing social learning and cultural transmission, in that avoiding toxic food and predators is crucial for survival.

Camberfort (1981) describes the "feeding culture" as "the total knowledge about the diet, which is shared by troop members and transmitted from one generation to another, allowing them to survive in their chosen environment" (p. 244). Jouventin, Pasteur & Camberfort (1976) showed how, in captive mandrills (*Manndrillus sphinx*), juveniles learned from adults to discriminate between palatable and unpalatable food. In contrast, testing baboons and vervets did not show social learning in this domain (Camberfort, 1981).

Visalberghi and colleagues conducted several experiments to test the role of social influence on novel food choice (e.g. Addessi & Visalberghi, 2001; Galloway *et al.* 2005; Visalberghi *et al.* 2003). The results of all these experiments point to social facilitation of general eating and not necessarily to matching of the novel food items. There was no evidence for higher social learning mechanisms.

Reviewing studies with avian and non-avian species shows that avian species are able to socially learn to avoid noxious foods whereas there is no evidence for such social learning in non-avian species (Sherwin *et al.* 2002). However, there is recent evidence that cotton-top tamarins (*Saguinus oedipus*) are able to learn to avoid noxious foods through observation of conspecifics (Snowdon & Boe, 2003; Prescott *et al.* 2005).

Brosnan & de Waal (2004) tried approaching the problem of socially learning food preference from a different angle. The negative results found in laboratory tests, they claimed, may be due to the presence of many possible non-social cues. They therefore tested their subjects on the ability to learn the value of tokens by observing others use the tokens. Thus, the monkeys were not demanded to learn new skills but rather to extract information from the conspecific's behaviour alone. The results showed that the subjects were indeed able to form a preference for one token as a result of watching the preference of a conspecific. In a non-social situation, when the subjects watched tokens held by the experimenter with their corresponding food without the active conspecific, they were not able to develop the same preference. However, subjects were not able to learn new values for familiar tokens; once the association was made it was difficult to change. The authors explain this by the fact that in nature different foods have constant values.

This experiment, as opposed to food choice experiments cited earlier, show positive results for social learning, as the only information for the preference was the shape of token that was chosen. Thus monkeys had to rely on the social cue for learning. With real food, more cues exist, such as odour and taste. In such a situation the social cue may be less salient and may be overlooked (Dewar, 2003).

2. Social learning of object manipulation and tool use

Imitation is thought to have a role in the spread of tool use in hominids (Parker & Gibson, 1979). The ability to copy tool use thus is considered by some to require a high degree of imitative ability (Mitchell, 1994).

Spontaneous imitation of object manipulation

Perucchini *et al.* (1997) (cited in Visalberghi & Fragaszy, 2002) tested dyads of capuchin monkeys while they were playing freely with objects. Each monkey in the dyad had the exact same set of objects as the other. The authors checked for any instances of imitation, stimulus enhancement or social facilitation, which would be seen if subjects contacted the same object their partner did. No imitation was found in this experiment, in contrast to results for children as young as 12 months, who did imitate in a similar setting (Camaioni *et al.* 1988). The monkeys did show social facilitation, replicating common actions with the objects, as well as stimulus enhancement. However the monkeys paid little attention to each other.

This conflicts with data from chimpanzees where most anecdotal evidence for imitation comes from play settings and not from problem solving tasks (Hayes & Hayes, 1952). Russon & Galdikas' (1993, 1995) examples for orang-utans will be discussed in the section dealing with the effect of enculturation.

Nut cracking

Two different experiments (Antinucci & Visalberghi, 1986; Visalberghi, 1987) tested capuchin monkeys' ability to open nuts by using different tools, such as stones and wooden blocks. In each group one member learned to use the tool. The other monkeys in the group were seen to watch closely but did not show any acquired nut cracking skills.

Fragaszy & Visalberghi (1989) aimed to directly check social influence on behaviour acquisition in terms of the temporal relationship between behaviours of observers and tool users. In this experiment, too, the authors concluded, “immediate, direct imitation of a model’s pounding open nuts did not occur” (Fragaszy & Visalberghi, 1989, p. 164). Monkeys were not more interested in the tool after watching a conspecific, and exploratory behaviours were not enhanced: “In fact, the data suggested that relevant exploratory behaviours were performed by several subjects not only independently but preferentially while alone” (Fragaszy & Visalberghi, 1989 p. 164).

There were also no effects of social facilitation in pounding without a tool while near a solver, by contrast to behaviours such as biting the apparatus. Non-solvers were seen to scrounge. They learned that when a solver was near the board there was a chance of obtaining opened nuts, so scroungers were present at the board with solvers.

Ottoni *et al.* (2005) found that capuchin monkeys actively chose which monkey to observe. To do so, they must have had some understanding of the relative proficiency of their conspecifics while nut cracking and thus watched the more skilled nutcrackers. This might be done purely for the benefit of scrounging payoffs, but the authors claimed this behaviour provided more social learning opportunities as well.

Fragaszy *et al.* (1994) found that young monkeys did not learn to crack nuts from the older monkeys but the young juveniles preferred to be in the side of the housing where the adults were, whereas older juveniles preferred to operate the apparatus in the crèche to which adults had no access.

Some of the solvers in the Fragaszy & Visalberghi (1989) study first succeeded while they were alone at the board. The authors took this to suggest that their successes were not related to what the other monkeys were doing, and concluded that there was no evidence for imitation in either of these experiments.

It seems to me that the fact the solvers pounded more while alone may rule out social facilitation but does not necessarily rule out social learning. Later solvers could have used information from observing earlier solvers in order to then open the nuts while they were alone and not be threatened by the presence of others. The fact that not all monkeys learned the task may be due to individual differences.

Furthermore, nut cracking is a difficult task to accomplish. It usually takes young capuchins until two years of age to master this behaviour (Ottoni *et al.* 2005; Westergaard & Fragaszy, 1987a) hence longer than other tested tool use behaviours, such as dipping and raking (Visalberghi, 1990). Thus, an experiment testing naive monkeys' acquisition of nut cracking from short observation sessions may be too demanding for some monkeys.

Nut cracking is thought to be one of the principal tool use behaviours of chimpanzees in the wild. Even for chimpanzees, this is a very complex behaviour to master, as it includes using the right anvil (surface) and hammer (stone or other object) placed at the correct angle (Boesch & Boesch, 1983). The acquisition of nut cracking skills has been considered to be aided by social learning (Hannah & McGrew, 1987). However, young chimpanzees need many years of learning and practice in order to be skilful nut crackers (Boesch, 1993). What then is the role of social learning in mastering this behaviour?

Inoue-Nakamura & Matsuzawa (1997) studied the development of this nut cracking behaviour in wild chimpanzees of Bossou, Guinea. The authors concluded that the chimpanzees did not copy the behaviours of the model or the way to place the different objects, but were rather showing goal emulation. Sumita, Kitahara-Frisch & Norikoshi (1985) looked at the acquisition of nut cracking behaviour of individual apes in a captive group. As the learning was gradual, they concluded that it was based on trial and error and local enhancement. Thus, nut cracking with a tool may be too difficult to learn through short observational sessions for *Cebus* and *Pan* alike.

Probing with a stick

In Westergaard & Fragaszy's (1987a) study, the subjects had to use a stick as a probe to obtain syrup. The authors suggested that observational learning was taking place as a monkey detached a stick to use as a tool immediately after viewing another monkey in the group dip a stick into the apparatus. However, such results should be treated with caution, as other explanations could be given as well: the tendency to play and manipulate sticks is common in capuchin monkeys even without a noticeable goal. Previous individual experience could also not be ruled out (Visalberghi & Fragaszy, 1990a). Fragaszy *et al.* (1994) tested young capuchins on the same task where adult monkeys served as models. They found that although the juveniles did not learn to solve the task through observation, they did operate the apparatus more after observation. Thus, adult activity facilitated younger monkeys' activity, which could eventually lead to individual learning. The authors term this type of influence "coordination in time", where the activity of a model facilitates the activity of the observer, yet not in the specific way demonstrated, which they refer to as "coordination in space".

The same apparatus was used with lion-tailed macaques (Westergaard, 1988). Naïve macaques that were present with competent conspecifics were faster to learn the task than monkeys that were not next to such models. However, the author did not give any information about whether attention was directed towards the competent monkey, thus not being able to rule out mere social facilitation. Furthermore, one of the successful monkeys had also been part of the first phase of the study where he had access to the apparatus and thus had much more time to work it out through trial and error. Negative results were found on a similar task with *Macaca tonkeana* (Anderson, 1985).

A different way of using a stick was tested by Fragaszy & Visalberghi (1989). In this study, monkeys had to insert a stick into the apparatus and use it to push a sliding door, which then released sunflower seeds. Five of the monkeys solved the problem and were apt tool users, but this did not result in more exploration by the other monkeys, some of which never even contacted the tool. In this experiment, too, the inhibiting effect group mates had on their companions might have obscured what the observers learned. The authors, realizing this, tried two variations:

a. The most dominant female was taken out of the room and as a result other monkeys approached the apparatus more. One monkey inserted the stick in the tube (although not successfully).

b. More rods were given to the group. This resulted in greater general activity. Further, three non-solvers used the sticks to insert them in the tube (although not proficiently). Thus, it seems that if the question is 'can *Cebus* imitate', testing each monkey separately after they had a chance to observe a solver might give different results.

In a study by Visalberghi & Trinca (1989), four capuchin monkeys were presented with a horizontal transparent tube with a reward in the middle. The monkeys had to push a stick to retrieve the reward. Three monkeys succeeded and one female did not. She was then put together with the solvers but did not learn the task from observing them, although she did contact the apparatus more, showing stimulus enhancement. Later, she learned to solve a similar task and was then presented with the same unsolved tube task again - and solved it in less than 30 minutes. The authors concluded that "individual experience in a similar task was a more powerful aid to the monkey than was the information she was able to acquire from the behaviour of models" (Visalberghi & Fragaszy, 1990a p. 263).

Testing what an observer is looking at may be a good indicator of what information he is utilizing from the model. In the tube experiment, Visalberghi (1993b) reports that by analyzing which part of the apparatus the observers were looking at, it was found that they were looking straight at the reward and not at the tool, which was used to take the food out or at the model's behaviour.

Unlike the capuchin monkeys, human infants of 15-21 months were able to benefit from watching a model obtain a reward from the tube (Modena &Visalberghi, 1998). Younger infants showed no learning from such observation.

Probing is the basis of termite fishing, which is the second well-known tool use behaviour of chimpanzees in nature. Young chimpanzees watch attentively while the adult skilfully use sticks to fish termites. Yet, it takes many years of practice for a chimpanzee to skilfully use a stick (Goodall, 1986; McGrew, 1977). Mothers allow their young to participate in fishing activity and thus allow their infants to learn different parts of the activity. Some may play with the sticks too and learn their affordance.

Paquette (1994) investigated the importance of imitation in the acquisition of such tool use in chimpanzees. Local enhancement was found to play the main role in the discovery process and mastering the task took place through trial and error, similar perhaps to situations in nature, where chimpanzees use fishing holes, which were used by others and have sticks next to them (McGrew & Collins, 1985). The precise technique, Paquette concluded, was too complex to learn through imitation.

Raking

Raking an out-of-reach reward was tested on eleven capuchin monkeys (Vancatova, 1984). After a baseline phase, the dominant male was taught to use a T-shaped stick to reach the reward and serve as a demonstrator. Two monkeys used the stick, yet did so differently from the method they had observed. Thus, in this experiment the two monkeys had learned the affordance of the stick as a tool to get the food, but were not able to learn the action to use the stick, nor the correct relationship between the stick and food (i.e. that the stick has to be behind the food in order to pull it in). Once again, not all monkeys showed signs of social learning. However, as the monkeys were tested in a group setting, inhibition effects could also have taken place. Further, there was no control for stimulus enhancement, such as a control group viewing the T- stick being manipulated without the presence of food.

Beck tested a group of captive hamadryas baboons (Beck 1972, 1973a), Guinea baboons (Beck, 1973b) and pigtailed macaques (Beck, 1976) on a raking task. There was no sign of social influence on learning the tasks in the baboons. However, the dominant macaque male was influenced by the behaviour of the first solver and used the same technique he observed.

Zuberbühler *et al.* (1996) found that a group of longtailed macaque (*Macaca fascicularis*) failed to imitate raking by one of the adult males although they had ample time to view him. Several monkeys were seen to manipulate sticks more when the tool user male raked in the fruit, implying an increase in general activity as a result of the observation. It took a year for one individual to learn the behaviour and almost another year for two other individuals. This can be attributed to individual learning or perhaps stimulus enhancement as the three monkeys were peers from the same matriline and were able to be close to the model, who was tolerant of them.

Experiments were carried out with apes to test social influence on learning to rake. These experiments were designed more carefully and used suitable control groups. Tomasello *et al.* (1987) employed an extra control group, which viewed the demonstrator when she was not operating the apparatus. Results showed that the chimpanzees observing the demonstration learned to use the tool in only a few trials. Most of the subjects in the control group did not learn to use the tool. In both groups the chimpanzees manipulated the tool as often, thus ruling out stimulus enhancement. However, the chimpanzees in the experimental group did not copy or imitate the actual action they saw and used a variety of actions with the bar. As with the capuchin experiment previously mentioned, the chimpanzees learned the affordance of the tool and succeeded to solve the task through emulation. Nagell, Olguin & Tomasello (1993) further tested this process of emulation. Two groups of chimpanzees and two groups of human children viewed a human model demonstrating either an efficient or non-efficient way of using a tool as a rake. Results showed that the children had copied the model in both conditions while the chimpanzees, on the other hand, used the same method no matter which method they observed. Similar results were found with orang-utans (Call & Tomasello, 1994a). The debate whether chimpanzees emulate or imitate (or both) has been going on ever since (Call *et al.* 2005).

3. Puzzle box tasks without tools

Testing social learning with tool use tasks has its limits, as seen in the previous section, since these tasks may be difficult for the subjects to learn. Adams Curtis & Fragaszy (1995) and Adams-Curtis (1988 in Fragaszy *et al.* 2004) used a different approach and presented a multi stage apparatus to capuchin monkeys. Choosing a sequential task has its logic as it is accepted that imitation is more probable when the problem is too complex to be learned through individual learning. Furthermore, success on such tasks cannot be explained by social enhancement or stimulus enhancement. In these studies, a three-stage puzzle was given to twelve *Cebus* monkeys. Only one out of the twelve monkeys in the experiment solved the problem and hence acted as model for the other monkeys in the group. The researchers aimed to see whether the observers would contact the apparatus in the same order as they had seen. The authors concluded that there was no evidence that the monkeys were matching the behaviour they had seen nor the order in which it was shown (see also Adams-Curtis, 1987 for similar results).

More recently, de Resende & Ottoni (2002) gave their subjects a complex three-step task. The monkeys viewed a model open three bolts in a defined order. When the observers were given the box to open by themselves, two out of six subjects succeeded but did not use the same order of opening the bolts as they had witnessed. The mechanism enabling their learning was claimed to be stimulus enhancement. The authors stress that the two subjects who managed to open the box were those who were attentive to the demonstration.

4. Two-action experiments

From all their experiments mentioned above, Visalberghi, Fragaszy and colleagues concluded that there was no evidence for imitation in *Cebus* monkeys. Monkeys did benefit from viewing a model but made use only of environmental information, showing stimulus enhancement. However, there are two more recent experiments carried out by these researchers, making use of better controls and using the two-method design.

This design, first used by Dawson & Foss (1965) with budgerigars (*Melopsittacus undulates*), compares two or more groups and presents the subjects with an apparatus, which can be manipulated in two or more different ways. It is suggested that if the subject then manipulates the apparatus using the action it was shown and not the other, non-imitative mechanisms such as facilitation and enhancement can be ruled out , hence making the interpretation of imitation more plausible. In this method, the relative frequency of performing A after observing A is compared with the relative frequency of performing A after observing B.

Gardner (1997, cited in Visalberghi & Fragaszy, 2002) replicated Heyes & Dawson's (1990) study with rats, which employed a two-method paradigm in which monkeys could obtain a reward by either sliding a door to the left or the right. Five monkeys in each group observed a conspecific demonstrator. Only two out of the ten observers copied the direction the door was opened. Those who did not copy the demonstrator's method were then put with the demonstrator in the same cage for phase 2, thus watching the door slide from the same direction as the model did. This time, seven out of eight subjects slid the door in the same direction as the model. The results showed object movement re-enactment, as copying was only possible when observer and demonstrator saw the apparatus from the same side.

Fragaszy *et al.* (2002, unpublished manuscript cited in Fragaszy *et al.* 2004) tested twenty juvenile *Cebus apella.* The monkeys could obtain juice from a dispenser by either turning a little wheel with their finger or pressing a lever. After a baseline phase designed to control for individual learning, the apparatus was placed in the group with one of the methods enabled. Most of the adult monkeys learned the enabled methods and thus served as demonstrators for the two different techniques. Most of the juveniles learned how to solve the problem after viewing the adults and used the same techniques they had witnessed also when approaching the apparatus, which was enabled for both methods.

However, Fragaszy *et al.* (2004) do not regard these results as necessarily resulting from observing the adults and suggest a further test in which naïve juveniles without previous access to the apparatus should be compared to juvenile monkeys that did have such access. If these naive monkeys also quickly master the techniques it will be, they claim, evidence for imitation.

It seems that the implications of these results have been underestimated. It may be true that monkeys were not learning the action of the model but rather showing object movement re-enactment. However, these results show more complex social influence on learning than the studies previously described. On the other hand, even if a naïve group is tested, as the authors suggest, and shows rapid learning this could still be attributed to object movement re-enactment and not imitation.

The two-method paradigm has been very useful in testing for social learning in other species of primates, too. Bugnyar & Huber (1997) tested marmosets on a bi-directional task. They found that two out of their five subjects showed signs of imitating the direction in which the model opened a door to retrieve food. In order to confirm their conclusions, a microanalysis was carried out to show that the probability of the marmosets behaving in the relevant combination of actions by chance was extremely low. Tomasello & Carpenter (2004) claimed that instead of imitation the marmosets could have learned the affordance of the box. Visalberghi & Fragaszy (2002) also suggested that the monkeys had learned to operate the box through object movement re-enactment and not through imitating the model's action.

A response to these criticisms was provided in a later study with marmosets in which Voelkl & Huber (2000) showed that marmosets that observed a model open a lid either with hand or mouth clearly used the same body part they observed to open the lid themselves. Thus, object movement re-enactment or affordance emulation could not be taking place in this case. A different line of criticism to this study was that the learned behaviour was most probably already in the learner's repertoire and thus could have been an example of response facilitation[1] (Byrne & Russon, 1998). It was also argued (Mitchell, 2002) that opening with the mouth corresponded to attacking, while opening with the hand corresponded to exploring and this (i.e. general mood) was what the marmosets had learned from the observation and not what body action to perform. This criticism could also apply to Caldwell & Whiten's (2004) results with marmosets.

The two-action design has not always yielded positive results with monkeys. Ham (1990) tested two groups of *Macaca arctoides*. The groups saw a model either twist or push a bar. No difference was found in the performance of the two groups. More recently, Rigamonti *et al*. (2005) tested 13 pig-tailed macaque (*Macaca nemestrina*) and 30 human infants (*Homo sapiens*), to probe for localized stimulus enhancement and object movement re-enactment. Four different puzzle boxes were used with two ways possible to solve each puzzle. Only very weak evidence for object movement re-enactment was found with one of the boxes. Children, on the other hand, showed clear evidence for choosing the method they had watched.

Conclusions

Although observations in the wild indicate social transmission of a variety of behaviours in *Cebus* monkeys, studies in the laboratory do not seem to show the same trend. Studies conducted to find complex social influence in the domains of food choice, object manipulation and tool use behaviour in capuchin monkeys have not yielded positive results. Visalberghi, Fragaszy and colleagues conclude that capuchin monkeys are not able to learn a new behaviour from observing a model: "for these monkeys, imitation of a model is indeed a very limited way to learn to use a tool" (Visalberghi & Fragaszy 1990a, p. 263).

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[1] This is an important criticism to bear in mind when designing two - action experiments, since if the actions are indeed well in the subject's repertoire the results can only be explained by facilitation effects. Thus, using a two - action design does not automatically fit the criterion of novelty for imitation discussed in Chapter 1.

There is only some evidence from their experiments for stimulus enhancement. However, they claim that “successful monkeys differed from others in their interest in the task, not in their talent” (Fragaszy & Adams-Curtis, 1991b pp. 261).

Results also showed some inhibiting effects of the group. Monkeys were usually more successful when trying to solve the tasks when other group mates were not close. This inhibiting effect should be taken into account when designing new experiments.

The incoming data about traditions in groups of capuchins in natural environments imply that more complex social learning processes may be taking place than what is seen in laboratory experiments. And, indeed, signs of more positive results have been found when testing designs were changed, thus shedding a different light on the issue of the social influence on learning. Further experimentation should:

a. Test simpler tasks, which can be mastered in short experimental periods (e.g. Brosnan & de Waal, 2004).
b. Take into account the different effects of scrounging. Scrounging may inhibit learning when the reward is obtained from a locus not directly related to the tasks (e.g. rolls out of an apparatus; Giraldeau & Lefebvre, 1987). Yet, it may facilitate learning as it allows the observer close contact with the apparatus (Caldwell & Whiten, 2003) and the possibility of making an association between the action and reward. Scrounging may inhibit the *production*, but not the *learning*, of a behaviour in a group setting. It may be needed, if possible, to test the observer individually for evidence of learning (Lefebvre & Helder, 1997).
c. Use suitable controls. Controls are important for avoiding false positive results but at the same time may also help understand what information the monkeys *do* extract from the observation. Learning through observation is not an “all or none” process and subtle ways in which the monkeys are learning may be overlooked without such suitable controls.

Using a two-action design is one step in this direction and has already yielded interesting results, as shown in Fragaszy *et al.* (2002) and with marmosets (Bugnyar & Huber, 1997; Voelkl & Huber, 2000).

III. The Effect of Enculturation

The concept of *enculturation* is a key issue as regards this dissertation since some of the capuchin subjects were raised by humans from the age of 8-10 weeks. The term enculturation is used to describe primates raised by humans in their homes in close relation with their human caretaker, almost the way a child would be raised (Tomasello *et al*. 1993b).

Some authors use the term in a looser way to describe close relations with humans during infancy. This usage has its problems and it is important to differentiate “tame”, implying only human contact from “enculturated”. There is a difference between a primate that is familiar with humans and interacts with them (e.g. in zoo or laboratory environments) and raising the primate as a child, i.e. treating it very much as a child would be treated. This point was also made by Gomez (1993), who stressed that not all hand-reared primates are enculturated. This is manifested, for example, as Gomez points out, in Premack & Premack's (1983) results showing a difference between enculturated and hand-reared apes.

Call & Tomasello (1996) describe five levels of human–ape interaction:

> "WILD. Apes that have spent their entire lives in their natural habitat.
> CAPTIVE. Apes in human captivity who have interacted directly with humans and their artifacts only minimally; this includes many zoo and some laboratory settings.
> NURSERY-RAISED. Apes raised from a young age with peer conspecifics and a good deal of contact with humans and their artifacts, but without human training aimed at specific behavioural outcomes.
> LABORATORY-TRAINED. Apes raised mostly in human captivity who have been trained in particular tasks, sometimes multiple tasks over many years (some of which might be symbolic).
> HOME-RAISED. Apes raised by humans in something like a human cultural environment (sometimes including exposure or training in symbolic skills); the environment need not literally be a home but must include something close to daily contact with humans and their artifacts in meaningful interactions” (p. 372).

Call & Tomasello (1996) provide an extensive review of the effect of human-ape contact on the behaviour and cognitive development of apes. They describe four different routes this influence may take, some of which can be achieved also without a high level of enculturation:

1. Learning different tasks, which are usually carried out by humans; here the non - human primate (usually an ape), does not understand in any way what he is doing. In

this case, the primates' cognitive abilities are not elevated in any way. This could also be achieved with tamed primates.

2. The human environment gives rise to abilities, which are in the range of the primate's capability but nevertheless are not evident in nature. Tool use is a good example. Tool use is not seen much in nature, except for chimpanzees, but in captivity with the access to different objects and artifacts, tool use and object manipulation is more widespread (McGrew, 1998; Tomasello & Call, 1997). This is apparent even without the close relation with humans that characterizes enculturation.

3. Learning concepts, such as categorization through training. Here again the capability to learn is in the range of the primate but is latent and requires tutoring.

4. The fact of being raised by humans channels the cognitive development of the primate in ways, which are not species typical. There may be a critical period for this to take place (Rumbaugh & Savage Rumbaugh, 1992). This could be achieved in several ways:

a. Tomasello & Call (1997) first suggested that through the process of enculturation, human- raised primates were treated as intentional beings (Kaye, 1982) and were rewarded for looking at and doing things with humans, engaging in activity that "presupposes a reciprocity of understanding" (p. 393). Thus humans, by acting in such ways, socialized the primate's attention (Vygotsky, 1978) and through this process primates eventually were able to gain the understanding of others as intentional beings. The enculturated primate "experiences social contingences, such as joint attention and intentional agency", which in turn may "produce species-atypical cognitive abilities", which are manifested in higher imitative abilities (Bering *et al.* 2000; Bjorklund *et al.* 2000; Tomasello, 1996; Tomasello & Call, 1997; Tomasello *et al.* 1993).

In such an environment, as opposed to the natural environment, the primates are "constantly interacting with humans, who show them things, point to things, encourage (even reinforce) imitation, and teach them special skills - all of which involve a referential triangle between human, ape and some third entity" (Tomasello, 1999 p. 35).

However, on the basis of new results showing that apes without close relations with humans also have some basic understanding of the fact that others have goals (Tomasello *et al.* 2003), Tomasello & Call have modified the idea of enculturation to – "…it is likely that human experience only serves to modify existing social interactional and attentional skills rather than creating new ones" (Tomasello & Call, 2004 p. 214).

b. Enculturation involves an increase in attentiveness to social cues. According to Dewar's (2003) theory of social cue reliability, raising apes much the way human children are raised may make them more sensitive to social cues from humans and more motivated to duplicate the actions of humans, without actually altering the underlying cognitive operations involved in social learning in any significant way.

c. Johnson (2001) claims that through the process of enculturation primates are "being treated as if they could participate" (p. 8) with an emphasis on how the primate and human interact and coordinate behaviour. The context of interaction is the key to development. Fragaszy & Shaffer (1994) describe some of the contextual features that are influential in a human rearing environment. Some of these include: "responsiveness of others to infant, provision of multiple and frequent affective signals, practice with taking turns, exposure to varied activities where others are clearly more competent, scaffolding of tasks for the infant by others".

d. The apprenticeship idea of enculturation suggests that through enculturation the child or primate "is an apprentice who learns … through a guided process of participation and reinvention aided by scaffolding" (Miles, 1994 p. 256). Along the same lines Bering (2004) describes such ape-human relationships, in which the influence of enculturation may be explained in terms of learnt behavioural strategies towards new objects or situations by using the human agent, rather than influencing underlying cognitive ability.

Some authors see the impact of human-primate contact in a simpler way. De Waal (1998) claimed "all that human-rearing does is affect the range of identification objects. Animals probably identify the easiest with the species they know best…. rehabilitant orang-utans and language-trained bonobos may see themselves as partly human. Rather than transforming cognitive capacities - as implied by the concept of 'enculturation' - the simpler view is that rearing by another species increases the willingness to imitate this species". However, if that was the case, non-enculturated chimpanzees would imitate chimpanzees, the ones they are most close to, just as much as enculturated chimpanzees imitate humans. This, as we shall see, is not the case.

This difference between human-reared and mother-reared chimpanzees (discussed in the following sections), some say, is not because the enculturation process has elevated apes' social skills but rather that they have not lived in impoverished conditions such as those found in caged apes (Boesch, 1993a; Whiten, 1993; Suddendorf & Whiten, 2001). Thus, most authors would agree that:

> "enculturation cannot facilitate performance beyond a species' inherent limits but can help it reach its maximum potential…The immersion of chimpanzees in an artifact-laden human culture, with long-term, highly social, stable human relationships, affects the animals' access to attentional resources in dramatic ways. Such changes, in turn, can facilitate acquisition of complex cognitive concepts, encourage emergent skills, and can also override behavioural predispositions, which would preclude or diminish the chimpanzees' ability to grasp new concepts or comprehend task demands" (Pepperberg *et al.* 1997, p. 66).

How is enculturation manifested in apes' behaviour?

Call & Tomasello's (1996) review of enculturation surveyed the different studies carried out with enculturated apes and apes with other human contact.

The first domain explored is the physical domain, which includes the use and understanding of objects and artifacts. Studies show that object manipulation and tool-use increase and are more sophisticated with the exposure to artifacts and objects. What apes learn through enculturation is the affordance of many objects and tools, thus making them more available for more complex behaviours. This may be due to the fact that enculturated apes are very attentive to what humans do. Carpenter *et al.* (1995) found that home raised bonobos and chimpanzees were more attentive to how humans were manipulating objects and engaged more in this triadic joint attention with humans than captive conspecifics.

Through such exposure, affordance emulation, and training, apes may also learn more abstract properties of objects allowing for more sophisticated categorization abilities (Hayes & Nissen, 1971 for chimpanzee; Miles, 1990 for orang-utan; Patterson & Linden, 1981 for gorilla).

However, on some level, mere exposure to objects can also contribute to more complex object manipulation behaviour. Thus, in this physical domain there is apparently only a quantitative difference in the behaviour of apes as a function of different levels of contact with humans.

Pretend play or symbolic play seems to benefit from the enculturation process. Exposure to objects and learning their affordances may be part of the explanation. However, such play, although rare, has only been found in enculturated apes that have learned symbolic language (Patterson & Linden, 1981, for gorilla; Hayes, 1951 for chimpanzee; Savage-Rumbaugh & McDonald, 1988 for bonobo). As with children, pretend play and symbolic communication may emerge together in enculturated apes along with “imitation, nonverbal referential communication, labelling, elaborate object manipulation and categorization” (Gomez & Martin-Andrade, 2005 p. 167). On the other hand, some anecdotes from non-enculturated apes might be interpreted as pretend play as well (Goodall, 1986).

In the social domain, enculturation has a greater effect but not in all areas. Social attention and gaze following exist in all apes and close interaction with humans is not necessary (e.g. Brauer, Call & Tomasello, 2005). Yet, there does seem to be a strong effect of enculturation on the sophistication of this ability (see Itakura & Tanaka, 1998 for orang-utans; Peignot & Anderson, 1999 for gorillas).

Further, attention-getting behaviours do increase in enculturated apes. Gomez (1996) found that enculturated chimpanzees, more than other chimpanzees that were used to human contact, used attention getting behaviours to get food from an inattentive human, whose eyes were closed or was with his back to the chimpanzee. They used behaviours, such as touching or trying to make eye contact (see also Gomez, 1990 for gorillas; Savage-Rumbaugh *et al.* 1986, for chimpanzees). Imperative pointing was also found to be influenced by enculturation (Miles, 1990 for orang-utans; Savage Rumbaugh *et al.* 1986) as well as in chimpanzees with close contact with humans (Leavens & Hopkins, 1999). Several studies also showed that enculturated apes understood human pointing better than other apes (Woodruff & Premack, 1979 for chimpanzees; Call & Tomasello 1994b for orang-utans; Inoue, Inoue, & Itakura, 2004 for gibbons; but see Yerkes & Nissen, 1939), as well as doing better on the “object choice” paradigm, which makes use of such behaviour (Itakura & Tanaka, 1998; Call *et al.* 2000).

Declarative gestures were only found in enculturated apes although there may be other interpretations for this behaviour (Patterson, 1978, for gorillas; Carpenter *et al.* 1995 for bonobos).

Imitation in enculturated apes

In Whiten & Ham's (1992) review of imitation there are many anecdotes of ape imitation in enculturated apes. One of the earliest reports of imitation in great apes comes from Kellogg & Kellogg (1933), who raised a baby chimpanzee named

Gua with their son of a similar age. The project lasted only nine months and Gua learnt only a few behaviours through imitation. In the same short time, the human infant had imitated many of the ape's behaviours, stressing the point that humans are "imitation machines" (Tomasello, 1999). The Kellogs concluded "we are accustomed to regard the chimpanzee, as a splendid imitator... yet the child is a more versatile and continuous imitator than the animal" (Kellogg & Kellogg, 1933 p. 230).

Imitation of action on objects

Mignault (1985) described how young enculturated chimpanzees imitated humans using a variety of objects (such as a hair brush). Tomasello (1990) criticized this study as no control group was used. Further, an earlier study showed that chimpanzees can work out what to do with conventional human objects on their own (Schiller, 1957).

Tomasello, Savage-Rumbaugh & Kruger (1993b) conducted a more systematic study of imitative skills in chimpanzees and bonobos. They compared mother - reared apes, enculturated apes and two - year old children on how they reproduced twenty-four different novel actions on objects. The mother-reared apes hardly reproduced any ends and means, thus there was no imitation**.** The enculturated apes and the children imitated, and there was hardly any difference between them, although Tomasello & Call (1997) stated later that at least in some of the trials emulation and not imitation could have been taking place.

Arbitrary body movements

Hayes & Hayes (1952) used the "Do as I Do" paradigm to test whether their human-raised chimpanzee Viki could learn to imitate various body movements and gestures. In general, after the twentieth item she had reproduced the task faithfully and quickly. Frantz, a chimpanzee that had not been raised the way Viki was, showed no signs of any type of social learning in this set of problem- solving tasks and usually needed more than ten demonstrations to solve the problem.

The interpretation of Viki's behaviour has been criticized. Heyes (1994) stated that the results could be outcomes of stimulus enhancement. Miklosi (1999) noted that some description of baseline behaviours is needed in order to determine imitation in this study, and reproduction of behaviours, such as nose touching, could be defined as response facilitation.

Custance, Whiten & Bard (1995) conducted a more rigorous study and reported similar abilities in two nursery-reared chimpanzees after they were trained for a period of several months in a manner similar to Viki.

Eye blink was difficult for chimpanzees to imitate (Hayes & Hayes, 1952; Custance *et al.* 1995), but an enculturated orang-utan, Chantek, mastered this task (Miles *et al.* 1996). Chantek, a human-raised orang-utan, was also seen to imitate a number of arbitrary movements and gestures (Miles, Mitchell & Harper, 1992; Call & Tomasello, 1995). Call & Tomasello (1995) gave Chantek several arbitrary body movements to reproduce following the command "Do this" which Chantek managed to do (replicating Miles *et al.* 1996 findings). However, when Chantek was given the same request – "Do this" in a problem solving context - he failed. Chantek understood the mimicking game of "Do this" at the sensorimotor level of arbitrary body movements but could not apply this knowledge to a problem solving task.

Tomasello & Call (1997) concluded that "the understanding of what another is doing in instrumental problem solving situations in a way that is relevant for one's own problem solving attempts, requires an understanding of the intention of others, which apes may not be able to do without certain specific types of experience and training from humans, or at all" (p. 294).

Communicative skills

Perhaps the most impressive evidence involves the communicative skills of enculturated chimpanzees. This raises the question of language acquisition.

Terrace *et al.* (1979) claim that signing apes can reproduce the previous (familiar) utterances signed by their human partners, but new signs are not learnt through imitation (Gardner & Gardner, 1969). Fouts (1972) showed that apes learn ASL easier through shaping and moulding than through imitation. Tomasello *et al.* (1985) did not find much evidence either to prove that chimpanzees were learning communicative gestures through imitation. Rather, gestures seem to be shaped through a process of conventionalization (Tomasello *et al.* 1985) or, as Tomasello & Call (1997) termed it, "ontogenetic ritualization", in which primates learn to associate specific gestures with a particular outcome.

Yet, some results do indicate an ability to imitate in this domain. Tomasello, Gust & Frost (1989) showed how young enculturated chimpanzees learned playful gestures through what seemed like imitation. Savage-Rumbaugh *et al.* (1986) claimed that Kanzi, the famous bonobo, began spontaneously demonstrating some lexigrams, which he had learned from observing his mother being trained by humans. The researchers concluded that Kanzi could only have learned the lexigrams through observational learning, but this has never been experimentally tested.

Deferred imitation

As mentioned earlier, deferred imitation is considered a complex mode of social learning, which requires the representation of the task and its components in order to reproduce it later. Parker & Gibson (1979) suggested the existence of deferred imitation in apes on the basis of anecdotal reports in the literature, such as those concerning home- reared chimpanzees who exhibited behaviours remarkably convergent with those of their human house mates (e.g. Hayes & Hayes, 1952). Orang-utans that were being rehabilitated into the wild are reported to reproduce complex human actions commonly done by the workers at the camp such as chopping weeds and then piling them up neatly, tying a hammock between two trees, digging and weeding with a hoe (Russon & Galdikas, 1993, 1995). What exact mechanism underlies these behaviours is hard to say as this was not an experimental context with the needed controls (Stoinski & Whiten, 2003). Furthermore, the history of these orang-utans - what they had learned in the past - was not known.

Studies have shown deferred imitation in enculturated chimpanzees (Bering, Bjorklund, & Ragan, 2000; Bjorklund, Bering, & Ragan, 2000; Bjorklund *et al.* 2002). Tomasello, Savage-Rumbaugh & Kruger (1993b) found that on the delay trials of their experiment, the enculturated chimpanzees significantly outperformed the mother- reared chimpanzees and human children. “We conclude from these results that a human-like socio-cultural environment is an essential component in the development of human-like social-cognitive and imitative learning skills for chimpanzees, and perhaps for human beings as well” (pp. 1688). Deferred imitation was found to increase over the juvenile period for enculturated chimpanzees (Bjorklund & Bering, 2003). The authors concluded that this could be a result of typical ontogenetic development (Boesch, 1996; Whiten *et al.* 1999) or a result of atypical development due to enculturation.

If enculturated apes are able to imitate on a higher level than non-enculturated apes this implies that the ability is there and simply needs to be nurtured. The effect of enculturation may suggest that "the learning processes may themselves be nurtured and shaped *by* the culture in which they are embedded" (Whiten, 2000 p. 485).

In conclusion

Given recent results showing at least rudimentary intention understanding in mother-reared apes, the core concept of Tomasello's enculturation process- understanding intentionality - has been toned down.

It would appear that the more parsimonious perspective to take, for the time being, as regards enculturation is not how the human culture changes the ape but rather what the ape learns about humans and their artifacts. Through its very close interaction with humans, the ape learns not only the affordance of objects but also the affordance of the human as a (social) tool. The human is perceived as a worthwhile model, a good problem solver, not only allowing but encouraging the ape to be in very close contact, usually ready to share and even more, reinforcing the ape through their interaction. (This contrasts with the more competitive interaction between mother and infant chimpanzees while manipulating objects, e.g. Bard & Vauclair, 1984).

The enculturated ape may receive two-fold reinforcement: the first is its actual success in achieving the goal, and the second is the social reinforcement from the human for this success. This is supported by data showing better imitation in enculturated apes as well as for communicative skills and attention getting behaviour.

Enculturation in capuchin monkeys

Can capuchin monkeys also benefit from the process of enculturation by humans? Itakura (2004) claims that "the effects of enculturation are presumed to be emphasized in species with a greater degree of behavioural plasticity, such as great apes" (p. 220). No doubt capuchin monkeys can be placed in this category as well (Fragaszy *et al.* 1990; Fragaszy, Visalberghi & Fedigan, 2004).

Furthermore, enculturation has its greatest effect when started in infancy. Capuchins are long-living monkeys (up to 42 years) with a long childhood and a relatively slower infant development than other Cebidae (Fragaszy, 1990b; Fragaszy & Adam-Curtis, 1991c) more resembling the slow development of apes (Spinozzi, 1989). Such slow development may lend itself more to the effects of enculturation.

Although capuchin monkeys have been kept as pets for hundreds of years, hardly anything has been written about the effect of enculturation on *Cebus*. Fragaszy (1990) compared the difference in development between a hand-reared and a mother-reared capuchin monkey (*Cebus apella*), during the first six months of their lives. It was found that the hand-reared infant spent more time manipulating objects than the mother-reared one, and this behaviour also started earlier in age. Thus, the human environment had an effect on the ontogeny of manipulative skills' development.

Gibson (1990) describes 'Andy', a male capuchin, who lived in her home for more than ten years. However, the nature of his upbringing in the first five years, in which he lived with a different owner, is not known. Also, the description of the years he spent at Gibson’s house does not provide much information about the type of human- monkey contact that was taking place. Andy showed little apparent imitative ability and Gibson concluded that most of his behaviour in this domain was probably due to stimulus enhancement.

The first attempt to test imitative ability directly with enculturated capuchin monkeys was carried out by Hervé & Deputte (1993) who tested an eight month old infant capuchin monkey who was part of the French “Helping-Hands” program aimed at preparing monkeys to aid quadriplegics.

The infant was given an array of objects to play with together with his human foster mother in order to see what influence the mother had on the objects the monkey chose to play with (social enhancement) as well as his actions on them (imitation). Results showed that the foster mother did influence the interest of the infant capuchin in objects. This was especially true for simple objects, which the monkey did not show an interest in to begin with, and which were manipulated more after the mother pointed to or manipulated the object. However, there were no signs of imitation in his behaviour.

Later, Hemery *et al.* (1998) and Fragaszy *et al.* (cited in Visalberghi & Fragaszy, 2002) applied the “do-as-I-do” paradigm with three of their enculturated capuchin monkeys from the same French project, who were older by now. The monkeys were first trained through reward to act upon an object or combine two objects in a familiar way. Both attention to the demonstration and fidelity of reproduction were coded on a four-point scale. Results showed that two of the monkeys contacted the same objects, which were contacted by the human in 60% of the demonstrations but the third monkey did so only in 30% of the demonstrations.

However, the monkeys seldom matched the actions they observed (only in 20%, 11% and 4.3% of the trials). Monkeys were more successful when they were more attentive. Also, actions involving objects were matched more than those involving the body alone.

The best performing monkey was then moved to the second phase of the experiment, in which novel actions were demonstrated to him in between the familiar ones (it is not clear whether these were novel actions on the same objects, or novel objects as well). However, most of the novel actions demonstrated (36 out of 48) were not copied. Also, in the remainder of the demonstration, although the correct object was contacted, the action did not resemble the demonstrated one. Visalberghi & Fragaszy (2002) note: "the authors concluded that capuchin monkeys predictably contact objects that have been acted upon by the demonstrator, as found also in Hervé & Deputte (1993) and (with a much lower probability) they will move an object to achieve (or toward) a demonstrated movement or new position of object. However, except in this circumstance, capuchins do not match the action performed by others" (p. 12).

These studies highlight the salience of the human as a model for the enculturated capuchin. By watching and interacting with humans monkeys develop "an understanding of special relations about objects from the human's actions on those objects" (Visalberghi & Fragaszy, 2002).

Experiments conducted to this day have not demonstrated the enculturated monkeys' ability to attend to the action of the human model. The difficulty of copying actions on oneself as opposed to actions with objects has also been reported in chimpanzees (Myowa-Yamakoshi & Matuzawa, 1999).

Nevertheless research perspectives dealing with the effects of enculturation on the imitation ability in *Cebus* monkeys are far from exhausted. Firstly, the experiments above tested infant (8 months old) and juvenile (4.5 years) monkeys. As the only longitudinal tests of imitative abilities in enculturated chimpanzees shows a development in the ability to imitate (Bjorklund & Bering, 2003) enculturated *Cebus* monkeys may also develop this ability with age.

Secondly, a more systematic experimental design is needed in order to test what components the monkeys *are* capable of extracting from the demonstration, not only an "all or nothing" design.

Finally, only a very small number of subjects were tested in the experiments described in this chapter. Individual differences in behaviour, attention span and cognitive ability among capuchin monkeys are considerable and testing imitative abilities in a larger group of enculturated monkeys is needed. This objective is met in the current thesis, which tested a larger group of enculturated monkeys from "Helping-Hands" Israel.

Israeli "Helping-Hands" capuchins were raised in homes by humans from the age of about 8-10 weeks. Foster families were instructed to raise them 'like a child' in the home where the monkey is part of the family in all aspects of everyday life. Just as described for chimpanzees, capuchin monkeys in the home participated together with humans in different activities on objects, were reinforced socially for paying attention to things humans did, and for social communication. The role of social reward for communicative and interactive behaviour with the human can for instance be seen in the way the enculturated capuchin monkeys seem to use the play-face more often than non-enculturated monkeys (personal observations). This is perhaps because of the social reward they received from humans from infancy for this behaviour - vocalizing, hugging, cuddling, smiling etc. Thus it may tentatively be inferred that social reward had an effect on other social behaviours of the monkeys as well.

There has been only one systematic study of other cognitive abilities in this group of monkeys that tested their understanding of physical causality (Fredman, 1995). Utilizing the data above for enculturated chimpanzees, a comparison can be made as regards communicative behaviour. Imperative gesturing has been seen in enculturated capuchins as well as different actions made by the monkeys to urge humans to act in a certain way for the monkey. These behaviours include taking the human's hand, and bringing an object to be manipulated such as opening a bottle (personal observations).

Thus, it may be expected that, like apes, enculturated capuchin monkeys have learned the affordance of tools as well as the affordance of humans, enabling them a more complex ability for social learning than mother-reared monkeys.

In the next chapter, I will discuss the first attempt to test imitation carried out with this group of enculturated capuchin monkeys. This experiment which was carried out before this thesis was the starting point for the experiments in Chapters 6, 7 and 8.

Chapter 3

THE ARTIFICIAL FRUIT BOX STUDY

This chapter describes experiments with an artificial fruit box apparatus (AF) which was designed to test social learning in different species as it does not rely on tool using abilities. The experiments using the AF are based on the two-action paradigm, which was claimed in the previous chapter to be most suitable for testing social learning. The results for primate and non- primate animals are discussed in comparison to results from enculturated monkeys. The AF experiment was the first to elicit positive results in capuchin monkeys, and was the impetus for the empirical studies in this thesis.

The two-action task has been shown to be a powerful method for studying social learning in human and non-human subjects (Dawson & Foss, 1965; Zentall, Sutton & Sherburne, 1996; Meltzoff, 1996; Moore, 1992). It has the advantage of ruling out stimulus enhancement explanations since both methods employ the same object but in a different way (see Chapter 2). It may also rule out general emulation explanations because in both cases the main end result is the same.

These were the considerations that prompted the design of the Artificial Fruit box (AF) (Whiten *et al.* 1996) as a two-method apparatus simulating the complex food processing techniques animals may use when dealing with embedded food items in natural environments. Because opening the AF does not demand tool-using behaviours, the task can be tested on many different species and comparative issues can be dealt with.

There are two aims to this chapter:

1. A discussion of the first experiment carried out with the enculturated group of capuchin monkeys (see Chapter 4 for information on subjects), which triggered the battery of experiments described in this thesis.

2. A comparative examination. The AF experiment is the only social learning experiment to my knowledge which has been carried out with several species, thus allowing for tentative comparisons concerning social learning in the capuchin monkey and other primate and non-primate species.

The artificial fruit box (AF)

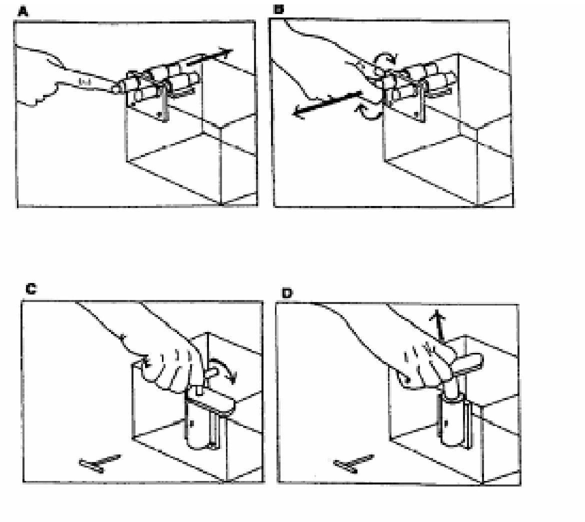
The AF is a Plexiglas box with two types of defences securing its hinged lid. Each type of defence can be removed using one of two alternative methods:

The **bolt latch-** two plastic rods are placed in two metal rings on the lid. The rods can be poked with the finger from the actor's side outwards or twisted towards the actor while pulling them out (See Fig 3.1 a and b).

The **barrel latch** - a T bar is slotted into a hollow barrel on the side of the lid with a wide lip which closes the lid. The T bar is secured by a pin.

The **pin** can either be pulled out or spun out while the T bar can either be pulled out or turned allowing the lid to be opened (See Fig 3.1 c and d).

If observers watching one method use this method significantly more than the subjects viewing the alternative method, their behaviour is thought to be based on imitation. It is important to note that the twisting actions of the bolt as well as the spinning actions of the pin are not necessary actions for moving these parts; thus copying these actions would be stronger evidence for action- centred social learning.



(Adapted from Custance, Whiten & Fredman, 1999)

Figure 3.1 Actions performed on the artificial fruit box. They include (a) poking the front of the rod, (b) twisting the front of the rod (c) turning the handle, and (d) pulling the handle**.**

Custance, Whiten & Fredman (1999) tested eleven enculturated capuchin monkeys, divided into two groups. Each group saw one of two methods of removing the bolts and one of two methods of disabling the barrel latch (only one type of defence was attached each time).

Two main types of analysis were carried out:

1. Overall rating. Two independent coders, familiar with the task but having no knowledge as to which subject observed which method, were asked to estimate which method the monkey had seen in each trial.
2. A microanalysis of the frequency of the actual movements the subjects performed.

The results showed that there was no significant difference between the groups regarding their behaviour with the barrel latch. However the independent coders were able to differentiate between the two groups in terms of their behaviour on the bolt latch. When trying to assess what factors influenced this perception it was found that although there was no significant difference between the groups in the amount of poking and twisting actions, there was a significant difference in more general actions on the bolts. All target-like behaviours related to poking, such as pushing the bolts while using different parts of the hand as well as the mouth, were plotted together. In the same way target-like behaviours related to twisting, including pulling out the bolts with the hand and mouth, were also plotted together. Comparing the groups on this level showed a significant difference between the groups.

Thus it was concluded that the social learning mechanism underlying the behaviour of the capuchin monkeys in this study was either object movement re-enactment (OMR) in which the monkeys re-enacted the movement of the rods yet did so in mainly in their own way, or a simple form of action imitation. More controlled testing to differentiate between the two was needed.

Since this experiment, several others using the same AF or a slightly modified version of it have been carried out with other species (see Table 3.1). Together with the original experiments using the AF with chimpanzees and children (Whiten *et al.* 1996, Whiten, 1998a) it is now possible to make some tentative comparative comments.

1. Mother - reared capuchins

Custance (1994) tested six group-housed capuchin monkeys. There was no significant difference in the behaviour of the monkeys towards either of the latches.

The author concluded that “although the capuchin data was not significant the general trend was in the predicted direction for imitation” (p. 200).

2. Other species of monkeys

(a) Marmosets.

Marmosets (*Callithrix jacchus*) were tested on a simplified version of the AF (Caldwell, Whiten & Morris, 1999; Caldwell & Whiten, 2004) as it was found that the manipulative skills of this species would not be sufficient to open the original latches. The AF was scaled down in size for this study and only the handle was used. The monkeys first had to turn the handle which then enabled them to lift open the lid. It was not possible to train a model to open the box in two different ways so an additional group, which controlled for stimulus enhancement (SE) was used in which a model licked food off the lid. This experiment also included a third control group that only observed the box, without a demonstration of any kind.

Although none of the monkeys managed to open the box, differences in the behaviours of the monkeys towards it were found as a function of what they had observed. Monkeys who had observed the demonstrator open the box showed more exploratory actions towards the box than the SE group monkeys. Furthermore, monkeys who had watched the demonstrator open the box manipulated the box more with their hands whereas the monkeys who had watched a conspecific lick the box in the SE group used their mouth more. This showed what the authors called a “crude level of imitation”- in which observers preferably use the same body part as they had witnessed (similar to results found in Zentall *et al.* 1996, for pigeons). However interpreting this behaviour as action imitation was challenged by Mitchell (2002), who claimed this could be explained by observational conditioning of the mood towards the box, in which foraging is associated with the hand and attacking associated with the mouth. Byrne (2002) claims this type of learning is not action-centred social learning but rather context imitation, where the context in which to reproduce behaviours from the animals’ repertoire is learned socially.

Although stimulus enhancement was controlled for in this study, localized stimulus enhancement was thought to be taking place because the monkeys were concentrating more on the different, specific parts of the box they had seen manipulated in the demonstration.

(b) Pig-tailed Macaques.

Custance *et al.* (2006) tested pigtailed macaques (*Macaca nemestrina*) using only the bolt-latch. There was no significant difference between the groups for either of the behaviours. Independent coders were only able to differentiate between the groups on the first trial. It was impossible to isolate the factor which brought about this difference although the authors suggested that the mechanism of social learning was mainly object movement re-enactment.

One of the reasons suggested for the lack of a significant effect of observation in these macaque monkeys was the small amount of attention they paid to the demonstration; they showed only “limited and sporadic attention” (p. 311).

3. Great Apes

(a) Chimpanzees

In the first experiment using the AF, Whiten *et al.* (1996) tested 8 chimpanzees (*Pan troglodytes*). Independent coders were able to differentiate between the two chimpanzee experimental groups for behaviours performed on the bolt-latch but not on the barrel latch. Although spinning the pin was only seen in the group viewing “spin”, this behaviour only rarely occurred. Behaviours on the rods were significantly different between the groups on the less rigidly defined 'target- like' behaviours.

The AF was also used to test imitation of a sequential structure (Whiten, 1998a). In this study, both latches were present together and different sequences, as well as different methods to open the latches were demonstrated. The results showed that in the third – final - trial the chimpanzees copied the sequence with statistically significant high fidelity, thus showing the first evidence for imitation at the sequence level in primates.

(b) Orang-utans

Custance *et al.* (2001) tested 14 wild born orang-utans. The results showed no evidence for social influence on learning. The authors suggested this might be due to the young age of the subjects as two out of the four adult subjects did seem to match the method they had observed more closely, as well as being the only subjects that managed to open the AF. Further, most of the subjects had a traumatic history (they were orphans in a rehabilitation camp) which could have affected their cognitive development. In this experiment, as with the chimpanzees (Whiten, 1998a) both latches were present and different sequences were demonstrated to the two groups. No evidence for imitation of a sequence was found.

Stoinski & Whiten (2003) used the same paradigm on 15 older subjects with a more normal childhood than the orphans in the previous study. These subjects also had some experience with different experimental procedures; thus the authors thought they would reflect more faithfully the capabilities of orang-utans. Independent coders were able to differentiate between the experimental groups according to their actions on the bolt latch. Further microanalysis showed this was not due to a difference in poke vs. twist actions on the bolts or to general target–like actions. The significant difference was found in the *direction* in which the bolts were removed, thus indicating the work of an object-centred learning mechanism.

Further, this study incorporated a third control group which did not observe any demonstration. Seven out of the ten orang-utans in the experimental groups managed to open the box at least once but one out of five control subjects succeeded as well. Thus, having an additional control group provided evidence for the benefits of social learning.

(c) Gorillas

Stoinski *et al.* (2001) tested ten gorillas using the complete version of the AF. However the actions on the pin were modified and instead of demonstrating spinning of the pin, the pin was pulled out. Perhaps as a result, basic action-centred imitation was found regarding actions on the pin. However such interpretations should be made with caution as, at least for other species, pulling the pin was the typical way of acting on it. Object centred imitation was thought to underlie the actions towards the bolts. As for the orang-utan subjects, no imitation of sequence was found in this experiment.

Thus, experiments testing great apes on the AF have shown a division between chimpanzees on the one hand, showing object and action centred imitation as well as imitation of sequence, and the orang-utan and gorilla subjects, for which only object focused social learning can be confidently attributed.

4. Humans

Studies with humans have included children and adults. Children are often tested in comparison to non-human primates with the idea that the ontogenetic development of social learning may give insights into the processes underlying social learning, as well as other cognitive aspects of non-human primates.

Whiten *et al.* (1996) tested 2, 3 and 4 year old children. Independent coders were able to significantly differentiate between the two experimental groups at each age. This was based on the actions on the bolts, which showed high fidelity copying, as well as on the actions on the handle of the barrel latch.

Testing adults provides a different perspective to understanding the behaviour of subjects towards a given task. The ability of adults to imitate is not questioned; rather the level at which they choose to imitate, if at all, is tested. Horowitz (2003) found that although the majority of adult subjects did imitate the method they observed, almost a third pulled the bolts out no matter what method they saw. Thus the adults were imitating less than the children in Whiten *et al.* (1996) who seemed to show high conformity in that they imitated even when it was not necessary (twisting the bolt). In adults, no significant effect of imitation was found for the pin, as with experiments with other species.

In the Custance *et al.* (2006) experiment, adult subjects were tested and showed more faithful matching, even to the extent of matching the digit used. Nevertheless, although starting with the demonstrated method, the subjects very quickly invented their own. This was perhaps due to the fact that the subjects saw more demonstrations (three as opposed to one demonstration in Horowitz, 2003) and were paying more attention to the demonstration than subjects in Horowitz' study in which some used the demonstration time to do other things. The significance of attention to imitation will be addressed later.

5. Non- primate species

Huber, Rechberger & Taborsky (2001) used a modified version of the AF to test social learning in New Zealand Keas (*Nestor notabilis).* Although there was no evidence for copying the action the keas viewed, results showed that subjects that observed a demonstrator were more explorative of the box and were more successful in opening its different locks. Further, an effect of localized stimulus enhancement was found, as with the marmosets (Caldwell & Whiten, 2004). Thus observing the model emphasized to the observer which part of the box was more important (Huber, 1998) which led to higher rates of success. The authors suggest that the lack of imitation could be a result of

a. The two methods being too similar in the Keas' eyes.
b. The model demonstrated very quickly and professionally, which is one of the common features problems of conspecific demonstration in such tests, as opposed to human demonstration
c. Keas are known for their explorative and playful tendencies (Diamond & Bond, 1999), which might have overpowered the need to copy.

Visual Attention

One of the factors which may influence the extent and complexity of social learning is the amount of attention paid to the demonstration and more precisely to the different components of the demonstration.

I further analyzed the data from the enculturated capuchin monkeys and found that the rate of attention to the demonstration was very high, with five monkeys showing maximum attentiveness and six others showing just a slight deviation. On average, the capuchins were attentive to the demonstration 97.67% of the time.

This is a higher rate of attention than the one found for the Macaque monkeys in Custance *et al.* (2006) study, that only watch 36% of the time. The results for the enculturated capuchins resemble those found for children and chimpanzees in Whiten *et al.* (1996) who were reported to attend to virtually the entire demonstration. Unfortunately, no comparable results are given for the orang-utan, gorilla or mother-reared capuchin monkeys in the studies cited earlier

Table 3.1 Artificial fruit box experiments with eight different species. N= number of subjects. Model column indicates human or conspecific. Results are given for each latch as well as latency effects in studies which employed a control group**.**

Species	**Reference**	**N**	**Model**	**Bolts**	**Pin**	**Handle**	**Control**	**Latency benefit**
Chimpanzee	Whiten *et al*. 1996	8	Human	***Action centred***	No	No	-	-
	*Whiten, 1998	4	Human	***Action centred***	No	No	-	-
Orang-utan	*Custance *et al*. 2001	14	Human	No	No	No	-	-
	*Stoinski & Whiten, 2003	15	Human	**Object centred**	No		Yes	Yes
Gorilla	*Stoinski *et al*. 2001	10	Human	Object centred	*Action centred?*	No	Yes	Yes
Macaque	Custance *et al*. 2006	11	Monkey	No	-	-	-	-
Capuchin	Custance, 1994	6	Human	No	No	No	-	-
	Custance, Whiten & Fredman 1999.	11	Human	**Object centred**	No	No	-	-
●Marmosets	Caldwell, Whiten & Morris 1999; Caldwell & Whiten, 2004	12	Monkey	Not used	-	No	Yes	No
● Kea	Huber, Rechberger & Taborsky, 2001	5	Kea	Object centred	Not used	Not used	Yes	Yes
Children	Whiten *et al*. 1996	24	Human	***Action centred***	No	***Action centred***	-	-
2 year old		8		Yes	No	No		
3 year old		8		Yes	No	Yes		
4 year olds		8		Yes	No	Yes		
Adults	Horowitz, 2003	48	human	***Action centred***	No	Yes	Yes	
Adults	Custance *et al*. 2006	24		**Action centred**			Yes	Yes

* In these experiments both latches were attached to the box, thus testing for imitation of sequential structure was possible.

- A modified version was used (see text for details).

Discussion

The AF, to my knowledge, is the only apparatus tested on such a relatively large number of species. This makes it possible to put forward tentative suggestions about behavioural and cognitive similarities and differences between the species in terms of what information each species extracts from the demonstration and how it makes use of it in its performance. This, however, calls for caution, as the small number of subjects tested may not faithfully reflect a species' ability. Further, although the apparatus is similar, there may be differences between the species in aspects not related to their cognitive ability to learn socially which may confound with the results. An example of this may be seen in the fact that the orang-utans were more hesitant to manipulate the AF than the chimpanzees, capuchins, and children. This may "reflect underlying species differences in motivation, specifically in situations involving novelty" (Stoinski &Whiten 2003, p. 287). Caldwell & Whiten (2002), addressing this issue, identify additional problems in trying to compare species on cognitive tasks. Such pitfalls may include, amongst others, differences in motivation for a given reward, differences in social tolerance levels of the species, and the level of habituation to humans who often serve as models, as well as differences in motivation to copy them.

Bearing all this in mind I now examine how the enculturated capuchin monkeys stand in comparison to the other species tested.

Mechanisms of social learning

None of the non-human primate species matched their behaviour on the barrel latch, except for the gorilla, yet the action demonstrated was different in that experiment from the others, rendering comparison difficult.

This could be a result of:

a. A difference in the saliency of each latch,

b. A difference in the way the two latches are released. In the case of the bolts the two methods are mutually exclusive: poking outwards is not followed by twisting inwards, whereas with the pin both spinning and pulling could be used together. Subjects could recognize this, incidentally, by very brief touching of the pin (Whiten *et al.* 1996).

This is true for the handle, too.

The fact that children did make the effort to copy the actions on the barrel latch shows a high fidelity of action-centred imitation not seen in the non-human species or the human adults.

The bolt latch is thus more useful in comparing different species. Chimpanzees and children were seen to use information about the action of the model on bolts yet children showed a higher fidelity in doing so (Whiten *et al.* 1996).

Some of the enculturated capuchins faithfully reproduced the actions on the bolts, yet a significant difference was only found for the more general target-like actions. This may imply a low fidelity action centred imitation, but it is more parsimonious to conclude that the monkeys' behaviour was based on object-centred imitation. This was the same type of imitation found for the gorillas and adult orang-utans.

The macaque monkeys and mother-reared capuchins did not show significant signs of imitation.

I further analyzed the data from the enculturated capuchin monkeys and found they were very quick at opening the box (median for first trial with bolt latch 45 seconds compared to 390 sec for the mother- reared capuchins; chimpanzees 38 sec, two year olds 77 sec, three year olds 17 sec). Information is not comparable for the gorilla and orang-utan subjects, as they had to open both latches.

One way to explain the difference in the enculturated capuchins' behaviour is to relate it to their rich experience with objects and tools. This may result in the absence of neophobia (noted in the orang-utans tested) as well as the relatively short time it took the monkeys to open the box. Nevertheless, such experience in itself cannot explain the difference in behaviour found between the two experimental groups. The process of enculturation (see Chapter 2) could have influenced their behaviour. However, at least for the orang-utan subjects, enculturation did not make a difference between Chantek, the enculturated subject, and the performance of the other subjects in the study.

The comparison of the enculturated monkeys with the mother-reared subjects in the Custance (1994) study requires caution. Therefore, further experimentation with mother-reared capuchin monkeys that are more relaxed in the experimental setting was included in my research and will be discussed in the following chapters.

Emulation versus imitation

Heyes (1998; Heyes & Ray 2000) and Tomasello (1996) claimed that the chimpanzees' behaviour could better be explained as emulation learning. The chimpanzees, they claim, learned the affordance of the rods and more than children used their own methods to achieve the goal of opening the box. Emulating in this case was more adaptive as chimpanzees opened the box with the barrel-latch faster than children. Thus chimpanzees in these studies seem to imitate in a more selective way and emulate when it is more efficient. This trend was also found in Horner & Whiten's (2005) study with chimpanzees. Whiten (2000) argues that "imitation and certain emulation effects should be considered a continuum and not dichotomous". Others claim that attention to results, as seen in emulation, predominates over attention to action in social learning situations, and thus subjects, although capable of action imitation, may mainly reproduce results.

Testing human adults on the same apparatus gives a different perspective on what the AF might be testing. In fact, as Horowitz (2003) claims, each behaviour on this task, as well as other tasks, may be subdivided into so many levels and when a subject is asked "which part of an act should be copied? The variation of adult performances indicates that subjects, and likely, species, answer this differently" (p.333).

The AF, as it was used in these experiments, could not make the fine differentiation between low fidelity action-centred imitation, emulation or object movement re-enactment. Further control groups are needed in which different groups see the same movement produced on different sides of the rods. An additional control for object movement re-enactment versus action imitation should have a control group only see a demonstration of the intended action without the actual movement of the bolts, thus viewing for example an exaggerated twist action without moving the bolt, complemented by the end state of open box.

Experiments employing a "ghost" condition in which the apparatus is seen moving without the model's intervention have been found useful in showing the importance of watching the model act, in order for copying to take place in chimpanzees (Hopper *et al*. 2007)

Although the idea of a two-method task is that the groups serve as a control for each other, the use of a control group in the studies cited, in which subjects do not observe a demonstration at all, gives a better differentiation between social learning and individual learning, emphasizing the benefits of social learning, when latency to success is different.

Sequence learning

Testing the imitation of a sequence has its values from different perspectives. Whiten (1998a) proposed that a sequence can overcome the problem of novelty as the sequence may be based on behaviours from the subjects' repertoire but the distinct combination of the components into a sequence could be novel. The ability to imitate a sequence may also lend weight to the Associative Sequence Learning theory (ASL) (Heyes & Ray, 2000), which claims that social learning is based on an imitation repertoire an individual acquires through experience, which is then used when imitating a novel sequence.

The AF was found very useful in testing sequence level imitation. Chimpanzees but not the other primates tested showed the ability to copy a sequence. The ability to imitate the sequences implies that the chimpanzees were able to represent the "basic plan" of what they had seen (Whiten, 1998).

The more striking results were that the orang-utan and gorillas did not show sequence level imitation, thus disconfirming Byrne & Russon's (1998) claim that gorillas in nature learn complex leaf processing techniques through program level imitation rather than action-level.

The ability to copy a sequence does not specify at what level its components are imitated. It is possible to imitate a sequence using object-centred as well as action-centred imitation, which is what the chimpanzees did in so far as the imitation of the barrel latch was object-centred.

Imitation of sequence in the AF has not yet been tested with monkeys. As the capuchin monkeys showed the ability for object-centred imitation it may be possible that complex food processing in nature (Boinski *et al.* 2003, Panger *et al.* 2002) may be transmitted socially also on the basis of sequence imitation. This still has to be experimentally tested. Some support for this reasoning was found by Subiaul *et al.*

(2004) who showed that macaque monkeys were able to socially learn to tap on a series of pictures in the sequence they had watched another monkey apply.

To conclude

Fragaszy & Visalberghi (1996) claimed that capuchin monkeys only evidence stimulus enhancement. However the AF results showed that at least for the group of enculturated capuchins, higher levels of matching did not fall far short of results for great apes on this task. However it has already been shown (Anderson, 1996; Visalberghi, 1997) that although *Cebus* and *Pan* may seemingly behave in an identical fashion on some tasks, the underlying cognitive mechanisms behind the behaviour of the two may be different.

In the following experimental studies in this thesis I explore the nature of capuchin social learning strategies and capabilities, also testing mother-reared capuchin monkeys living in a more naturalistic environment than the laboratory capuchin monkeys tested in the studies discussed up to now. Before these studies were carried out I conducted a survey of the object manipulation repertoire of these monkeys in order to have as much information about them as possible so as to avoid false positive interpretation of their behaviour in the social learning experiments I planned to carry out. The results of this observational study will described after the following Subjects chapter.

Chapter 4

SUBJECTS

The Capuchin subjects were drawn from two different populations: a mother-reared population and a hand–reared, enculturated population.

The three groups in the mother-reared population were originally one large group living in a petting zoo on Kibbutz Maabarot north of Tel-Aviv. The group belonged to "Helping-Hands" Israel. Six monkeys were taken out of this group in 1994 and housed in a separate cage, as aggression in the group was increasing at that time.

In 1995, when Monkey Park opened, part of the group was brought to the Park and housed in a spacious enclosure. They were named the Enclosure group. Several months later, the six monkeys who had previously been separated from the group were also moved to Monkey Park. They were housed on a separate small island thus giving them the name, the Island group.

All the monkeys in the enculturated group, except for Cheppy, Cheppa and Cacao, were born in the original big group in the petting zoo. Cheppy and Cheppa came from outside Israel and Cacao was born in the enculturated group.

Further information about each monkey is given in Tables 4.1, 4.2, 4.3. and 4.4.

Table 4.1 Subjects in the petting zoo group. Name, gender, short known history and the experiments they took part in**.**

Name	**Gender**	**History**	**Fruit Box Std.**	**Coffee Tin Std.**	**Dipping Box Std.**	**Do As I Do**
Blacky	M	Born 1999 to female in petting zoo group. Middle rank.		√		
Ktantan	M	Born 1997 to female in petting zoo group. Middle rank.		√		
Max	M	Born approx. 1982. Middle rank.		√		
Ziva	F	Born approx. 1980. High rank.		√		

Table 4.2 Subjects in the Enculturated group. Name, gender, short known history and the experiments they took part in.

Name	**Gender**	**History**	**Fruit Box Std.**	**Coffee Tin Std.**	**Dipping Box Std.**	**Do As I Do**
Cheppa	F	Born approximately 1975. She was smuggled into Israel and lived as a pet until she was given to "Helping Hands" in 1984. She moved to my home in 1989. In 1997 moved with the group to the IPSF.	√			
Cheppy	M	Born 1983 in "Helping Hands" USA. Lived in foster families until 1989 then entered training and later placed with a quadriplegic. He returned to the group in my home in 1991.	√	√		
Amy	F	Born 1990 lived in foster family until 1990 then moved to the group in my home.	√			
Sifu	F	Born 1990. Lived in foster family until 1997 then moved to live with Adam and Koko in IPSF.	√	√		
Viva	F	Born 1988. Lived in foster family until 2000.	√			
Koko	M	Born 1990. Lived in foster family until 1995 then housed with Adam in IPSF.	√	√	√	
Hezda	F	Born 1991. Lived in foster family until 1994 then moved to live with the group at my home. In 1996 moved with the group to IPSF.	√	√	√	√
Rusty	M	Born 1990. Lived in foster family until 1994 then moved to live with the group at my home. In 1996 moved with the group moved to IPSF	√	√	√	√
Mango	F	Born 1990. Lived in foster family until 2001. Then moved to the petting zoo group.	√			
Kim	F	Born 1990. Lived in foster family until 2001 then was housed with Koko and Adam in IPSF.	√	√		
Lulu	F	Born 1988. Lived in foster family until1999 then left Israel.	√			
Adam	M	Born in 1988. Lived in foster family until 1996 then housed with Koko in IPSF.		√	√	√
Cacao	F	Born 1995, daughter of Amy and Rusty. In 1996 moved with the group to IPSF.		√	√	√

Table 4.3 Subjects in the Enclosure group. Name, gender, short known history and the experiments they took part in**.**

Name	Gender	History	Fruit Box Std.	Coffee Tin Std.	Dipping Box Std.	Do As I Do
Scarface	M	Born 1975. Alpha male.		√		
Dark	M	Born 1991. Middle ranking.		√		
Dor	M	Born 1995. Eldest son of alpha female.		√		
Dali	M	Born 1998. Youngest son of alpha female.		√		
Dolche	F	Daughter of alpha female.		√		
Hozelito	M	Born 1997. Entered the group at the age of 10 months		√		

These subjects as well as the rest of the Enclosure group participated in the object manipulation observational study described in Chapter 5.

Table 4.4 Subjects in the Island group. Name, gender, short known history and the experiments they took part in.

Name	Gender	History	Fruit Box Std.	Coffee Tin Std.	Dipping Box Std.	Do As I Do
Milky	M	Born in 1990 to a female in the petting zoo group. Alpha male		√	√	
Seffie	M	Born in 1991 to a female in the petting zoo group. Middle ranking.		√	√	
Shpigler	M	Born in 1990 to Dina (now alpha in enclosure group). Low ranking		√	√	
Zorba	F	Born in 1995 to Zed and Milky. High ranking.		√ demonstrator	√	
Zed	F	Born in 1990 to Ziva in the petting zoo group. Alpha female		√	√ innovator	
Duba	F	Born in 1991 to Dina (now alpha in enclosure group). Low ranking			√	
Drorit	F	Born in 1996 to Duba and Milky. Middle ranking.			√	

All the island group subjects participated in the object manipulation observational study described in Chapter 5.

Chapter 5

OBJECT MANIPULATION AND TOOL USE IN THE ISLAND AND ENCLOSURE GROUPS

A survey of object manipulation and tool-use behaviour was carried out on the Island and Enclosure groups. This was done in order to verify that the groups were similar enough in this domain to be used as two equivalent experimental groups for testing social learning. An ethogram of actions with objects was defined for the monkeys. Between and within group differences and similarities are discussed.

Introduction

Capuchin monkeys are one of the few species of primates that have been seen to use tools in nature (van Schaik, Deaner & Merrill, 1999). In a captive environment their tendency to manipulate objects and use tools is even more widespread and more varied (Visalberghi, 1990).

1. Object manipulation and combination

Eye-hand coordination develops early in *Cebus*, and varied precision grips are observed by 13 weeks of age (Costello & Fragaszy, 1988). Infant *Cebus* monkeys start manipulating objects after six month of age (Fragaszy & Adams Curtis, 1991; Natale, 1989) and do so considerably more than infants of other species (Poti & Spinozzi, 1994). According to Gibson these are “species-typical infantile behaviours that help to channel intellectual development in particular directions” (Gibson, 1990, p. 215). Through this complex manipulation of objects these monkeys may learn about the properties of the objects, facilitating adult tool use behaviour (Byrne, 1995).

Comparative studies have found that as adults, capuchin monkeys show a higher tendency to manipulate objects than other primates (Torigoe, 1985) and do so using a wider variety of manipulatory responses than most other animals in terms of the variety of actions observed, the way they combine objects and the body parts they use (Fragaszy *at al*. 1990, Glickman & Sorge, 1966; but see Parker, 1974). In nature, capuchin monkeys have been observed pounding fruits on trees (Izawa & Mizuno, 1977), demonstrating a case of skilful object manipulation which may be enhanced by *Cebus*' high tendency to “explore and manipulate familiar objects and substrates persistently and routinely engage in many actions. This can allow them to discover the consequence of actions, combining objects and surfaces” (Fragaszy, Visalberghi & Fedigan, 2004 p.177).

In captivity this behaviour is even more prominent. Capuchin monkeys show a high degree of curiosity towards objects (Jalles-Filho, 1995), even towards novel ones, something that wild animals tend to avoid at first (Visalberghi *et al*. 2003). Furthermore, *Cebus* in captivity may continue to show interest in the object over time (Visalberghi, 1988; Westergaard & Fragaszy, 1985).

2. Tool use

Beck (1980, p. 10) defines tool use as: "The external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries a tool during or just prior to use and is responsible for the proper and effective orientation of the tool". Such tool use is thought to be a sign of higher cognitive abilities and used to be considered as the trait differentiating humans from other animals (See Beck, 1980 for a review).

Table 5.1 Capuchin monkeys' tool use in nature and captivity.

Purpose	Description	In Nature Reference	In Captivity Reference
Tools for foraging	Using a stone or hard object such as a hammer to open hard husked fruits or oysters	de Oviedo, 1526/1990 (in Fragaszy *et al* 2004); Fernandes, 1991; Struhsaker & Leland, 1977; Boinski *et al*. 2000; Rocha *et al*. 1998*; Langguth & Alonso, 1997; Ottoni & Mannu, 2001; Jalles-Filho *et al*. 2001; Oxford, 2003; Fragaszy *et al.* 2004a.	Erasmus ,1794*; Nolte, 1958; Vevers & Weiner, 1963; Anderson, 1990; Antinucci & Visalberghi, 1986; Westergaard & Suomi, 1993b; Romanes 1883
	Stones as spades to dig in the ground	Moura & Lee, 2004.	
	Stones as knives		Westergaard & Suomi, 1994a; Westergaard & Suomi,1995b; Westergaard & Fragaszy, 1987a.
	Stick for probing for insects or liquids	Chevalier Skolnikoff, 1990.	Romanes, 1883; Westergaard & Fragaszy, 1985; Westergaard *et al*. 1997.
	Stick for raking in out- of -reach object		Romanes, 1883; Harlow & Settlage, 1934; Kluver, 1937.
	Stacking boxes to reach suspended food		Harlow & Settlage, 1934; Kluver, 1937.
	Leaves to scoop up water	Philips, 1998.	
Tools as weapons	Throwing at enemies.	Boinski ,1988; Chapman, 1986; Boinski, 1988; Chevalier Skolnikoff, 1989; Panger, 1997.	Romanes 1883; Cooper & Harlow, 1961; Vitale *et al.* 1991; Fredman, personal observations.
Tools for treatment			Westergaard & Fragaszy 1987b; Ritchie & Fragaszy, 1988; Renan, Fredman & Eizenberg, 2006.

Table 5.1 lists the variety of tool use actions cited in the literature for capuchin monkeys living in nature and in captivity. This table by no means aims to cite all the references for tool use behaviour in capuchin monkeys but rather gives examples of the main purposes for which capuchin monkeys have been seen to use tools.

3. Tool making by *Cebus* monkeys

Some researchers go even further to claim that capuchin monkeys not only *use* tools but also *manufacture* them.

Beck (1980) defines tool manufacture as “any modification of an object by the user or a conspecific so that the object serves more effectively as a tool” (pp. 11-12). This includes actions such as: ‘detach’, ‘subtract’, 'combine’, and ‘reshape’.

Cebus have been seen to detach branches from a tree and subtract the twigs and leaves, in order to prepare twigs for probing (Anderson & Henneman, 1994; Westergaard & Fragaszy, 1987a; Westergaard *et al.* 1997; Westergaard & Suomi 1994c; 1995a), and combine and re-shape leaves and paper in order to create effective sponges (Westergaard & Fragaszy, 1987a).

Westergaard & Suomi (1994a) described how their subjects prepared flaking tools by combining two tools to create chisels and hammers using three different striking techniques. These techniques, the authors claim, resemble stone flaking techniques which pygmy chimpanzees use as well as those used by Oldowan hominid tool-makers.

However it is unclear from their report whether the monkeys understood what was wrong with the tool and modified it accordingly, or whether failure prompted the monkeys, perhaps in frustration, to break or bite on the stick, perhaps even making it less suitable, for example breaking it when in fact a longer stick was necessary? Capuchin monkeys are often observed biting and breaking twigs and branches without using them, or behaving in such a manner in what seems to reflect mere frustration or excitement such as while waiting for food to be brought by the keeper (personal observation).

Goals of the observational study

The object manipulation and tool use tasks employed in this thesis were designed to test social learning. It was therefore important to obtain answers to the following questions before planning the tasks and starting the experiments:

1. What were the subjects of the studies already doing with objects they had in their home areas? This was important to know in advance for two reasons:

    a. In order to design a task which did not include a learned, commonplace action with objects.

b. In order to design a task within the monkeys' capabilities.

2. Were the different groups similar enough in the domain of object manipulation and tool use for valid comparisons about social learning? This was important as the groups were living in very different environments. Further, it was not possible to select subjects randomly from the different groups for the different experimental conditions.

Subjects:

Two groups were observed: the Enclosure group (N=25 , fourteen females and eleven males, age range 2-28 years) and the Island group (N=7, three females and four males age range 2.5-8 years) (see Chapter 4 and Tables 5.2. and 5.3). The Petting Zoo group monkeys (see Chapter 4) were not observed as they were living in a very impoverished cage with no toys or natural objects in it.

The Enculturated group (see Chapter 4) subjects could not be extensively observed, but Table 5.6 describes the actions they were known to do in their foster families. These data were obtained through interviews with the families during the time "Helping-Hands" was still in existence. For six of the monkeys who had lived in my home, the behaviours were personally observed.

Three years after the Enclosure group monkeys were first observed, a second period of observations was conducted on young monkeys who were born in the enclosure during that period. These subjects were thus termed Enclosure Stage 2 group (N=9, five females and four males age range <1-3).

Table 5.2 Monkeys in the Island group. Names in *Italic*s indicate the offspring of the female in the row above.

Monkey	**Gender**	**Age At Testing**
Milky	Alpha Male	8
Seffie	Male	7
Shpigler	Male	7
Zed	Alpha Female	7
Zorba	Male	3.5
Duba	Female	8
Drorit	Female	2.5

Table 5.3 Monkeys in the Enclosure group. Names in *Italic*s indicate the offspring of the female in the row above. Stage one = first observation. Stage two= second observation carried out three years later on the monkeys born in the enclosure during that period.

Stage One			**Stage two**		
Monkey	**Gender**	**Age at testing**	**Monkey**	**Gender**	**Age at testing**
Scarface	Alpha Male	25			
Dark	Male	9			
Sami	Male	9			
Samba	Male	7			
Dvash	Male	7			
Hozelito	Male	3			
Layla	Female	8			
Lymon	Male	2	*Leachy*	Female	3
Diki	Female	28			
Kokus	Male	4	*Kiwi*	Female	2
Cinamon	Female	2			
Kunts	Female	3	*Tsupchik*	Male	1
Lachats	Female	8			
Chets	Female	2	*Chamsa*	Male	2
			Chanita	female	1
Dina	Alpha Female	27			
Dor	Male	4			
Domino	Female	3			
			Nuni	Male	Less than 1 year
Dulche	Female	3			
Dali	Male	2			
Yafa	Female	13	*Yukatan*	Female	3
Yogly	Male	3			
Yoffee	Female	7			
			Ponsho	Female	3
Yuli	Female	2			
Mimi	Female	6	*Mango*	Male	3
Ginger	Female	8			

Procedure:

Each monkey was observed for six sessions lasting twenty minutes each in which all incidences of object manipulation and tool use were recorded. Sessions were carried out twice at three different times of the day, morning, mid - day and afternoon.

An action was recorded as one instance from the moment the monkey moved an object until it changed direction of movement or broke contact with an object or between the object and a surface or second object.

For example one instance of “Scratch” (see Table 5.4) was recorded from the moment the monkey moved the stick on the surface until it changed the direction of movement or broke contact between stick and surface.

Results

I. Modes of action and their frequency

1. Frequency of actions on objects.

In order to compare the frequency with which the monkeys manipulated objects in the groups, the average number of actions used per session was calculated for each monkey (see Table 5.4).

Table 5.4 Frequencies of action on objects in each group; N= number of subjects**.**

	Enclosure Group	**Stage 2 Group**	**Island Group**
N	25	9	7
Mean	5.033	8.13	6.31
Median	4.33	9.17	4.67
Std. deviation	3.71	4.86	3.43
Range	0.50-15.67	1.50-16.0	3.67-13.17

A one way ANOVA test was carried out in order to test whether there was a difference in the frequency of actions with objects between the three groups. The difference was not significant; df(2) f =2.084 p=0.138. Thus, monkeys in the three environments were similarly active with objects.

2. Number of modes of actions observed. An ethogram of twenty five different modes of action on objects was identified in the Enclosure group which was observed first (see Table 5.5). Twenty one of these action modes were also seen in the Island group. One of the modes not found in the Island group was "rake" as there is no mesh on the island and no need to rake-in out-of-reach objects. The fact that three other modes were not seen in the Island group may be due to the much smaller number of

monkeys in that group compared to the Enclosure group (7 and 34 respectively). There were no actions observed in the Island group which were not seen in the Enclosure group and thus the 25 modes were used for comparison between the groups.

One session for each monkey was videotaped. A correlation between the coding from the video and the coding carried out while observing the monkeys using a checklist of behaviours was significant (N=25, r= 0.99, p=0.0).

3. Most frequent actions. Although the two groups live in different enclosures it is evident that the main modes of actions used on objects are similar, and actions which are frequently used in one group are also frequently used in the other (see Table 5.4). The most frequently used action was "pounding" with different objects either on the surface or on a second object. This was followed by "carrying", "hitting" "probing", and "raking". The frequency of each of the 25 different modes of action was ranked for each group. A Spearman rank correlation test shows that there was a high similarity between the Enclosure and Island groups in the frequency at which the different modes were used (N= 25, rs = 0.550, p = 0.004). There was also a high correlation between the two stages of the Enclosure group (N= 25, rs = 0.509, p = 0.009).

4. Distribution in the group. Actions were also coded by the number of monkeys using the action in the group. McGrew & Marchant (1997) classified four levels of tool-use. These are: anecdotal, idiosyncratic, habitual, and customary.

> "*Anecdotal* reports show the possibility of an act, but are always subject to the alternative interpretation of being an accident, an observer's error, or a subject's mistake. Thus, anecdotes alert us to the potential of an organism, especially in striking cases" (p. 790).
>
> "*Idiosyncratic* cases are performed repeatedly by only one individual. Such uniqueness may indicate an innovator or a genius and, so, cannot be generalized as explanations for a population or species" (p. 791).
>
> "*Habitual* events are those repeated by several individuals over time….in captivity limited results may be due to context-specific constraints, such as having only one experimental device for a group of subjects, so that one or a few can monopolize it" (p. 791).
>
> "*Customary* events are enacted regularly or predictably by all appropriate members of a group or population. Lack of universality may result from seasonality of resources or age- or sex-specific influences, and there may be intergroup or population differences" (p. 791).

Applying this classification to the data gathered in this study regarding object manipulation and tool use, the following definitions were made:

Anecdotal - only one incident seen.

Idiosyncratic - only one monkey in the group seen using the mode of action.

Customary - 90% or more of the monkeys seen using the mode of actions (22 or more monkeys in the Enclosure Group, 8-9 monkeys in the Stage 2 Group and 6-7 in the Island group).

Habitual - the remaining 2-21 monkeys in the Enclosure Group, 2-7 in the Stage 2 Group and 2-5 monkeys in the Island Group) (see Table 5.5).

Table 5.5 A description of modes of action with objects found in the Enclosure group and the Island group. The first column for each group gives the percentage for each action/total number of actions for each group. The second column gives the number of monkeys in the group which were seen using the action.

	Enclosure group		**Enclosure Stage 2**		**Island group**	
Action	**% of total group actions**	**monkeys acting**	**% of total group actions**	**monkeys acting**	**% of total group actions**	**monkeys acting**
Pound. Pound object with one or two hands on surface or on a detached object.	18.01	22 (c)	56.7	8 (c)	47.5	7 (c)
Carry. Carry object with hand, mouth or tail**.**	12.97	23 (c)	5.11	4 (h)	11.7	6 (c)
Hit. Hold one end of stick and hit the distal end on surface or object.	10.46	22 (c)	1.46	1 (i)	4.9	3 (h)
Probe. Probe stick in hole.	9.27	14 (h)	2.43	2 (h)	7.55	5 (c)
Rake. Use stick to rake out- of- reach-object.	7.15	9 (h)	-	-	-	-
Rub. Quickly move object on surface, detached object or body with one or two hands**.**	5.43	20 (h)	7.3	5 (h)	6.07	3 (h)
Throw. Throw object on surface or other object/animal using one or two hands**.**	4.9	10 (h)	0.97	2 (h)	4.5	4 (h)
Hide. Put object on head or hold with mouth while covering eyes**.**	4.37	10 (h)	0.49	1 (i)	1.13	2 (h)
Roll. Roll object on surface, body or detached object with one or two open hands.	4.11	14 (h)	0.24	1 (i)	4.9	5 (c)
Scratch. Move stick up and down surface while holding it upright with one or two hands and /or mouth.	3.05	10 (h)	4.9	2 (h)	-	-
Shake. Quickly move either detached object in the air or connected object with one or two hands.	2.91	10 (h)	5.11	4 (h)	0.76	2 (h)
Soak. Soak food in water.	2.78	9 (h)	0.73	2 (h)	1.51	2 (h)
Grate. Grate food on edge of object	2.65	1 (i)	4.6	2 (h)	1.1	2 (h)
Lever. Insert stick in hole or under object. Pull up the stick or sit on it.	2.51	3 (h)	-	-	1.13	1 (i)
Bounce. Bounce object on surface with one or two hands.	1.6	8 (h)	2.43	2 (h)	0.76	2 (h)
Rest. Place food or object on surface or on second object and bite it.	1.46	6 (h)	2.25	5 (h)	-	-
Dig. Use object to dig in the ground.	1.46	5 (h)	-	-	2.26	2 (h)
Spin. Hold object at its middle and spin on surface.	1.06	4 (h)	1.22	2 (h)	0.37	1 (i)
Play with sand. Collect or push away sand either with hands or with object.	1.06	4 (h)	0	0	1.13	3(h)
Draw. Use object to make circle around self.	0.66	2 (h)	2.19	1 (i)	1.51	1(i)
Self treatment. Use twig to insert in nostril or penis or for self grooming.	0.66	3 (h)	-	-	-	-
Contain. Use object to contain water or food.	0.4	3 (h)	0.97	1 (i)	0	0
Look through. Put transparent object on eyes.	0.4	1 (i)	0	0	0.76	1 (i)
Press/mash. Place food or object on surface and push with force.	0.4	3 (h)	0.73	1 (i)	1.13	2 (h)
Toy. Initiate social play by pulling object or splashing water.	0.27	1 (i)	-	-	1.13	2 (h)

a = anecdotal, i= idiosyncratic, c = customary, h = habitual. "-"= absent

Table 5.6 Comparison of the results of the present study, as well as information for the Enculturated group, to the survey of studies of *Cebus apella* described in McGrew & Marchant (1997). In *italic*s is the way the action was observed in the subjects of this study.

Mode	**Mcgrew & Marchant Summary**	**Island & Enclosure Groups**	**Enculturated Group**
1. Absorb/sponge	c	h	c
2. Bait	a	-	-
3. Balance/climb	a	-	-
4. Brandish/flail	a	h	c
5. Club	a	-	i
6. Contain	a	h	c
7. Dig	h	h	c
8. Drag *(carry)*	h	c	c
9. Drape *(wear on head)*		h	h
10. Drop	c	-	-
11. Hammer/pound	a	c	c
12. Ladder	c	-	-
13. Probe	a	h	c
14. Prod/jab	a	-	-
15. Pry/lever *(to break tool)*	h	h	-
16. Reach/rake	a	h	c
17. Stack	-	-	-
18. Swing	h	-	-
19. Throw (aimed)	-	h	c
20. Throw (unaimed)	h	h	c
21. Wipe	-	-	c
22. Cushion	-	-	h
23. Toy	-	h (island)	h
24. Groom	a	h	h
25. Cut/pierce	h	-	h
26. Chisel	a	-	-
27. Grind	h	h	h

a = anecdotal, i= idiosyncratic, c = customary, h = habitual**.** "-"=absent

II. Differences between monkeys – gender and age.

As seen above, there was no significant difference between the groups; thus the enclosure in which they were living did not have an influence on their activity. However, were there differences within the groups?

1. Gender differences: There was a difference between males and females in the frequency of interacting with objects. Males in the Enclosure group (mean=7.24) manipulated objects significantly more than females (mean =3.30) (t (23) =3.07, p =

0.005). Males in the Island group (mean =6.92) also manipulated objects more than females (mean =5.50) but this difference was not significant (t (5) = 0.506, p = 0.635). There was no gender difference between the Stage 2 monkeys in the Enclosure group: males (mean =8.125) manipulated objects just as often as females (mean = 8.13). (t(8)=-0.002, p=0.998) This may be related to the fact that all monkeys were juvenile and gender differences in activity levels may reveal themselves more with age However, when comparing all subjects together, the difference between genders was significant (male mean=7.36; female mean=4.70, t (39) =2.201, p =0.034) (see Table 5.7).

Table 5.7 Gender differences in frequency of actions on objects in each group.
N= number of subjects.

	Enclosure Group		**Stage 2**		**Island Group**		**All**	
Gender	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
N	11.00	14.00	4.00	5.00	4.00	3.00	19.00	22.00
Mean	7.24	3.30	8.13	8.13	6.92	5.50	7.36	4.70
Median	6.67	2.83	7.83	9.19	5.42	4.17	6.50	4.17
Std. deviation	4.18	2.13	4.77	5.49	4.29	2.46	4.09	3.65
Range	0.83-15.67	0.50-7.67	2.83-14.00	1.50-16.00	3.67-13.17	4.00-8.33	0.83-15.67	0.50-16.00

2. Age differences: Two age groups were considered: Juvenile (1-5 years) and Adult (over 5 years). As there was only one infant (under one year) in the group at the time of testing, its results were added to the Juvenile group. The juvenile monkeys manipulated objects significantly more than older monkeys
(Island: adult mean=4.54, juvenile mean=10.75, t (5) =4.215 p=0.008; Enclosure adult mean= 3.00, juvenile mean= 7.24, t (23) =3.44 p= 0.002). This effect was also found when comparing all subjects including the Stage 2 juvenile monkeys (adult mean= 3.43, juvenile mean=7.91, t (39) =4.16, p = 0.00) (see Table 5.8).

Table 5.8 Age differences in frequency of actions on objects in each group.

N= number of subjects.

	Enclosure Group		**Stage 2**	**Island Group**		**All**	
Age	**adult**	**juvenile**	**juvenile**	**adult**	**juvenile**	**adult**	**juvenile**
N	13.00	12.00	9.00	5.00	2.00	18.00	23.00
Mean	3.00	7.24	8.13	4.54	10.75	3.43	7.91
Median	2.17	6.50	9.16	4.17	11.01	3.17	7.67
Std. deviation	2.41	3.67	4.86	0.98	3.80	2.20	4.13
Range	0.50-7.50	3.00-15.67	1.50-16.00	3.67-6.17	8.33-13.70	0.50-7.50	1.50-16.00

III. Complexity of manipulation.

Matsuzawa (1996) presented a system to describe different levels of actions on objects (similar to Greenfield's 1991 system for the development of tool- use and language). The system first identifies the objects involved in the action and then the actions upon these objects. Using a tree structure it is possible to identify the hierarchical organization of object manipulation. This system has already been used by Westergaard (1999) to analyze reports on tool use in C*ebus apella* in the wild and in captivity. The levels can be described as follows:

Level 0 - manipulating one object.
Level 1 - manipulating an object on a surface.
Level 2 - manipulating two objects and surface.
Level 3 - manipulating three objects.

The hierarchical level of the action is characterized by the organization of nesting clusters. The data collected in this survey were analysed using this hierarchical system (see Table 5.9).

Table 5.9 Complexity of Manipulation. Results for all subjects combined were analyzed according to level of hierarchical organization. The percentage of the actions out of the total number of actions in the survey is in brackets.

	Structure Level 0	**Structure Level 1**	**Structure Level 2**
Pound		Pound object on surface (27.6%)	Pound object on object; Pound object on object while holding them in both hands (6.5 %)
Carry	(10.5%)		
Hit	Hit hand with stick (0.3 %)	Hit surface or body with object (6.3%)	Hold object in hand and hit it with a stick (0.2%)
Probe		(7.0%)	
Rake		(3.8%)	
Rub	Rub on body (0.1%)	Rub object on surface (6.2%)	Rub object on object while holding both objects (1.0%)
Throw	Throw sand in the air (0.4%)	Throw object at other object/animal; splash water at duck (3.4%)	
Hide	(2. 5%)		
Roll	Roll object from arm to palm; between two hands; on inner thigh (1.6%)	Roll object on surface or in paddle (1.5%)	
Scratch		(2.3%)	(1.4%)
Shake	(2.6%)		
Soak		(1.7%)	
Grate		(1.7%)	
Lever		(1.5%)	
Bounce	(0.5%)	(1.7%)	
Rest		(1.1%)	Stand stick in sand then rest food on it (0.3%)
Dig		(1.2%)	
Spin	(1.0%)		
Play with sand	Pull or push sand with hands (0.2%)	Using a stone to pull or push sand (0.5%)	
Draw		(1.3%)	
Self treat	(0.3%)		
Contain		Use object to contain water (0.5%)	Put object in object and carry (0.1%)
Look through	(0.3%)		
Press/mash	(0.6%)		
Toy		(0.3%)	
	20.9 %	**69.6 %**	**9.5 %**

Most actions observed were of Level 0 (20.9 %) and Level 1(69.6%). The higher percentage of Level 1 manipulations than Level 0 is in line with previous accounts of the high tendency of *Cebus* monkeys to bring objects in contact with other objects or surfaces (e.g. Fragaszy & Adams Curtis, 1991).

Level 3 actions were observed, but very rarely (see Table 5.10)

Table 5.10 Level 3 actions. The first column for each group gives the number of instances an action was observed**.**

	Enclosure Group		**Island Group**	
Action	Number of occurrences	monkey	Number of occurrences	monkey
Soak pellets then crush them by pounding stone	3	Mimi	2	Zorba
Put pellets in container then put container with pellets in water to soak	1	Yogly	-	-
Break stick then probe in hole	4	Domino	-	-

Conclusions

1. Juvenile monkeys manipulated objects more frequently than adult monkeys. This finding is similar to earlier accounts of *Cebus apella* (Jalles-Filho, 1995; Visalberghi, 1988). Gender differences were found only in the Enclosure group with males manipulating objects more frequently than females.

2. The most important result for the studies in this thesis is that the Island and Enclosure groups were similar in terms of activity levels and frequency of using the different action modes. This justified using these groups as the two experimental groups in the study despite the differences in group size and environments.

3. Most actions with objects observed in the monkeys were Level 0 and Level 1. Thus, tasks to test social learning involving these levels should be designed to be in the range of capability of the monkeys. A task using Level 2 actions could be used to test the strength of social learning over individual learning as this level of action on objects is not usually seen in these monkeys' activity but is still within their capacity. This level was used in the Dipping-Box task (see Chapter 7).

Chapter 6

OBSERVATIONAL LEARNING FROM TOOL USING MODELS BY HUMAN-REARED AND MOTHER-REARED CAPUCHIN MONKEYS (*Cebus apella*)[2]

Studies of wild capuchins suggest an important role for social learning, but experiments with captive subjects have generally not supported this. Here we report social learning in two quite different populations of capuchin monkeys (*Cebus apella*). In experiment 1, human raised monkeys observed a familiar human model open a foraging box using a tool in one of two alternative ways: levering versus poking. In experiment 2, mother-raised monkeys viewed similar techniques demonstrated by monkey models. A control group in each population saw no model. In both experiments, independent coders detected which technique experimental subjects had seen, thus confirming social learning. Further analyses examined fidelity of copying at three levels of resolution. The human-raised monkeys exhibited fidelity at the highest level, the specific tool use technique witnessed. The lever technique was seen only in monkeys exposed to a levering model, by contrast with controls and those witnessing poke. Mother-reared monkeys instead typically ignored the tool and exhibited fidelity at a lower level, tending only to re-create whichever result the model had achieved by either levering or poking. Nevertheless this level of social learning was associated with significantly greater levels of success in monkeys witnessing a model than in controls, an effect absent in the human-reared population. Results in both populations are consistent with a process of canalization of the repertoire in the direction of the approach witnessed, producing a narrower, socially shaped behavioural profile than among controls who saw no model.

Introduction

Capuchin monkeys are renowned for their tool using ability, which among non- human primates in the wild is surpassed only by chimpanzees (Beck 1980; Visalberghi 1990). Capuchin (spp) monkeys have been seen using a stick to club a snake (Boinski**,** 1988; Chapman, 1986) drop or throw objects at conspecifics and intruders (Chapman, 1986; Chevalier-Skolnikoff, 1990; Klein, 1974), crack oysters with a hard object (Fernandes, 1991; Hernandez**-**Camacho & Cooper 1976), pound palm-nuts together to crack them open (Struhsaker & Leland, 1977) and use leaves to scoop out water from tree cavities (Philips, 1998). More recent reports have described use of a branch to crack open nuts (Boinski *et al*. 2000), using stone hammers for a similar purpose (Langguth & Alonso, 1997; Ottoni & Mannu, 2001;

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[2] This chapter is based on a paper published in Animal Cognition: Fredman, T. & Whiten, A. (2008). The nature and consequences of observational learning from tool using models in human-reared and mother-reared capuchin monkeys (*Cebus apella). Animal cognition, 11, 295*-309.
The introduction for this paper repeats much of what is said in the earlier review chapters.

Fragaszy *et al.* 2004a) and using stones to dig up roots and sticks for various probing tasks (Moura & Lee, 2004).

In captivity, where capuchin monkeys may have contact with a larger set of objects and more “leisure“ time to manipulate them, they have been reported to exhibit an even broader range of object manipulation and tool use behaviours (Beck, 1980; Gibson, 1990; Visalberghi, 1990; Fragaszy *et al.* 2004).

Capuchin monkeys, especially the young, show attentiveness to the actions of other group members in captivity (Fragaszy *et al.* 1997) as well as in the wild (Boinski *et al.* 2000, 2003) and other free-ranging environments (Ottoni & Mannu 2001; Ottoni *et al.* 2005) raising the question of what the observers are able to extract from watching the behaviour of others. Nishida (1987) suggested that the sophisticated food-processing behaviour of capuchin monkeys in the wild may imply cultural learning. More recently, systematic comparisons across three field sites supported this, identifying variations in processing methods for 20 of 61 foods eaten, and demonstrating a correlation between dyadic proximity and shared techniques (Panger *et al.* 2002). Further evidence that capuchins sustain local traditions has come from studies of social behaviour (Perry *et al.* 2003). However in the wild, it is extremely difficult to disentangle the various social and individual learning processes that may be responsible for regional differences in behaviour patterns. In the case of functional foraging techniques, it is particularly difficult to be sure that environmental constraints do not channel individual learning to produce the variations observed. Discriminating between different grades of social learning is even more challenging.

For these reasons we have examined social learning of tool use experimentally. Because authorities including Tomasello (1990) and Galef (1992) have emphasized imitation as a potentially crucial mechanism permitting cultural transmission, and because Custance *et al.* (1999) found tentative evidence of imitation in one of the populations of capuchin monkeys available to us for the present study, we designed our experiments to identify any imitative fidelity occurring, but also examined subjects' behaviour for evidence of other kinds of social and non-social learning.

Visalberghi, Fragaszy and colleagues have tested social learning of tool use in an extensive series of studies with capuchins, *Cebus apella* (e.g. Antinucci & Visalberghi, 1986; Westergaard & Fragaszy, 1987a; Visalberghi, 1987, Fragaszy & Visalberghi, 1989 Visalberghi & Trinca, 1989; reviewed by Visalberghi & Fragaszy

1990, 2002). Results did not support the hypothesis that these monkeys were imitating. For example, capuchin monkeys were unable to learn, through observation, the use of a stick to push a reward out of a horizontal transparent tube (Visalberghi, 1993). Based on many similar results, Visalberghi & Fragaszy (1990, 2002) have concluded that the capuchin monkeys they studied do not acquire tool use through imitation, although more basic social learning processes such as stimulus enhancement may influence manipulative behaviour. Whereas imitation requires learning "some aspect(s) of the intrinsic form of an act" (Whiten & Ham, 1992) from a model, stimulus enhancement involves only the drawing of attention to relevant items. Visalberghi and Fragaszy noted evidence of stimulus enhancement in the tube-task, where monkeys observing a proficient tool user would be more likely to touch or manipulate the stick and tube; however, they did not imitatively integrate the objects into a copy of the expert's technique.

By contrast, Custance *et al*. (1999) reported more evidence of matching in a study employing capuchin monkeys that had been reared by humans and exposed to human home environments, in readiness for induction into a 'Helping Hands' program for quadriplegics. In this study, the model was a human caretaker. Each monkey saw bolts that held shut an "artificial fruit" box either pulled and twisted out, or poked out. The monkeys later tended to make the bolts move in the same way as had their human model. Custance *et al*. concluded that this indicated either a crude level of imitation, or 'object movement re-enactment', in which the movements of the bolts themselves were copied.

These results raised the question of whether, if faced with one of two alternative methods of employing a tool, more evidence of tool-use copying would be obtained with this population of monkeys than others studied elsewhere. This question was addressed in Experiment 1, below. For Experiment 2, utilising a different population of capuchins, we trained monkey models to perform each of the same two techniques in front of other group members, all of whom had been reared by their mothers, rather than by humans. Potential contrasts in social learning in these human-reared and capuchin reared populations is of interest in relation to controversies about
the issue of 'enculturation' (Tomasello, Kruger & Ratner 1993; Bering 2004; Tomasello & Call 2004). This issue has hitherto centred on evidence that apes reared in intimate interaction with humans appear to have heightened powers of social

cognition that include imitation. One of the populations of capuchins we studied could be considered ‘human enculturated’: would it behave differently in relation to social learning of tool use?

We note that an ideal experimental design for teasing apart factors influencing social learning in these different populations would involve four conditions, generated by the combination of human versus capuchin rearing, and human versus capuchin models. Insufficient subjects were available to achieve this. We judged that, given this constraint, it would be a valuable first step to perform two separate parallel experiments. For one of these, it made obvious sense to use capuchin models for the capuchin-reared subjects. In the second, since the human-reared capuchins were primarily familiar with, and indeed apparently bonded to, a human caretaker, we thought it logical to make this person the model for that population. However, it is important to stress that the resultant multiple differences between the circumstances of the two experiments significantly constrain conclusions we can draw about causes of any differential results. They are better thought of as two complementary windows upon social learning propensities of capuchins.

For each population, the two-action design (Dawson & Foss, 1965) outlined above was supplemented by addition of a control group of monkeys that did not view a model open the box, but instead found the box baited and in its final, already-opened state; they also witnessed the tool tapped on the apparatus, to provide some stimulus enhancement. Thus we wished to know if watching either of the modelled techniques had an effect over and above this combination of stimulus enhancement and opportunity to learn from the end state normally achieved in a modelled episode.

Experiment 1: Enculturated Capuchins Observing a Human Model

Subjects

Subjects were ten hand-raised capuchin monkeys (*Cebus apella*); four males and six females with a mean age of 8.25 years (range from 3.5 to 14 years). All were raised in a close relationship with human foster families for at least their first 3 years of life as part of a "Helping Hands" project in Israel, which prepared capuchin monkeys to aid quadriplegics (Willard *et al.* 1982).

Six of these subjects were still with their human foster families at the time of the study. Only one of them, Cheppy, had been systematically trained and had worked with a quadriplegic. His training was based on behavioural shaping (for a description of the tasks he had learned, see Custance *et al.* 1999).

Apparatus

The centre of a lid (5 cm diameter) of a coffee tin was cut out and thick paper was glued across this hole. The entire lid was then painted with brown paint so as to give the impression of a homogeneous surface. The inside of the tin was padded so that the monkey could easily reach the reward once the lid was opened. To change the overall appearance of the tin, a class of object that subjects might have seen while living with the foster family, it was embedded in a wooden box (18 x 18 x 10 cm). A screwdriver was attached to the box by a nylon cord approximately 60 cm long (see Fig. 6.1).

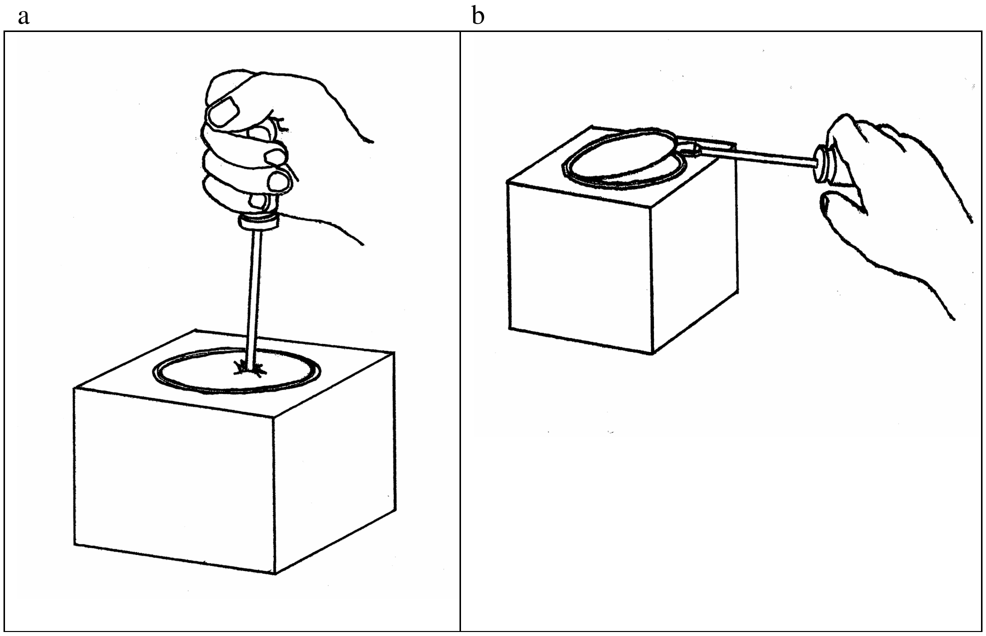


Figure 6.1 The apparatus. Two methods of using the tool in order to gain the reward were: (a) poking through the centre of the lid (b) levering open the lid at its rim

Procedure

Two alternative techniques to obtain the reward were demonstrated by T.F., who was familiar to all the subjects:

Poke technique: The screwdriver was held in the right hand and was used to poke a hole in the centre of the lid, by stabbing down twice. After the second stab the screwdriver was not raised again but was used to enlarge the hole made in the paper in the centre of the lid by moving it twice from side to side. The reward (raisins) was thus visible and the hole was big enough for the subject to put its hand in and obtain the reward.

Lever technique: The screwdriver was held in the right hand and its distal edge was inserted between the rim of the lid and the top of the tin. The lid was then popped off by pulling down the handle of the screwdriver and using it as a lever.

The monkeys were randomly assigned to one of two experimental groups (observe poke vs. observe lever) or to a control group. Each group had a mixture of ages and genders (see Table 6.1).

Table 6.1 Assignment of Human-Raised Subjects to Experimental and Control Groups.

Name	Gender	Age (Yr)	Condition
Rusty	Male	8	Poke
Cacao	Female	3.5	Poke
Viva	Female	10	Poke
Hezda	Female	7	Lever
Kim	Female	8	Lever
Cheppy	Male	14	Lever
Adam	Male	10	Control
Koko	Male	8	Control
Sifu	Female	8	Control
Mango	Female	9	Control

Each monkey was tested individually by TF, with the monkey's foster parent required to sit entirely passively to the rear of the monkey. Tin opening was demonstrated to the monkeys in the experimental groups three times before their first trial and then once before each of their second and third trials. This procedure is comparable to that used by Whiten (1998a) in a study with chimpanzees. The monkeys were allowed to take the reward after the demonstration (Caldwell & Whiten, 2003 found that marmosets learned more in such a scrounging context). Each demonstration lasted approximately 6 s and monkeys were typically attentive.TF made no vocalisations whilst demonsrtating. The tin was reloaded out of sight and the subjects were then allowed two minutes to manipulate the box.

The subjects in the control group were shown the open tin with a reward in it.

The lid was torn in the centre and placed next to the box. Thus, the monkeys were given clues to both kinds of end results experienced by animals in the experimental conditions; torn in the middle as by "Poke", and detached from the tin as resulting from "Lever". In addition, the screwdriver was handled for several seconds, as for experimentals, and tapped onto the tin and lid. This was a control for stimulus enhancement in the experimental groups. Each session lasted for no more than twenty minutes. All sessions were videotaped and subsequently coded by TF and two independent judges, as explained in different sections of the results.

Because of small sample sizes, principal pairwise comparisons between the two experimental groups, and between these and controls were tested through Mann-Whitney U tests. For each variable so tested, we first provide a Kruskal Wallis test across the three groups. However, even where this test did not attain the level of p = 0.05 or below required to offer confidence in the pairwise statistics, we report all of these because the overall pattern of marginal significant trends may be instructive (Table 6.3). One tailed p values are reported as the predictions are clearly uni-directional that watching a method will enhance the success of using it.

Results

Manipulation of Tool

Given the tool had been handled by an experimenter during demonstration and also while presenting the apparatus to the control group subjects to control for stimulus enhancement, it was predicted that if stimulus enhancement occurred, all subjects would manipulate the tool in some way or other when tested.

There was indeed no difference between the number of subjects in the experimental groups and the control group in whether the tool was handled (Fisher test, p = 0.6). All monkeys handled the tool, with the exception of one in the “Lever” group.

Influence of type of model: human coders’ overall judgments.

Did the monkeys learn through observation how to use the tool? If so, we would expect to see a difference between the two experimental groups in the way they used the tool to solve the task. In order to test for such a difference, two independent judges first viewed the behaviours of the ten subjects without knowing what each monkey had seen. The coders were also unaware of the fact that a control group was included in the study.

Judges scored the behaviour of the subjects on each trial on a scale from one to seven:

A score of 1 indicated that they were confident that the monkey had seen a "Poke" technique, whereas a score of 7 indicated that they were confident the monkey had seen the "Lever" technique. A score of 4 meant the judge could not tell by the behaviour of the monkey what technique that subject had seen. Each monkey's scores were averaged across trials. The independent coders showed a high degree of agreement in their scores with a Spearman's Rank correlation of Rs(10)=0.85, P=0.002.

There was a significant difference in the scores across the three groups (Kruskal Wallis test, $\chi^2(2)=6.162$, $p<0 .05$). Scores were significantly higher in the Lever group (median=6.15) than the Poke group (median=2.0); (Mann–Whitney test, U=0, $n_1=3$, $n_2=3$, p=0.05); see Fig. 6.2. Thus, viewing the overall behaviour of each monkey, the judges were able to correctly determine which of the two techniques the subjects in the experimental groups had seen. There was also a significant difference between the Control (median=4.19) and Poke (median=2) groups (U=0, $n_1=4$, $n_2=3$, p=0.029) but not between the Control and Lever group (U=3.5, $n_1=4$, $n_2=3$, p=0.229); (see Fig. 6.2.)

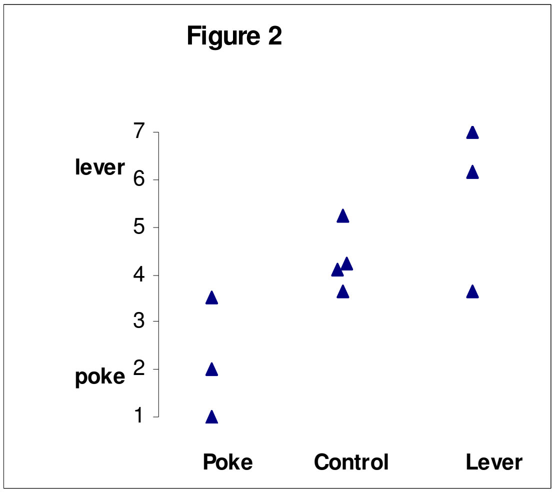


Figure 6.2 Mean scores of the two independent coders' confidence ratings for each hand-reared monkey that had witnessed models poke or lever, or as controls saw no model. A score of 1 indicates that the coders were confident the subject had observed Poke. A score of 7 indicates that the coders were confident the subject had observed Lever. A score of 4 indicates the coders were not able to decide what method the subject had observed.

Influence of type of model: behaviour counts.

Which components of the demonstration were monkeys copying? To answer this question, twenty five different modes of behaviours were identified and coded by T.F. (See Table 6.2). Additionally, a naive observer coded one trial, taken at random, for each monkey. There was a high degree of agreement between the two sets of codings across subjects and behaviour categories. ($rs_{250} = 0.93$, $P=0.001$). A behavioural profile was produced for each monkey by calculating the percentage of times each of the twenty-five movements was used out of the sum total of movements used by that monkey. These behavioural profiles enabled an analysis of Behaviour Modes and Orientation of Behaviours, explained further below.

1. Behaviour Categories

A. "Poke" versus "Lever" tool-use behaviour. To first measure the extent to which a monkey tended towards being a "leverer" or a "poker", behaviours most related to either "lever" or "poke" demonstrations were summed (categories 2+4+5+7+10+18+19=Lever; categories 1+8+9+22+23+24=Poke; see Table 6.2) The sum of all Lever behaviours was divided by the sum of all Lever and Poke behaviours, generating an index of the tendency to behave in one way as opposed to the other. An LP-index of 1 meant the monkey was a consistent "leverer" whereas an LP index of 0 meant the monkey was a consistent "poker".

Table 6.2 Coded Behaviour Categories. A = High fidelity matching with tool; B = General manipulation of tool; C = Low fidelity matching, no tool; D = Non-tool manipulation. Exp. 1= testing the enculturated monkeys; Exp. 2= testing mother-reared monkeys; Exp. 3= retesting a subgroup of the enculturated monkeys.

		Behaviour Categories	**Description**	**EXP. 1**	**EXP. 2**	**EXP. 3**
WITH TOOL	A	1. Poke	Pick up tool and bring it straight down on centre with/without piercing paper.	√	√	√
		2. Lever	Insert tool under rim and pull down handle of tool.	√		√
		3. Scratch	Move tool from side to side while the point of the tool is in contact with centre of the lid.	√		
		4. Lever gap	Insert tool in gap between tin and box and pull down the tool.	√		
		5. Lever centre	Pierce centre with tool and pull it down in a levering movement.	√	√	
		6. Lever near centre edge	Pierce paper close to the edge with tool and pull it down in a levering movement.	√		√
		7. Insert tool in rim	Place tool in rim without levering movement.	√		√
		8. Poke gap	Pick up tool and bring it straight down into the slight gap between the box and tin.	√		
	B	9. Poke box	Pick up tool and bring it straight down on wooden box.	√		√
		10. Lever box	Push edge of tool into wooden box and pull down tool handle.	√		
		11. Scratch box	Move tool from side to side while the point of the tool is in contact with the wooden box.	√		
		12. Bang tool	Hold tool horizontally and bang it on apparatus with one or two hands.	√	√	
		13. Roll tool	Roll tool horizontally on apparatus with one or two hands.	√		
		14. Handle object with tool	Bring unconnected object in contact with tool.	√		
		15. Bang tool on ground	Bang tool horizontally/ vertically on ground.		√	
		16. Move tool	Move tool away from apparatus.		√	√
		17. Hold or bite tool	Hold tool with one or two hands or bite tool	√	√	√
NO TOOL	C	18. Pull rim with teeth.	Hold rim with teeth and pull upwards.	√	√	
		19. Pull rim with fingers	Insert fingers under rim and pull upwards.	√	√	√
		20. Scratch near rim	Scratch lid on inner side of rim with index finger.		√	
		21. Scratch centre	Scratch centre of lid with index finger		√	
		22. Touch/tear centre with mouth	Place lips or teeth on centre and lick or bite.	√	√	
		23. Push centre with hand	Push centre with fingers or palm of hand.	√	√	
		24. Tear centre with hand	Tear centre with fingers.	√	√	√
		25. Put object on lid	Put unconnected object on lid.	√		
	D	26. Pull tin	Hold edge of tin and try to pull out of wooden box.	√	√	
		27. Push/pull box	Turn the wooden box.	√	√	
		28. Object on box	Put unconnected object on wooden box.	√		
		29. Scratch box	Scratch box with index finger		√	
		30. Bite box	Bite or lick wooden box.	√	√	

Overall, differences in the LP index across the three groups were not significant (Kruskal Wallis test, $\chi^2(2)=5.378$, $P=0.068$). However, the LP index was significantly higher for the Lever group (median=0.83) than the Poke group (median=0.0) ($U=0$, $n_1=3$, $n_2=3$, $p=0.05$); see Figure 6.3. This is consistent with the conclusions from the overall judgements above, that the two groups were behaving differently towards the apparatus as a function of seeing different models.

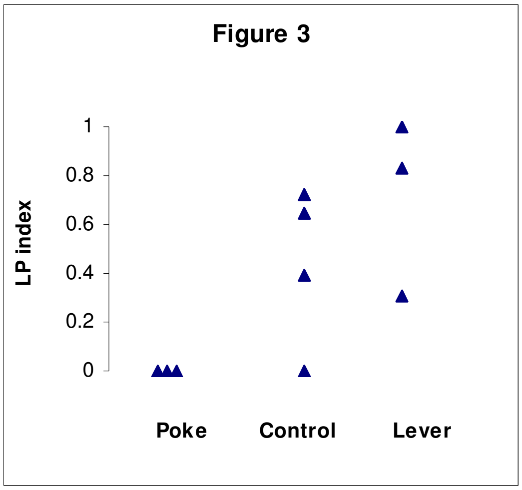


Figure 6.3 LP (Lever/Poke) Index of overall behaviour for each monkey in each condition. An LP-index of 1 indicates the subject was a consistent "leverer" whereas an LP index of 0 indicates the subject was a consistent "poker".

The control group produced intermediate LP indices, overlapping the distributions of both Lever and Poke groups ($P>0.05$) in both cases (see Fig. 6.3)

The LP index was based on a large range of behaviours. Further analysis was needed in order to tease out precisely where the difference lay. To this end, behaviour counts were analyzed at three different levels of potential matching:

Level 1: Target behaviour - using the specific behaviour demonstrated (categories 2 for Lever and 1 for Poke: see Table 6.2).

Level 2: Target-like behaviour - using a similar tool-use behaviour to that seen but used on different parts of the apparatus (categories 4+5+7+10 for Lever and 8+9 for Poke).

Level 3: Outcome-aimed behaviours- behaviours appropriate for the outcome witnessed but not using the tool (categories 18+19 for Lever and 22+23+24 for Poke).

Two subjects did not use the tool at all (although one of these did manipulate and bite it) and were therefore excluded from the analysis of the first two levels. Sufficient sample sizes for analysis were here achieved by combining controls with the experimental group who had not witnessed each act, as explained in the sections that follow. Median ranges and statistical results for these analyses are summarised in Table 6.3).

1. Target behaviours. There was a significant difference between the groups on Lever acts (Kruskal Wallis test, $\chi^2(2)=6.857$, $P=0.032$). In fact, Lever acts were found only in the Lever group (Table 6.3). This difference between the Lever and the two other groups combined was significant ($U=0$, $n_1=2$, $n_2=6$, $p=0.036$); see Fig. 6.4a.

Poke behaviour was found in all three groups (Kruskal Wallis test, $\chi^2(2)=4.5$, $P=0.105$), but more frequently in the Poke group than in the two other groups combined (Poke vs Control + Lever, $U=0$, $n_1=2$, $n_2=6$, $p=0.036$); see Fig. 6.4b.

Four monkeys in the two experimental groups very closely reproduced the behaviour they had observed. Two appeared to be "locked" exclusively onto the behaviour they had seen even when they did not succeed. Not being successful on their first attempt they stopped responding, but on seeing an additional demonstration they responded again using the same action that they had observed.

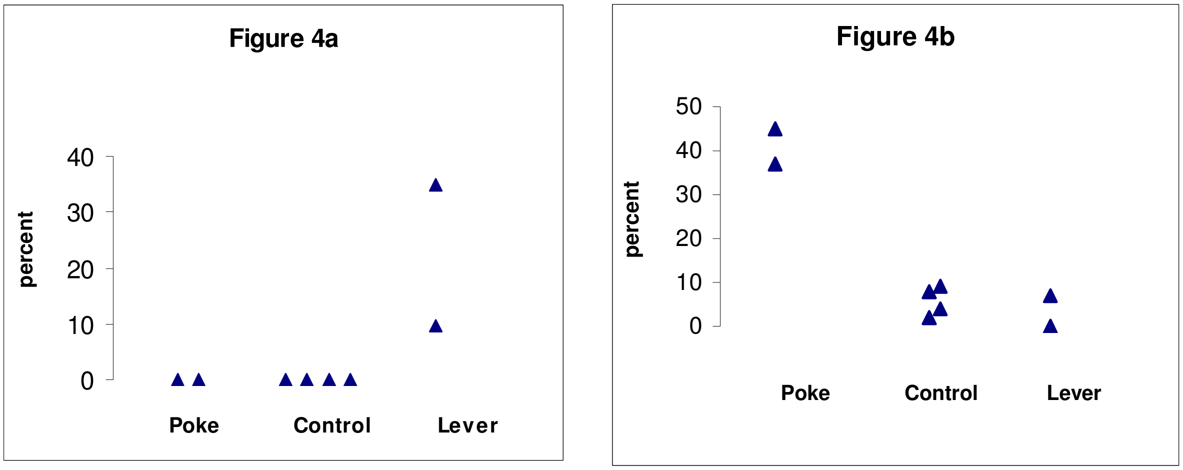


Figure 6.4 (a) Percentage of lever-target behaviours used by each subject.
(b) Percentage of poke-target behaviours used by each subject.

2. Target-like behaviour. A comparison between the groups in displaying Lever target-like behaviours showed that there was no significant difference (Kruskal Wallis $\chi^2(2)=4.38$, $P=0.11$). The difference in Poke target-like behaviour across the groups was not significant: Kruskal Wallis test, $\chi^2(2)=5.44$, $P=0.066$. Both Poke and Lever groups had higher values than Controls, but likewise this failed to reach significance ($U=0$, $n_1=2$, $n_2=4$, $P=0.067$ for both comparisons).

A closer look at the behaviour of the subjects in the control group showed that there was no difference in the tendency to use general poking as compared to general levering. Both behaviours were equally common in their repertoires (Wilcoxon test, $N=4$, $T = 2$, $p = 0.59$).

3. Outcome-aimed behaviours. If all that the monkeys had learnt from the demonstration was how the lid moved or opened they could have tried to re create this end result without necessarily using the tool. Thus, if the monkeys in the Poke group had recognised only that in order to gain the reward it was necessary for the lid to be pierced, we might expect behaviours aimed towards this outcome such as pushing the centre of the lid with the hand or tearing the centre with hand and teeth. The tendency to use these modes of behaviour was compared between the groups. This analysis was done including the two non tool-using subjects.

There was no significant difference between the groups in the tendency to use poke-outcome behaviours (Kruskal Wallis test, $\chi^2(2)=1.612$, $P=0.45$; see Table 6.3).

In the same vein, it was expected that if the monkeys in the lever group were focused on the movement of the lid they would tend to use behaviours such as pulling open the lid from the rim with the hands or teeth. A significant difference in the tendency to use lever-outcome behaviours was found between the groups (Kruskal Wallis test, $\chi^2(2)=6.636$, $P=0.036$; see Table 6.3). There was a significant difference between the two experimental groups ($U=0$, $n_1=3$, $n_2=3$, $P=0.05$). Comparing subjects who had seen Lever with all those who did not also showed a significant difference ($U=1$, $n_1=3$, $n_2=7$, $P=0.017$); see Fig. 6.5. Subjects in the Poke group were not using these behaviours at all and a comparison between them and the monkeys in the other two groups shows a significant difference ($U=1.5$, $n_1=3$, $n_2=7$, $P=0.033$). Viewing one technique thus had a negative effect on the probability of behaving in other ways.

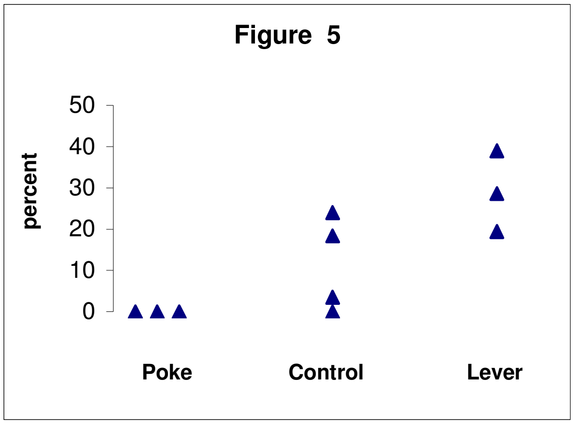


Figure 6.5 Percentage of lever-outcome-aimed behaviours used by each subject.

Monkeys in the Control group were using both sets of outcome behaviours almost equally (Wilcoxon N=4, T=4, p=0.71).

B. Range of behaviours. An index of "behavioural range" was calculated by awarding each monkey one point for each behaviour category recorded up to a maximum of 25. The comparison of interest here is between the two experimental groups combined (median 6.5) and the control group (median 12). The control group generated a wider range of behaviours than the experimental groups (U=2, n_1=6, n_2=4, P=0.014; see Fig. 6.6).

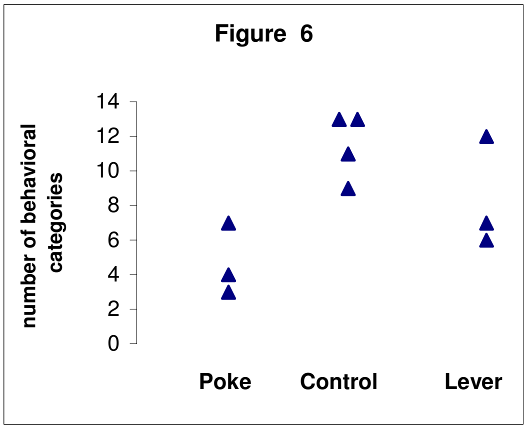


Figure 6.6 Number of behaviour categories (see Table 6.2) recorded for each monkey: its 'behavioural range index'.

Table 6.3 *Human* reared study, summary results. Medians (in bold), range (in brackets, rounded to whole numbers except behavioural index) and differences with p<0.1 (<0.05 in bold). Dashes indicate p>0.1.

	Lever	**Control**	**Poke**	**L vs. P**	**L vs. C**	**C vs. P**	**L vs. P+C**	**P vs.L+C**
Observer's judgment	**6.15** (4 –7)	**4.19** (3-5)	**2** (1-3)	**P = 0.05**	-	**P = 0.029**	Na	na
Lever target behaviour	**10** (0)-35)	**0** (0-0)	**0** (0)-0)	-	**-**	-	**P = 0.036**	-
Lever-like, with tool	**17.3** (0)-39)	**10.15** (0-31)	**0** (0)-0)	-	P = 0.071	-	-	P = 0.09
Lever-outcome no tool	**28.6** (19-39)	**10.95** (0-24)	**0** (0-0)	**P=0.05**	P = 0.057	-	**P = 0.017**	**P = 0.033**
Poke target behaviour	**0** (0)-7)	**5.95** (2-9)	**37** (0)-45)	-	-	P = 0.064	-	**P = 0.036**
Poke-like, with tool	**0** (0)-7)	**8.6** (8-33)	**0** (0)-5)	-	P = 0.067	P = 0.067	-	-
Poke-outcome no tool	**0** (0-63)	**8.75** (0-15)	**33.4** (7-52)	-	-	-	-	-

C. Orientation of behaviours

For another comparison between controls and the two experimental groups, points were summed across behaviours oriented towards the target parts of the apparatus (i.e. the lid of the tin, categories 1-7+18, 19, 22-24, 25). The experimental subjects were more orientated towards these target parts of the apparatus (U=2, n_1=4, n_2=6, p=0.019)

A comparison of the specific part of the lid to which the subjects were orientated (categories 2+7+18+19=Rim, categories 1+5+22+23+24=Centre) showed a significant difference between the groups (Kruskal Wallis χ^2 (2)=7.469, p=0.024). The subjects in the Lever group were significantly more orientated towards the rim of the lid than the subjects in both the "Poke" group (U (3, 3) = 0, p=0.050) and the Control group (U (3, 4) = 0, p=0 .029).

A comparable analysis of the difference between the groups in orientation towards the centre of the lid was not significant (Kruskal Wallis χ^2(2)=2.230, p=0.328). In summary, monkeys were in general more orientated towards the centre of the lid, but subjects in the Lever group showed a strong orientation towards the rim, which was absent in the Poke group subjects.

D. Benefit of Social Versus Individual Learning.

It has been established thus far that the behaviour of the monkeys that had viewed the model was influenced by what they had seen: they differed from each other and from controls. We assessed if these effects were beneficial to the experimental groups by comparing them to controls on two measures: rate of success and latency to success.

<u>Success rate</u>: Two of the subjects in the experimental groups did not succeed in obtaining the reward. One did not appear to be motivated at all; the other tried, but did not exert enough force into the movement. Two of the subjects in the control-group did not succeed either, although they manipulated the entire apparatus. A Fisher test showed no difference between the control and the experimental groups in whether individuals were successful (Fisher test, p=0.43).

<u>Latency:</u> The difference between the groups in the latency to first success was also not significant (Kruskal Wallis test, χ^2(2)=3.11, P=0.211) (subjects that did not manage to retrieve the reward during the three two-minute trials were coded as taking 361 sec).

Sample size and Bonferroni corrections

When several multiple comparisons are carried out on the same set of data there is a risk of making Type 1 errors, rejecting H_0 when it is true (e.g. it is statistically likely that one out of 20 comparisons will be significant at 0.05 by chance). The Bonferroni correction is a conservative way to safeguard against this mistake, by lowering the alpha value to account for the number of comparisons being performed. Thus, if there were n dependent or independent hypotheses tested, then the statistical significance level that should be used for each hypothesis separately is $1/n$ times what it would be if only one hypothesis were tested.

Using the Bonferroni correction does on the other hand dramatically increase the risk of making Type II errors, not rejecting a H_0 when it is false.

It is true that were Bonferroni corrections applied in the statistical analysis of the data of Experiment 1, most comparisons would have been statistically insignificant, especially as the sample size was very small. A significantly larger sample size is ideally needed, however such numbers of enculturated monkeys do not exist and the results do raise important issues discussed in the following section.

Discussion: Experiment 1

The following discussion is based on results obtained from uncorrected p values for multiple comparisons, and thus can be regarded as trends that will require larger sample sizes to rigorously test in future.

Viewing one behavioural method as opposed to another had a definite influence on the way observing monkeys later behaved, that was apparent at a global level to the independent coders. Quantitative analysis showed that watching a model was effective in influencing orientation of subjects even when not using a tool, towards the specific part of the apparatus contacted by the model (the lid) whereas control group subjects were orientating their behaviour towards all its parts. Furthermore, watching the model influenced the orientation to a very specific part of the lid, i.e. the rim for the Lever group. Since these analyses were concerned with actions not using a tool, the effect documented is not due to the monkeys simply replicating what they saw, but is better characterized as a highly localized stimulus enhancement effect. A similar effect has also been shown in marmosets (Caldwell &

Whiten, 2004).

Yet, localized stimulus enhancement can not in itself account for the different behaviour of the groups. Analyzing the subjects' behaviour on three different levels of fidelity to the model enabled us to see that the third level of outcome-aimed behaviours played a role too, consistent with what previous taxonomies of social learning have called 'emulation' (Tomasello, 1990) or more specifically, 'result emulation' (Whiten *et al*. 2004). However, whereas lever-outcome-aimed behaviours contributed to the difference between the groups, with monkeys pulling at the rim with hands and teeth instead of the tool, poke-outcome-aimed behaviours did not. In addition, subjects in the Lever group tended to use a levering movement when trying to pop open the lid using the tool, whereas the Poke group subjects, like controls, did not display this behaviour at all. First level behaviours were thus a prominent difference between these groups.

Several subjects were very persistent in using the observed movement although they were not always successful. The fact that they hardly (one subject) or never (two others) shifted to other movements from their wide potential repertoire (as indicated by the controls) emphasizes a strong influence of observation on the behaviour of the monkeys. But were they imitating?

Imitation, novelty and response facilitation

Target levering in the current study appears to meet Whiten and Ham's definition of imitation quoted earlier. Subjects produced very similar behaviours to the one they had watched the model perform. The fact that the subjects tried again and again to use the technique – in the case of levering, carefully inserting the screwdriver under the rim of the lid and levering despite lack of success, suggests a strong effect of social learning. Moreover, levering did not occur spontaneously in the control group. To this extent it is not part of these monkeys' repertoire (Helping Hands monkeys were not allowed to handle screwdrivers, knives or other similar objects that could be used as levers, nor is lid opening part of their training), and so not easily dismissed as mere facilitation of existing habits. The two target behaviours in the present experiment bear some resemblance to broad categories of "poke" and "lever" action schemes, which in a general sense are "in the monkeys' repertoire", as was seen in the behaviour of the subjects in the control group. However, several authors have acknowledged that an imitated behaviour is unlikely ever to be "totally novel", suggesting that it must suffice for *some aspects* of the behaviour to be novel (Whiten & Ham, 1992), or organized in a different way (Visalberghi & Fragaszy, 1990a) in order to imply imitative learning. In the present study, using a lever behaviour in a very precise way to pop open the lid was not in the repertoire of the monkeys. Subjects in the control group did not even try to use it. The type of general levering seen in controls was similar to that which is often used to break a piece of wood with a levering action (personal observations).

This was not true of the Poke technique, which was eventually used by two of the subjects in the control group. It is perhaps more parsimonious to argue then that target-poke behaviour was facilitating an existing response, although the present experiment nevertheless involved learning to direct it to a specific location on a novel task.

Canalization

Whatever conclusions are drawn on evidence for imitation specifically, our results indicate the operation of significant social learning. It seems that observing the behaviour of a conspecific may work as a "sieve": sifting out the inappropriate responses and concentrating on those functional for the task. In this study control animals were using a wide variety of actions towards the apparatus, whereas the monkeys in the experimental group were using a much smaller set of actions. Although capuchin monkeys may poke and lever in different ways and for different purposes, they are influenced by observation to use one of the movement types available to them rather than an alternative and to use it in a particular way and for a specific purpose, at the expense of alternative actions.

Boesch (1996) describes how young wild chimpanzees use only a subset of behaviours available in their repertoire when learning how to crack nuts by watching others. This subset is limited to the actions they observe when adults in their group crack nuts. Chimpanzees in Zurich Zoo, given the same materials, produced a greater range of actions. Boesch calls the focussing process “canalization”; “In nut cracking behaviour, social canalization through imitation is at work and it confines the individual learning possibilities to the different types of objects that could be used to pound the nuts" (Boesch, 1996 p.257). A somewhat similar process of canalization seems to be taking place in the capuchins we studied. Control group subjects were using many movements in their repertoire whereas the experimental group subjects chose mainly, and sometimes only, the movement they observed.

Thus, through a process of localized stimulus enhancement the monkeys are able to receive information about very precise parts of the object to be dealt with. If, in addition, viewing a conspecific canalizes specific behaviours from a wide repertoire, then these two processes acting together could be highly influential in learning a new task in a social environment.

Social vs. Individual Learning

A clear advantage of social learning over individual learning was not seen in this study. Overall, monkeys who had not observed a model were just as successful in gaining a reward as were those who saw a demonstration.

The process of social learning through canalization may appear to be potentially beneficial in avoiding the necessity to try out different behaviours in the repertoire, saving time. On the other hand, canalization may have a blocking effect, as seen with the persistence of some subjects in using the observed behaviour although it was not working for them. In a case like this it could have been more beneficial for them to try a different way of solving the task, and indeed one of the subjects (Kim) did this. This monkey, although observing the "Lever" technique, seemed to have guessed right from the beginning that the lid was not solid and tore through it with her teeth no matter what she saw and without using or touching the tool.

However, conclusions about functional issues should not be over emphasized in this particular experimental setting. In a captive environment, where manipulating objects and tools is a playful occupation and not necessary for survival, time saving considerations may be a less important factor. Since the subjects were tested alone there was also no competition with conspecifics. These factors may partly explain why lose-shift strategies appeared uncommon.

Enculturation

Visalberghi & Fragaszy (1990a) concluded that as far as tool-use behaviour is concerned, their capuchins did not show evidence of learning to perform a task from observing the performance of skilful others. The results of this study and of a previous study carried out with many of the same monkeys (Custance, Whiten & Fredman, 1999), imply that the capuchins we studied are showing a higher degree of social learning than others tested elsewhere. One possible explanation is that the subjects in the present experiment and in Custance *et al.* (1999) were brought up in a special environment with a very close relationship with a human care taker. Experiments with hand reared chimpanzees have suggested that these chimpanzees were more inclined to imitate than mother reared chimpanzees (Tomasello *et al.* 1993b). Call and Tomasello (1996) suggested that imitative abilities, among other skills, are a result of human raised chimpanzees being treated as intentional beings, as with human infants (Kaye, 1982).

During such interaction with a human, capuchin monkeys too may learn to be more attentive to the behaviour of the human “significant other”. It has not been established that capuchins understand the intentions of others, but monkeys may learn to be attentive to the behaviour of the familiar human through recognizing their utility as "social tools" without necessarily understanding their intentions (Bering, 2004). The behaviour of Cacao, one of the subjects in this study, illustrated this tendency. She tried to gain the reward using the action she had observed ("Poke") but was not using enough force to pierce the thick paper. She then consistently (10 times) tried to get help by taking the experimenter’s hand and putting the tool in it. When the experimenter did not react to her request she poked the lid gently with the tool and put it in the experimenter’s hand again. Similar behaviours are found in human raised chimpanzees who use imperative gestures to gain human attention when requesting (Call & Tomasello, 1996).

In addition, the fact that the human raised capuchins are almost always tolerated and close to the human while learning a new task enables them to benefit from the skilled human. Visalberghi & Fragaszy (1990a), while discussing the way young chimpanzees learn from their mothers, suggested that this "coaction of a skilled model and learner, in which the model allows the learner to participate intimately in its actions, is probably the most effective setting for learning a novel motor skill in nonhumans" (p.267). Possibly the special social context of our own studies encouraged such a tendency.

However, the influence of human rearing cannot be seriously addressed without testing mother-reared capuchin monkeys on the same task. This is the subject of the next experiment.

Experiment 2: Mother-Reared Capuchins Tested Socially

Our second experiment was designed to test social influence on the acquisition of the same tool use task as in Experiment 1 but in a more naturalistic environment. The monkeys in this experiment were mother-reared capuchin monkeys living in social groups. They were tested after observing conspecific models.

These monkeys did not have as much experience manipulating and using tools as the hand-raised monkeys; nevertheless, they have had access to natural objects such as sticks, stones and pieces of wood, which they occasionally manipulated and used as tools (e.g. using a stick to rake in out-of-reach objects, or a stone to break open hard-shelled food items).

Methods

Subjects

The subjects were 14 capuchin monkeys (*Cebus apella*); 11 males and 3 females (age range 2-25 years) living in three different groups, which used to constitute one big group. Two of the groups live in a Monkey Park near Tel Aviv in open outdoor enclosures (one of 80 m^2, the other 500 m^2). The third group lives in a large cage (120 m^2) in a nearby zoo.

Apparatus

The same task as in Experiment 1.

Table 6.4 Assignment of mother–raised subjects to experimental and control groups.

Name	Gender	Age (Yr)	Condition	Housing
Seffy	Male	8	Poke	Enclosure 1
Shpigler	Male	9	Poke	Enclosure 1
Milky	Male	8	Poke	Enclosure 1
Zed	Female	9	Poke	Enclosure 1
Blacky	Male	5	Lever	Cage
Ziva	Female	20	Lever	Cage
Max	Male	17	Lever	Cage
Ktantan	Male	3	Lever	Cage
Scarface	Male	25	Control	Enclosure 2
Dark	Male	9	Control	Enclosure 2
Dor	Male	5	Control	Enclosure 2
Dali	Male	2	Control	Enclosure 2
Dolche	Female	3	Control	Enclosure 2
Hozelito	Male	3	Control	Enclosure 2

Procedure

The procedure was similar to that in Experiment 1 but with four differences:

1. The groups, not the individual monkeys, were assigned to either one of two experimental groups or a control group (see Table 6.4). Due to different housing conditions, the group housed in the cage was assigned to one of the experimental groups and not the Control. This was done in order to make sure that their somewhat more barren housing, that might lead to less target behaviours overall, would not be confounded with the control condition.
2. The monkeys were not tested individually, but rather together with other members of their group. Separating these monkeys from their companions caused them to be

nervous. (The hand–raised monkeys were used to being alone). Several task boxes were used simultaneously in order that all subjects could gain access to the task.

3. The demonstrator was a high ranking (but not alpha) group-mate male likely to gain attention (these monkeys were not accustomed to being in close contact with humans, unlike the hand-raised monkeys).

4. The monkeys viewed all the demonstrations before being tested on the task themselves. They shared the reward with the model monkey. This was done since it was estimated that once the subjects would have the chance to try the box themselves it would be difficult to have the model demonstrate again. In the one group, the monkeys observed the model in an adjacent cage; in the second, the model was with the subject monkeys in their enclosure

The two monkey models were taught the different methods through shaping. Monkey models performed actively with the observer present, like the human model taking just a few seconds to open the tin, and observers appeared to attend well, perhaps encouraged by the opportunity top gain food at this time.

The procedure for the control group was similar to that in Experiment 1. The subjects were presented with both end states of the open tin: the lid was torn in the center and placed next to the box. The screwdriver was handled by the experimenter (familiar to the monkeys and known to sometimes show interesting objects) for a few seconds and tapped onto the tin and lid. Subjects were then allowed to take the reward out of the open tin. Each subject had three consecutive tests after five such experiences.

All sessions were videotaped.

Results

Occurrence of Tool Use and Tool Manipulation

Eleven of the fourteen subjects (78%) manipulated the tool, but only one of them used it as a means to open the lid. This monkey, Milky, had witnessed some of the training trials for the model and thus his behaviour should be treated with reservation. He used the tool to pierce through the lid as soon as the trial began. He used a poking movement as well as a levering movement on the paper covering the centre of the lid. By watching the model learn to use the tool this monkey had possibly learnt the behaviour but of course we cannot be sure. There was no significant difference between the number of subjects in the experimental groups and the control group in the tendency to handle or manipulate the tool (Fisher test, P=0.15)

Influence of Type of Model: Overall Judgments

Although tool-using behaviour was scarcely seen, the question still remained whether the groups differed in behaviours reflecting what they had seen.

Two independent judges viewed the behaviour of the subjects in the same way as in Experiment 1, so that scores of 1 and 7 corresponded to Poke and Lever respectively. The independent coders showed a high degree of agreement in their scores, with a Spearman's Rank correlation of Rs(14)=0.89, P=0.05. The difference in the behaviour of the monkeys in the three groups was tested using the mean score given by the two coders.

The overall differences between the groups on this score did not achieve significance (Kruskal Wallis $\chi^2(2)=5.316$, P=0.07), although scores were higher in the Lever group (median=5.73) than in the Poke group (median=2.75) (Mann Whitney test, U= 1.5, $n_1=4$, $n_2=4$, P =0.043). There was a significant difference between the Control (median=4.77) and Poke groups (U=2.5 $n_1=4$, $n_2=6$, P=0.024) but not between the Control and Lever groups (U=9.5, $n_1=4$, $n_2=6$, P=0.32); see Fig. 6.7.

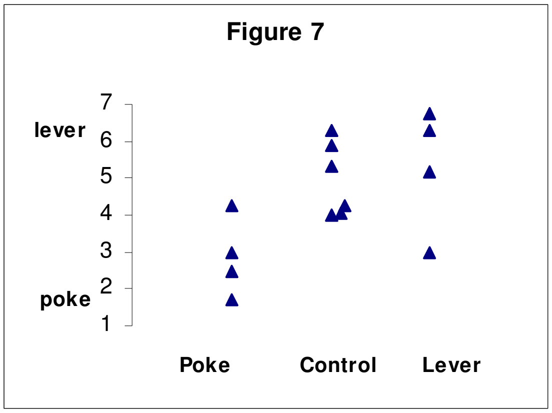


Figure 6.7 Mean scores of the two independent coders' confidence ratings for each mother-reared monkey that had witnessed models poke or lever, or as controls saw no model. Scores as for Figure 6.2.

Influence of Type of Model: Behaviour Counts

The monkeys in this experiment were not using as many behaviours as those in Experiment 1. On the other hand there were four extra non-tool use behaviours identified by TF for this group of monkeys (categories 15,16, 20, 21, 29; see Table 6.2).

A naive observer coded one random trial for each monkey. There was a high degree of agreement across subjects and behaviours between the two codings (Rs_{238}=0.99, p=0.001).

A behavioural profile was produced for each monkey, as in Experiment 1. As no tool use behaviour was seen (except for the one subject) analysis was carried out only on the third level, outcome-aimed behaviours.

Outcome-aimed behaviours. All behaviours appropriate for the outcome witnessed, either Lever (categories 18+19) or Poke (categories 1+21+22+23+24) were summed producing an index of outcome-aimed behaviours for each monkey**.**

The difference between the groups in lever outcome-aimed actions was significant (Kruskal Wallis $\chi^2(2)$=9.74, P=0.01). Subjects in the Lever group (median=54.1) scored significantly higher than the Poke group (median=0.0) (U=0, n_1=4, n_2=4, P=0 .014); see Fig. 6.8. As in Experiment 1, subjects in the Poke group did not use this method at all. There was no significant difference between the Control and Lever groups in this behaviour (U=4, n1=4, n_2=6, P=0.057).

Poke outcome-aimed behaviours were also significantly different between the three groups (Kruskal Wallis $\chi^2(2)$=6.214, P=0.045). The Poke group scored significantly higher on Poke outcome-aimed behaviours (median = 58.0) than the Control group (median=28.2) (U= 0, n_1=4, n_2=6, P=0.005, see Table 6.5)

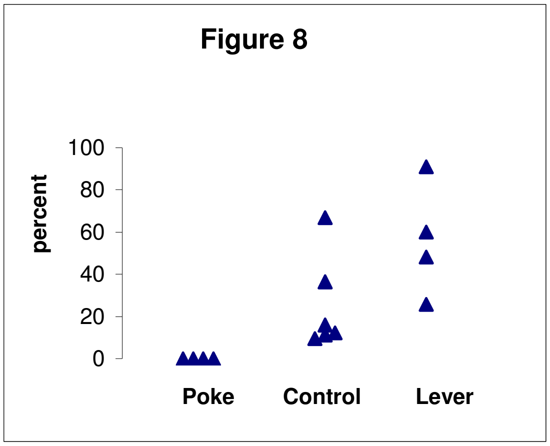


Figure 6.8 Percentage of lever-outcome-aimed behaviours used by each monkey

The difference between Poke (median=58.0) and Lever (median=5.0) groups was not significant, principally because one of the subjects in the Lever group mainly pierced the lid (U=3, n1=4, n_2=4, P=0.08). However, the Poke group showed more Poke outcome-aimed behaviours than Control and Lever combined (U= 3, n_1=10, n_2=4, P=0.007).

There was no significant difference in the tendency of the control group subjects to use Lever versus Poke outcome-aimed behaviours (Wilcoxon test n=6 T = 1.153, P=0.156).

B. Range of behaviours. An index of "behavioural range" was calculated as in Experiment 1. Each monkey was awarded a point for each behaviour category recorded up to a maximum of 16. The difference between the groups on this score was significant (Kruskal Wallis $\chi^2(2)$=9.491, P= 0.01). A comparison of this index between the two experimental groups combined (median=4) and the control group (median=7.5) showed a significant difference (U=5, n_1=8, n_2=6, P=0.001); see Fig. 6.9. Thus the subjects in the experimental groups were focused on a smaller set of behaviours than the controls.

Table 6.5 Mother reared study, summary results. Medians (in bold), range of behaviour counts (in brackets, rounded to whole numbers) and differences with p<0.1 (<0.05 in bold). Dashes indicate p>0.1.

	Lever	**Control**	**Poke**	**L VS. P**	**L VS. C**	**P VS. C**	**L+C VS P**	**P+C VS L**
Observers' judgment	**5.72** (3- 7)	**4.77** (4-6)	**2.75** (2-4)	**P = 0.043**	-	**P = 0.024**	-	-
Lever Outcome	**54.1** (26-91)	**14.15** (10–67)	**0** (0-0)	**P= 0.014**	P = 0.057	**P = 0.005**	-	**P= 0.012**
Poke Outcome	**5** (0-74)	**34.5** (18-42)	**58** (44–100)	-	-	**P = 0.005**	**P=0.007**	-

C. Orientation of behaviours. Orientation towards the target area (the lid) did not show an overall difference between the groups (Kruskal Wallis $\chi^2(2)=4.92$ P=0.085), but a significant difference was found in testing only between the Control group (median=55.7) and the two experimental groups combined (median=92.9) (U=7, $n_1=8$, $n_2=6$, P=0.015).

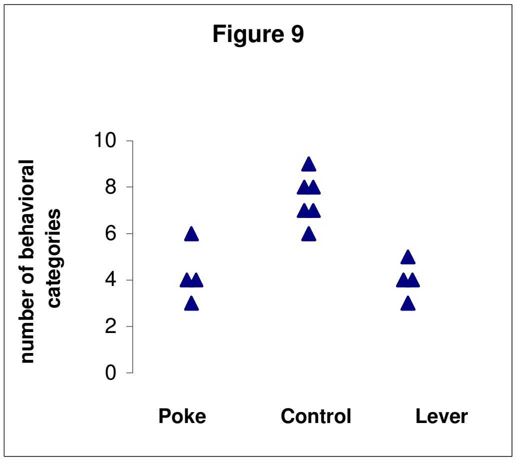


Figure 6.9 Number of behaviour categories (see Table 6.2) recorded for each monkey: its 'behavioural range index'.

Benefit of Social vs Individual Learning.

It has been established thus far that the behaviour of the monkeys viewing the model was influenced by what they had seen. Two measures for benefits of social learning were tested.

Success: Although only one applied the tool to the task, seven of the eight monkeys in the experimental groups were successful in obtaining the reward compared to only two of the six in the control group. A Fisher test showed a marginally significant difference in success rate between the control and the experimental groups combined (Fisher exact test, P=0.06).

Latency: Comparing the latency to first success showed a significant difference between the groups (Kruskal Wallis $\chi^2(2)=7.26$, P=0.027). Subjects in the control group (median=361 sec) were significantly slower gaining the reward compared to the subjects in the two experimental groups combined (median=26 sec) (U=4, $n_1=6$, $n_2=8$, P=0.003).

Discussion: Experiment 2.

Imitation, Emulation, and Object Movement Re-enactment

The monkeys did not learn tool using behaviour from watching the model, but experimentals were nevertheless faster and more successful than controls in opening the lid. There are several possible explanations for these results. One is that the observers had recognized a desirable result in the models' opening of the lid and were trying to attain this using their own method. This corresponds with Wood's (1989) definition of learning through emulation, later called result-emulation by Whiten *et al.* (2004). Being orientated to this outcome, many of the monkeys perhaps saw the tool as an obstacle rather than a means to reach their goal and so moved it aside. However, learning through result-emulation implies that only the end-state of the stimuli is learned whereas monkeys in the control group were also presented with the end-state of the apparatus taking the reward from the opened box, yet were less successful in later opening the box by themselves. This means that some aspect of what the model performed was important in order to produce successful goal orientated behaviours and not just the mere end-state of the object.

Several different aspects of this performance could have been important for learning. As discussed for Experiment 1, the difference in outcome-aimed behaviours implies greater matching to the results attained by the model than mere stimulus enhancement. Perhaps then, the monkeys were re-creating the movement of the lid, which they observed in the demonstration, a form of emulation sometimes called affordance learning (Whiten *et al.* 2004). Alternatively, the monkeys may have perceived the tool as an extension of the demonstrator's hand and roughly copied the action of the "tool-and–hand" on the apparatus, using their own hand but without a tool. This could be interpreted as a low – fidelity form of imitation. Differentiating such alternative explanations would require further experiments designed explicitly to do so such as 'ghost' conditions in which only the objects move (Tennie, Call & Tomasello, 2006).

Canalization

The process of canalization was evident for this population of monkeys as it was in Experiment 1. Monkeys who viewed a demonstrator used a much smaller set of actions than the ones who had not seen the demonstrator. Furthermore, although both sets of outcome aimed behaviours were in the repertoire of the monkeys, as demonstrated in the behaviour of the control group, monkeys who viewed one method hardly used any behaviours related to the other method. This effect was strong for the

Poke group but less so for the Lever group (one of the subjects in this group mainly used poke actions).

Social versus individual learning

In this experiment, as opposed to Experiment 1, social learning had a strong influence on the success rate. Monkeys who had not seen a model were less successful in gaining the reward than those who had. The two control subjects who did succeed in gaining the reward did so an order of magnitude more slowly than subjects in the experimental groups. As this experiment was carried out in a group environment, competing with conspecifics may have resulted in the subjects being more focused, attempting quickly to gain the rewards rather than playing with the apparatus as the subjects in Experiment 1 were perhaps more prone to do.

General Discussion

Canalization

In this context of social learning, canalization refers to a focusing or sculpting within the behavioural repertoire, neglecting potential responses to a situation that has not been witnessed, whilst strengthening, adapting and /or copying aspects of the actions observed to be performed by others. Canalization appears to be a strong underlying process of social learning in the capuchin monkeys we studied, although it took somewhat different forms in the two populations.

Hand Raised vs. Mother Reared Monkeys

The behaviour of the monkeys in both populations showed that they were definitely influenced by observing a model skilfully open the box. However, this influence was manifested in different ways, mainly in that the mother reared monkeys typically did not use the tool. As noted in the introduction, the feasibility of explaining such differences is constrained by the fact that multiple factors differentiate the groups. However of these, we judge two are relatively implausible. First, the human may have offered a clearer model, but even so, the capuchin models were assiduous tool users, so tool use was amply present in the displays witnessed. Second, the mother reared monkeys were tested in a group; yet again, they had ample opportunity to watch a tool-using model and use the tool if they wished. Accordingly we suggest that some other explanations are more worthy of discussion and further study, relating to either technical experience or cognitive abilities.

a. Experience in Tool Using

The human-raised monkeys had extensive experience with different objects and tools. During their lives they may have learned about the properties of these (Call & Tomasello, 1996), rendering it easier for them to socially learn relatively new ways to utilize a tool. This could be tested by supplying mother-reared monkeys with a richer variety of objects in the long term, offering tool and material experiences that human reared monkeys have typically had, then testing for imitation of tool use.

b. Different Cognitive Processes

Enculturation may alternatively have the effect of elevating some cognitive processes, which may facilitate imitation or other relatively sophisticated social learning mechanisms. If so so we might expect to find evidence for other cognitive abilities such as perspective taking or sensitivity to other' intentions in this population.

c. Perceiving humans as social tools

A third possibility is that the monkeys had learned to use humans as a "social tool", using a familiar human for help (as when we observed them handing over an object to receive help in manipulating it) as well as benefiting from carefully watching his/her behaviour. This would imply that a capacity for complex social learning is in the range of *Cebus* cognitive ability, being manifested when the monkey lives in a social environment that emphasizes and rewards close attention to a competent other. Discussing ape-human relationships, Bering (2004; see Tomasello & Call 2004, for a reply) described this as the 'apprenticeship hypothesis' and our results appear consistent with it. Further studies as indicated above will be needed to discriminate amongst these forms of 'enculturation' effect.

Experiment 3: Reversal of previous habits

Experiment 1 was carried out with a small number of subjects, as there are very few enculturated monkeys. In an attempt to override this limitation, four subjects were tested again after several years. Adding the results of this experiment to those of the corresponding experimental groups in Experiment 1 increases the sample size for statistical analyses. If the monkeys are more inclined to use the method demonstrated to them in Experiment 3, despite having seen and tried the other method in Experiment 1, this would strengthen the evidence for high fidelity social learning in the enculturated monkeys.

Method

Subjects

The subjects were two females, Hezda and Cacao, and two males, Adam and Rusty (see Table 6.6.).

Table 6.6 Assignment of enculturated subjects to experimental conditions.

	Gender	**Age(Yr)**	**Condition Ex. 1**	**Condition Ex. 3**
Hezda	Female	15	Lever	Poke
Adam*	Male	18	Control/Lever	Poke
Cacao	Female	11	Poke	Lever
Rusty	Male	16	Poke	Lever

* It should be noted that Adam was part of the control group in Experiment 1 but later was taught "Lever" as it was planned he would serve as a model in Experiment 2. Thus, for the sake of this experiment he was considered to have seen Lever in the past and therefore was shown Poke in Experiment 3. However the result of his behaviour in Experiment 1 is representive of the control group he was assigned to.

Apparatus

The same as in Experiment 1.

Procedure

The same as in Experiment 1.

Results

Influence of type of model: human coders' overall judgments.

Independent judges scored the behaviour of the subjects on each trial on a scale from one to seven:

A score of 1 indicated that they were confident that the monkey had seen a "Poke" technique, whereas a score of 7 indicated that they were confident the monkey had seen the "Lever" technique. A score of 4 meant the judge could not tell by the behaviour of the monkey which technique the subject had seen. Each monkey's scores were averaged across trials.

Unfortunately, there was no significant agreement between the independent coders (Spearman's Rank correlation of Rs (4) =0.4, P=0.6). This disagreement appeared to be a result of ranking Rusty's trials since he used elements of both methods together. Eliminating Rusty's trials results in a perfect correlation between the coders Rs (3) =1. Accordingly, these results were used together with the averaged results of the two coders for Rusty.

The results of the independent coders in Experiment 3 were then added to the corresponding results from Experiment 1 providing altogether 5 data points for each experimental condition. This involves using data from certain individuals twice. To this extent, these pairs of data points are not statistically independent. However, for the present analysis, the reversal of the demonstration type (e.g. from poke in Experiment 1 to lever in Experiment 3) means that the duplicated use of these subjects weights the study against finding statistically significant effects, rather than artifactually creating them. Thus below, the data are treated as if independent and a Mann-Whitney test applied.

There was a significant difference in the scores across the three groups (Kruskal Wallis test, $\chi^2(2)=6.45$, P=0 .04). Scores were significantly higher in the Lever group (median=5.33) than the Poke group (median=3.0); (Mann–Whitney test, U=0, $n_1=5$, $n_2=5$, P=0.016). Thus, the new results strengthen the conclusion that by viewing the overall behaviour of each monkey, it is possible to correctly determine which of the two techniques the subjects in the experimental groups had seen. There was also a significant difference between the Control (median=4.19) and Poke (median=3) groups (U=2, $n_1=4$, $n_2=5$, P=0.032) but not between the Control and Lever groups (U=6.5, $n_1=4$, $n_2=5$, P=0.23) (see Table 6.7).

Influence of Type of Model: Behaviour Counts

The monkeys' behaviour was coded using the categories in Table 6.2 . A naive observer coded one random trial for each monkey. There was a high degree of agreement across subjects and behaviours between the two codings (Rs=0.96, P=0.001).

In order to measure the extent to which a monkey tended towards being a "leverer" or a "poker", behaviours most related to either "lever" or "poke" demonstrations were summed (categories 2+4+5+7+10+18+19=Lever; categories 1+8+9+22+23+24=Poke; see Table 6.2) The sum of all Lever behaviours was divided by the sum of all Lever and Poke behaviours, generating an LP index of the tendency to behave in one way as opposed to the other.

The LP behavioural index was then calculated for each monkey. An LP-index of 1 meant the monkey was a consistent "leverer" whereas an LP index of 0 meant the monkey was a consistent "poker". These results were then added to the results of Experiment 1 in order to obtain a larger pool of data for this population of monkeys.

Overall, differences in the LP index across the three groups were now significant (Kruskal Wallis test, χ^2 (2) =7.49, P=0.024). The LP index was significantly higher for the Lever group (median=0.66) than the Poke group (median=0) (U=0, n_1=5, n_2=5, p=0.004). The difference in the LP index between the control group and each of the experimental groups did not reach significance even with the addition of these subjects (see Table 6.7).

The difference of the LP between Experiment 1 and Experiment 3 is illustrated in Fig. 6. For Hezda and Adam, who saw Poke in Experiment 3, the sum of 1-LP was calculated for each experiment. For Rusty and Cacao who saw Lever in Experiment 3 LP was plotted as it is (see fig. 6.10).

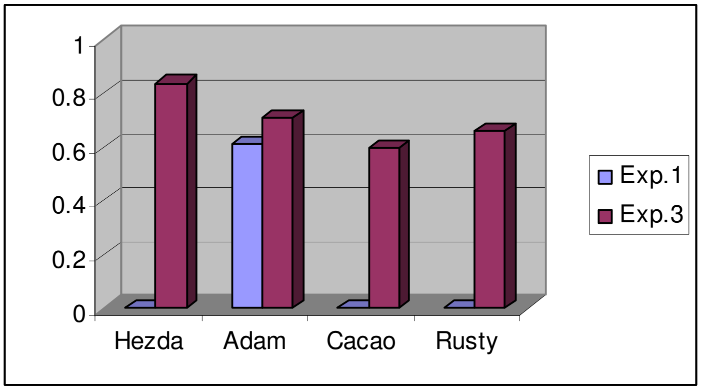


Figure 6.10 Change of LP for each monkey from Ex. 1 to Ex. 3.
For Hezda and Rusty who saw Poke in Ex. 3 (1-LP) was calculated.

Table 6.7 Enculturated monkeys' summary results. Medians (in bold), range of behaviour counts (in brackets, rounded to whole numbers, except for indexes) and differences with p<0.1 (<0.05 in bold). Dashes indicate p>0.1.

N =	**Lever 5**	**Control 4**	**Poke 5**	**L VS. P**	**L VS. C**	**C VS. P**	**L VS. P+C**	**P VS. +C**
Observers' judgment	**5.33** (4 –7)	**4.19** (4-5)	**3** (1-4)	**P= 0.016**	-	**P = 0.032**	NA	NA
LP index	**0.66** (0.31-1)	**0.52** (0-0.72)	**0** (0-0.29)	**P= 0.004**	**-**	-		
Lever Target Behaviour	**14** (0)-35)	**0** (0-0)	**4** (0)-15)	**P= 0.014**	**P=0.014**	-	**P= 0.011**	NA
Poke Target Behaviour	**7** (0)-26)	**5.95** (2-9)	**37** (0)-64	**P= 0.029**	**-**	**P= 0.014**	NA	**P= 0.011**

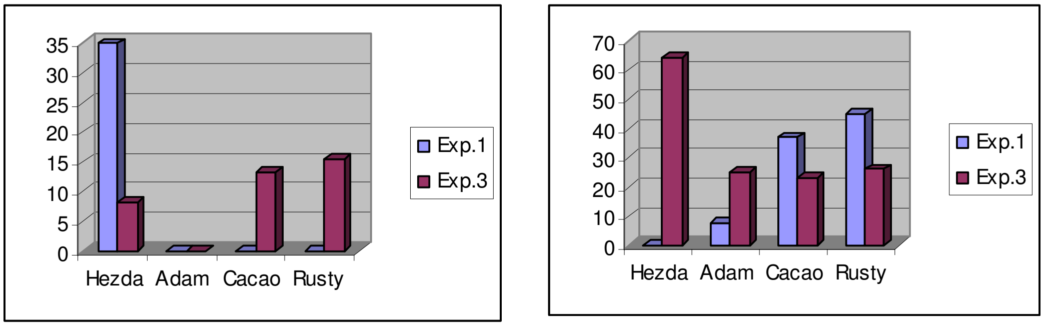
The four monkeys in this experiment were very focused on the target using only a few actions to reach it. Thus, only the level of Target behaviours was analyzed for these subjects.

Target behaviours. There was a significant difference between the groups on Lever acts (Kruskal Wallis test, χ^2 (2)=7.538, P=0.023). The difference between the Poke (median = 4) and Lever (median = 14.35) groups was significant (U=0 n_1=4, n_2=4 p=0.014) (see Table 6.7) as well as the difference between the Lever group (median = 14.35) and Control group (median = 0) was significant (U=0 n_1=4, n_2=4 p=0.014).

The addition of subjects in this experiment resulted in a significant difference between the groups in Poke behaviour (Kruskal Wallis test, χ^2(2)=6.731, P=0.035).

Monkeys in the Poke group (median =41) were significantly more focused on Poke than monkeys in the Lever group (median= 15) (U=1, n_1=4, n_2=4, p=0.029) as well as more than monkeys in the Control group (median= 5.95) (U=0, n_1=4, n_2=4, p=0.014).

The difference in percent of target behaviour between Experiment 1 and Experiment 3 is shown in Fig. 6.11a and b.


a.

b.

Figure 6.11 A comparison of the percent of target behaviour out of all coded behaviours for each monkey in Experiment 1 and Experiment 3. a) Lever target behaviour b) Poke target behaviour (In Exp. 3 -Hezda and Adam saw Poke, Cacao and Rusty saw Lever).

Discussion

The results of this experiment support the results of Experiment 1: enculturated capuchin monkeys show a higher fidelity of copying a demonstrator than has been seen in previous studies. The results of this experiment have an even stronger implication for this ability in the capuchin monkeys, as the four subjects have observed a different method in the past and used it with some degree of success.

The way Rusty combined both methods while trying to open the lid is interesting since there was no causal connection between the two parts of his behaviour; namely, punctuing a hole in the lid and taking the lid off. It was a combination of information Rusty gleaned from past experience together with the new information obtained from the current demonstration. Thus, Rusty's behaviour may be a good illustration of how new information acquired socially can be intergrated with previous information to create a change in the observer's behaviour. Adding more trials might have shown the course of change as by the third trial Rusty was already trying to insert the tool into the rim of the lid, which is required when using the Lever method.

The two subjects who saw "Poke" after having seen "Lever" in Expeiment 1 produced the Poke action as of the first trial. Hezda did show one instance of inserting the tool in the rim of the lid but did not pursue this method, which she had done so well in Experiment 1. However this does not mean that the monkeys were better imitators, as it has already been established in Experiment 1 that poking is an easier method for capuchin monkeys. This was seen in the fact that the control subjects in Experiment 1 also poked, whereas none of them levered.

Thus, poking may not need much practice in order to be used successfully.

Requesting help

As in Experiment 1, Cacao showed gestures for requesting help. Interestingly, these gestures were only seen in the last trial, the only trial where she tried to insert the tool in the rim, associated with lever target behaviour.

Conclusion

The results of Experiment 3 support the claim for high fidelity action copying in the enculturated monkeys.

The ability to switch from a known method to a different new one, as has been shown in this experiment, is the basis for cultural change through social learning. In a different situation, an animal may acquire a new behaviour which is based in some aspect of the old familiar one but has a new, advantageous element. This is the essence of cumulative culture learning which will be dealt with in the next chapter.

Chapter 7

TESTING FOR CUMULATIVE CULTURE IN CAPUCHIN MONKEYS

Cumulative cultural evolution is considered to be one of the characteristics of human culture. Only a few examples of such learning processes have been described in non- human animals. It has been already shown (Coffee Tin study, Artificial Fruit study) that two different variants of a behaviour seeded in two groups can result in socially transmitted behaviour of low fidelity in mother reared monkeys but higher fidelity in the enculturated subjects. The present study was designed to test whether these populations of monkeys could show cumulative social learning. In Experiment 1, seven mother reared capuchin monkeys were given a box with jam inside it. One of the monkeys retrieved the jam by inserting a stick into a little gap in the box, after which 5 other monkeys showed the same Gap behaviour. Next, they observed a monkey model demonstrate a more complex yet more efficient Poke method to obtain the reward. Five out of the seven monkeys who had demonstrated the Gap method switched to the new Poke method. In the next phase, the same model demonstrated an even more efficient Complex method. None of the monkeys managed to switch to this method although some behaviours related to the Complex method were seen.

In Experiment 2, four enculturated capuchin monkeys observed the same model. One monkey discovered the Poke method on his own during the baseline trials. The other three learned this method after observing a model. They were also able to switch to the Complex method after the same model had demonstrated this method.

Possible relevant differences between the two populations are discussed regarding the capacity for cumulative culture.

Introduction

In recent years there has been a vast amount of new findings on behavioural diversity among capuchin groups in their natural habitat in South America. In Chapter 3 of this thesis I reviewed these findings in detail. A range of behavioural domains has been observed including different food processing techniques (Panger et al 2002) substrate use (Boinski et al 2003), tool use (Ottoni & Mannu 2001) and hunting behaviour (Perry et al 2003; Rose et al 2003) as well as a diversity of social conventions between different groups (Perry 2003). Such diversity has been termed "tradition", implying that the difference in behaviours between the groups is based on social transmission and is not a result of ecological or genetic factors (McGrew, 1998).

However two issues still need to be addressed. Firstly, most of these observations of traditions in capuchin societies in nature have not enabled researchers to determine the mechanism underlying their spread since data on such a process are not usually available in natural conditions.

Secondly, in Chapter 3, I claimed that using Whiten & van Schaik's (2007) criteria for culture it is possible to portray the wealth of *Cebus* traditions as culture. However culture, as seen in human societies, is characterized not only by its behavioural diversity between different groups but also by the way it evolves cumulatively, by placing a new brick of knowledge upon an old one that usually results in more efficient behaviour. Some researchers have argued that high fidelity imitation is a prerequisite for this ratchet- like process of cumulative social learning (Tomasello et al 1993; Tomasello, 1999) since the behavioural variants must first be copied before they can be altered over the course of generations. Thus, such a cumulative learning process leads to an evolution of complex behaviours, which a single individual could not learn alone (Boyd & Richerson, 1985). Social facilitation, which could account for traditions in different communities, cannot account for a cumulative effect (Alvard, 2003). According to these authorities this is why only a very few suggestive examples of cumulative social learning have been found in non-human animals (Tomasello et al 1993; Boyd & Richerson, 1996; Tomasello, 1999). Such examples include nut cracking, parasite manipulation and well- digging by chimpanzees (Boesch, 2003), and tool manufacture in New Caledonian crows (Hunt & Gray, 2003).

On the other hand, McGrew (2004) put forward the idea that lower fidelity processes such as local enhancement can also be the basis for cumulative social learning. He argued that the change Japanese monkeys made to washing sweet potatoes in salty water after having washed them previously in sweet water is an example of cumulative learning through local enhancement. Matsuzawa (2003) states that the behaviour of pool making by Japanese macaque monkeys is an example of the ratchet effect in these monkeys. After the behaviour of washing sweet potatoes and rice had spread, a new behaviour started, which made use of the acquired one. Monkeys made little pools by digging in the sand until they got to the water. Then they would use these pools to wash the potatoes or throw wheat in the pools.

Thus cumulative social learning, according to McGrew and Matsuzawa, may be found in a species which does not necessarily show evidence of high fidelity imitation. It has been already shown (Coffee Tin study in Chapter 5, Artificial Fruit study, Custance, Whiten & Fredman, 1999) that two different variants of a behaviour seeded in two groups can result in socially transmitted behaviour although of low fidelity in mother reared monkeys and higher fidelity in the enculturated subjects.

Considering this, it is reasonable to predict that a naive monkey observing a new behaviour, without having been first exposed to another variant of it, could learn the behaviour through social learning. However, can the intermediate generation, those monkeys who are already accustomed to using a certain behaviour, appreciate a more advantageous variant and switch to the new behaviour after observing an inventor or immigrant monkey use it?

The following "Dipping- Box" study was carried out in order to address this question as well as others:

a. Would a new behaviour seeded in a group of capuchin monkeys spread to the rest of the group, and more importantly, how?

b. Can capuchin monkeys make use of knowledge learned socially in a cumulative way? Can a new tradition brought in by an immigrant monkey overpower an old established one or does the old one continue to exist? If a new tradition spreads, does each monkey continue to use both methods, or are the two traditions kept in the group with different subgroups using them?

In Experiment 1 of this study the Island group monkeys served as subjects to answer these questions.

In Experiment 2 of this study, the Enculturated monkeys were tested on the same Dipping-Box apparatus with the aim of answering the following questions:

a. As in Experiment 1, is social learning strong enough to evoke a quick shift from one method to the more effective other one?

b. In the Coffee-tin experiment we inquired whether the enculturated monkeys who showed the ability to copy the behaviour of a human model would also be able to do so if the model were a conspecific. In Experiment 2 of this study the model was a monkey so as to further explore this question.

Experiment 1: The mother-reared monkeys

Methods

Subjects

The subjects in this study were the monkeys of the Island group (see Chapter 4): four males and three females. However, by the time this experiment was carried out, these monkeys were not living on the island any more, but had moved to a 6 x 6 x 3 meter cage divided into 3 parts. The monkeys had access to all three parts of the cage.

Apparatus

The apparatus was a small Plexiglas box measuring 9 x 6 x 6 cm designed after Marshall-Pescini & Whiten (2008). On the top of the box was a little sliding door and on the side of the box there was a little hole, containing a bolt which locked the lid in place (Fig. 7.1a).

There were two planned methods by which a monkey could obtain the food placed inside the box:

Poke Method. The sliding door on the top of the box was opened with the finger of one hand, and while keeping the door open, a stick was inserted through it with the other hand and dipped into the jam at the bottom of the box. While the door was kept open with one hand the stick was taken out, and it was possible to lick the jam which stuck to it (Fig 7.1b).

Complex Method. This was a more complex method but also more efficient in terms of the amount of food obtained each time. By poking a stick into the little hole on the side of the box, the bolt was moved and the catch released (Fig.7.1c). Then, the sliding door on the top of the box was opened with a finger and the stick inserted with the other hand. It was then possible to open the lid of the box using the stick as a lever, obtaining all the jam that was in the box (Fig.7.1d).

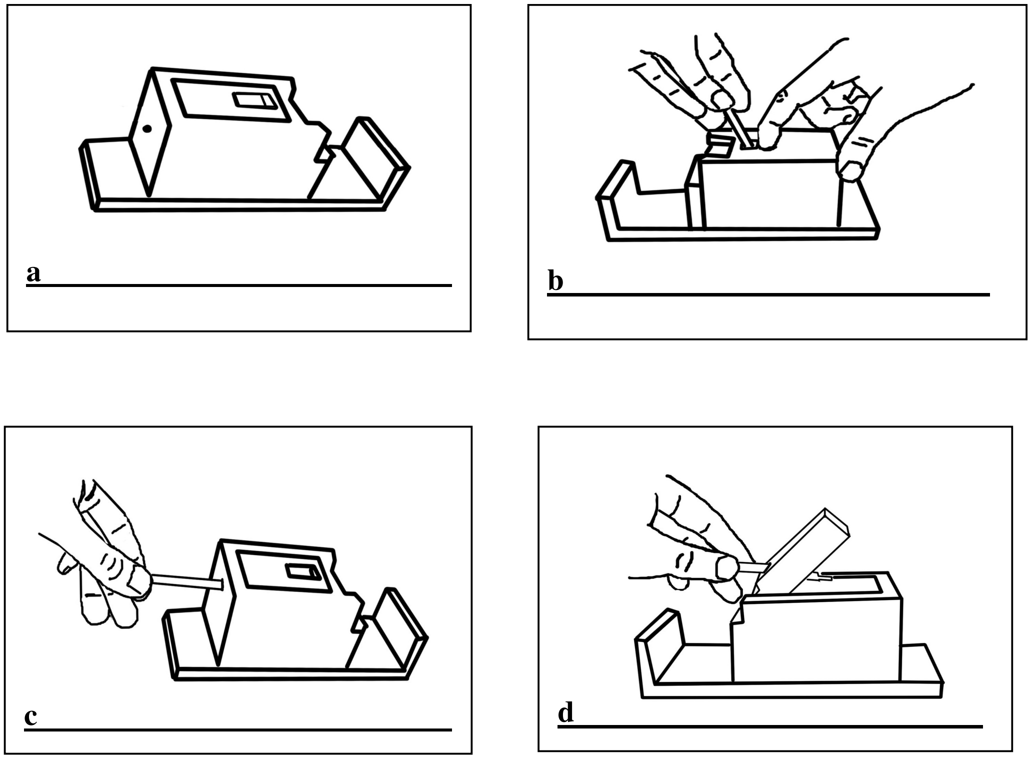


Figure 7.1 The Dipping-Box apparatus. (a) the unopened box (b) Poke Method –opening the sliding door with the finger and inserting the stick with the other hand.
(c) Complex Method: unlocking the bolt by poking the stick in the bolt hole and then (d) inserting the stick through the sliding door to pull open the lid**.**

Procedure.

The monkeys both viewed the demonstrator, and were tested, in a group setting in order to simulate as natural a context as possible.

The design had four phases:

Phase one: First Baseline. Six exploration sessions.

Phase two: Poke Method. Learning sessions in which the model demonstrated the Poke Method three times, then the monkeys were given 2 boxes to manipulate themselves, followed by two more single demonstrations. This phase was terminated when at least 5 out of the 7 monkeys used the Poke Method for at least two sessions. If this criterion was not met after 10 sessions, the phase was also terminated.

Phase three: Second Baseline. Three sessions allowing the monkeys extra time to discover the Complex Method by themselves.

Phase four: Complex Method. Learning sessions in which the model demonstrated the Complex Method as she did for the Poke Method.

Each session lasted approximately 30 minutes and was videotaped for further analysis.

The monkeys in this experiment saw a considerably greater number of demonstrations than in the previous Coffee-Tin or Artificial-Fruit experiments. This was done for two reasons:

(a). Monkeys in a natural environment most probably see more than just 3-4 demonstrations of a new behaviour: they may also observe more than one monkey using the new behaviour as it spreads in the group.

(b). Marshall- Pescini & Whiten (2008) found that some of the chimpanzees in their experiment needed many trials in order to learn the task. It was assumed that the capuchins would not learn faster than chimpanzees.

Phase one: First Baseline

The monkeys were given the box with some jam in and on it. Appropriate sticks and twigs were placed on the board to which the box was connected. This was done in order to give the monkeys enough opportunity to solve the task themselves as would happen if this group encountered unfamiliar fruit which was processed by another, in the natural environment.

In these first six sessions the monkeys showed neophobia towards the box, threatening it while standing on two legs, or touching it and running away. It was thus decided to leave the box longer until the monkeys were more relaxed and would start to manipulate it.

In the seventh session the monkeys started to manipulate the box. However, the box had a very thin gap on the side, which to human eyes, as well as to chimpanzee eyes (Marshall-Pescini & Whiten 2008) was apparently not salient. Yet, for the capuchin monkeys in this study, this gap was big enough to insert a very thin twig and obtain the reward. Size differences between capuchin monkeys and apes or humans may explain this difference in perception. This phase, which was then termed the "Gap-method" phase, continued until all subjects had at least contacted the box in some way.

Coding:

All the behaviours of the monkeys towards the apparatus and related to it were recorded. The behaviours were divided into seven levels (see Table 7.1 for a detailed description of these behaviours).

1. Target behaviours.
2. Incomplete Target behaviours with a tool (relevant for Poke Method & Complex Method).
3. Target- aimed behaviours without a tool.
4. Target- locus orientated behaviours without a tool.
5. Behaviour with a potential for social learning: these behaviours were coded as they had a potential for socially influencing later behaviours.
6. Non target behaviours on the apparatus.
7. Non-target tool-use behaviour: these behaviours included using tools on different objects or loci while another monkey was manipulating the box. This was done in order to check for some general tool use activation as result of watching a conspecific use a tool.

Table 7.1 Behavioural categories coded for each monkey in the different phases**.**

Behaviour categories	**Description**
Gap Method Target behaviour	Insert stick in Gap with one or both hands. Modify stick then insert in Gap.
Target- aimed no tool	Lick Gap, Poke finger in Gap and lick.
Poke Method Target behaviour	Open door with finger - Insert stick. Modify stick and then use the Poke method. Insert stick using one or two hands without first opening it with finger.
Incomplete target behaviour	Insert stick with mouth; Poke door- no success. Try to insert stick into wrong side of door. Take out stick with mouth. Move stick forward and backwards in door then leave. Move stick up and down in door, then leave.
Target–aimed no Tool	Open door with finger, insert other finger with/without licking finger. Open door with one or two fingers without inserting other. Open door with one or two fingers then look in box. Open door with mouth.
Target- locus orientation	Lick door, touch door then lick
Complex Method Target behaviour	Inset stick in bolt hole then lever lid with stick. Insert stick in bolt hole open lid with finger.
Incomplete target behaviour	Insert stick in bolt hole then do nothing. Lever box with stick without first inserting stick in bolt hole.
Target –aimed no tool	Pull lid with finger in door. Pull lid elsewhere. Poke bolt hole with finger.
Target –locus orientation	Touch, lick, or look in bolt hole.
Behaviours with potential for social learning	Watch other manipulate box. Scrounge: stick, gap or door
Non- target behaviours on apparatus	Put object on box, use stone on box, pound stick in door with stone, poke stick on wood to which the box is connected poke stick into close object, bite stick. Actions on box: Hold, shake, threaten, touch, lick, smell, and bite. Actions on board to which box is connected - shake, turn.
Non- target tool use	Pounding a stone, probing a stick on different loci of the cage while another monkey was manipulating the box.

Results

Target behaviour

The first monkey to obtain the food using the Gap method was Zed, the dominant female. Not only did she discover that the food could be obtained by inserting a very thin twig into the gap, she was also observed taking sticks and tearing off parts of them with her hand or mouth, modifying them to fit the gap. Drorit was also observed modifying sticks in the last session of the Gap method phase.

Most of the other monkeys were seen to observe Zed and thereafter four of the remaining monkeys were seen using little twigs to obtain the food from the box through the gap. Figure 7.2 shows the onset of performing the Gap method by each monkey. The connecting lines indicate that the monkey was watching Zed use the Gap method before s/he started using the method too.

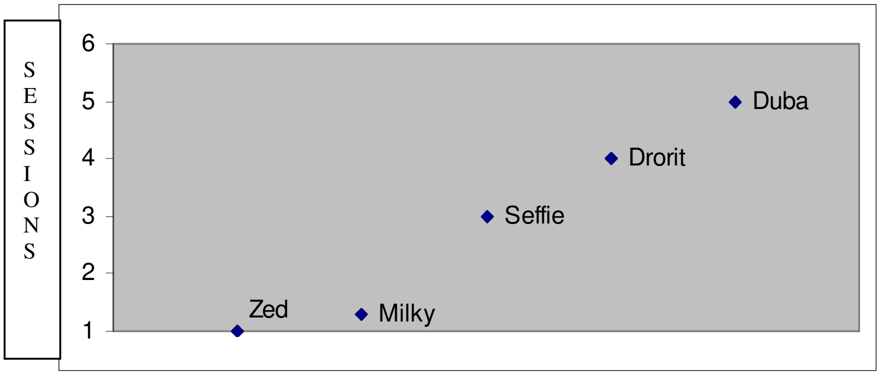


Figure 7.2. Order of Gap method acquisition. Lines indicate monkeys observing Zed.

Target-aimed behaviours without a tool

There were very few non-tool-use behaviours. Duba tried to poke the gap with her finger on the fourth session (on the fifth, she solved the task).

Target locus orientated behaviours without a tool

There were very few other behaviours which were orientated towards the significant locus, the Gap. Milky and Drorit were seen trying to look in the box through the gap on the sixth sesion.

Thus most of the behaviours towards the gap were target behaviours.

Behaviour with potential for social learning

a. Observing other monkeys solve the task.

A behaviour was recorded as an instance of observation when a monkey was seen watching the manipulation of the box while positioned no more than two meters from the box. Once the monkey moved away or moved his head, this was considered to be the end of the coded instance. It is of course possible that monkeys were also watching from furher away, but this was difficut to assess as well as capture on video.

Clear instances of monkeys observing a conspecific manipulate the box were recorded (see Table 7.2). Observing another monkey was recorded as one instance from the moment the monkey began watching a conspecific operate the box from a meter or less, until the observer moved his gaze away from the box or moved to another location. Seffie was observed watching a monkey manipulate the box, but this was seen a session after he had first solved the task. However, observing from further away before solving the task cannot be ruled out.

Shipgler was not observed watching other monkeys from a close distance at all. Zorba, on the other hand, showed the most bouts of observing other monkeys obtaining the reward (22 times). He was tolerated near the box as he is Zed's son. However, he did not try to obtain the reward himself .

Table 7.2 Number of instances in which a monkey was observed closely watching a conspecific manipulating the box using the Gap method. The last column indicates the percentage of these behaviours out of all coded behaviours for the monkey during the entire Gap phase. The shaded squares indicate the first session the monkey used the Gap method.

Session Name	**1**	**2**	**3**	**4**	**5**	**6**	**Sum**	**% Of All Behaviours**
Duba	2			2*	▨		**4**	**12.12**
Shpigler							**0**	**0**
Seffie			▨			1	**1**	**5.26**
Zorba	8	7	3	3		1	**22**	**66.67**
Drorit	4			5			**9**	**18**
Milky	7			2		1	**10**	**22.72**
Zed	▨				1	1	**2**	**4.88**

* In this session Duba showed general gap actions - poking finger in Gap

b. Scrounging

Scrounging was only rarely observed (see Table 7.3). Zorba was seen to take a used stick and lick it, or lick the gap after jam had been taken out of it. However, Drorit and Milky, who solved the task, were seen to scrounge just as much. Scrounging, then, does not seem to explain a lack of manipulation of the box, as in the case of Zorba.

Table 7.3 Number of instances in which a monkey was observed scrounging. The last column indicates the percentage of these behaviours of all coded behaviours for the monkey during the entire Gap phase. 1-6 = sessions in the Gap phase.

Session / Name	**1**	**2**	**3**	**4**	**5**	**6**	**Sum**	**% All Behaviours**
Duba							**0**	**0**
Shpigler							**0**	**0**
Seffie							**0**	**0**
Zorba	1	2					**3**	**9.1**
Drorit	1			3			**4**	**8**
Milky		1		1			**2**	**4.5**
Zed							**0**	**0**

Non-target tool-use behaviour

One of the alternative explanations of results claiming to show imitation in animals is that the subjects are showing response facilitation (Byrne & Russon, 1998a). If this is so, we might expect to find more general probing behaviour after viewing a monkey use a twig to probe in the gap and obtain the reward.

Inserting a twig elsewhere (i.e. in rocks or trees near the apparatus) was seen in only two of the monkeys in the group, Milky (2 instances) and Drorit (4 instances), in the second and fourth sessions respectively. Thus seeing other monkeys use a twig to insert in the gap did not significantly facilitate this response on other objects in the monkeys' environment. Milky was observed to perform other non-target tool use behaviour. This included manipulating stones or sticks next to the box while Zed was getting the reward out of it with the stick. It seems that this was a type of

displacement behaviour as Milky was not looking at the stones he was manipulating.

Discussion

Although the Gap method was not originally planned as such, it provided an answer to the first question as to whether a new behaviour in a group of capuchin monkeys can spread and how.

The new behaviour did spread in the group; 5 out of 7 monkeys were observed using it in a period of six sessions.

What mechanisms could underlie the diffusion of the behaviour? Inserting sticks into cavities is part of the capuchin repertoire in captivity as well as in nature. Thus, it would be most parsimonious to conclude that just as Zed figured out the Gap method on her own, the others with time could have achieved that too. However observing Zed might have accelerated the process by a combination of:

a. Social facilitation - once the first monkey Zed got the courage to approach the box the others quite quickly joined her.

b. Localized stimulus enhancement (Caldwell & Whiten, 2004) - the monkeys were attracted to the Gap after watching Zed.

As mentioned earlier, it is not possible to determine how Seffie solved the task as he was not observed to closely watch one of the solvers before solving the task himself.

Seffie and Drorit each showed a one- time interest in the sliding door, corresponding to the Poke Method, but did not pursue this direction and conformed to the Gap method which the others were using.

The Island group monkeys invented their own method, the Gap method, which was unintended in the design of the study but was just as relevant for the experiment. This could also be used as a basis for the second question mentioned earlier: Is social /imitative learning strong enough to change an established successful behaviour? Could a new invention spread in the group and replace the old, less efficient one?

In the original plan it was intended to demonstrate a more complex yet more efficient method after the monkeys learned the first one (door sliding).

The intended Poke method was expected to be more efficient than the Gap method the monkeys had adopted. As the sliding door on the top of the box was bigger than the gap, a larger stick could be poked in and more food could be taken out each time. Just as in the planned procedure, the Poke method was also more complex than the Gap method in that it demanded a two-hand action; namely, opening the door with one hand while poking the stick in with the other. Thus from the point of view of the experimental questions the situation the monkeys created was just as appropriate to the original plan.

Phase two: the Poke Method

Cacao, the enculturated monkey who lived next to the Island group, served as the model for this phase. Cacao spent a great deal of time next to their cage every afternoon. She shared food with these monkeys and played with some of them. Therefore it was possible for her to act as the model for these monkeys. She demonstrated in front of the whole group and then the box was placed in their cage.

It took three sessions of a maximum of 15 minutes each to bring Cacao, through shaping, to use the Poke method proficiently so that she could be a reliable demonstrator.

The demonstrations were carried out in eight sessions, one a day, lasting no more than 30 minutes each. Cacao demonstrated three times, and then the boxes were placed in the cage for the group to manipulate. She then made two extra single demonstrations in between which the monkeys were given the boxes for manipulation.

Statistical analysis

Non- parametric tests were used due to the small number of subjects. A Wilcoxon T test was used for within group comparisons between the different phases to determine whether the monkeys changed the method they used in the different phases. One -tailed P values are reported as the predictions that watching a method will enhance the success of using it is clearly unidirectional.

Results

The results showed that the monkeys started to use the Poke method behaviours immediately after viewing the demonstration in the seventh session. Further, the use of the Gap method during the Poke method phase decreased. Using a Wilcoxon test, a comparison was made of the average percent of Gap behaviours out of all actions each monkey exhibited in the Gap phase (median=25) compared to the Poke method phase (median=5.635). This comparison showed a significant decrease (N=7 T = -2.023, p = 0.031) (see Table 7.4).

Table 7.4 Average percent of Gap behaviours for each monkey in the Gap phase and the Poke method phase.

phase name	**Gap phase**	**Poke phase**	**Direction**
Duba	25.00	6.25	Reduced
Shpigler	0.00	0.00	-
Seffie	52.78	13.52	Reduced
Zorba	0.00	0.00	-
Drorit	37.43	5.02	Reduced
Milky	6.22	0.00	Reduced
Zed	44.05	28.41	Reduced

A comparison of the use of Gap behaviour alone is not enough to determine whether a switch between the methods was made. In order to test which method the monkeys were using more in each session a Method Index (MI) was obtained by calculating Poke method behaviours divided by the sum of Poke method behaviours + Gap behaviours: $MI= \frac{\text{Poke Method}}{\text{Poke Method + Gap}}$

Thus, MI = 1 indicates that the monkey was only using Poke method actions, whereas MI= 0 indicates that the monkey was only using Gap actions. This MI index was used throughout this study to determine whether a monkey was using one method predominately over the other. The comparisons were carried out on a different level each time; by comparing target behaviours, incomplete target behaviours, or target aimed behaviours (see Table 7.1).

Target behaviour

As of the first session of the Poke method phase two monkeys, Zed and Drorit, used the complete target behaviour of this method to obtain the reward. Zed however, returned to using the Gap method. Only by the fifth session of this phase did other monkeys use the complete Poke method. Table 7.5 shows the MI in each session for the two target behaviours alone.

Table 7.5 MI of target behaviours alone for each monkey in each session of the Gap phase (sessions 1-6) and the Poke method phase (sessions 7-14). MI=0 (shaded green) indicates that the monkey only used Gap target behaviour. MI=1 (shaded purple) indicates that the monkey only used Poke method target behaviours.

	Gap phase sessions						**Poke phase sessions**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Duba					**0.00**	**0.00**							**0.00**	
Shpigler												**1.00**		
Seffie			**0.00**	**0.00**	**0.00**	**0.00**		**0.50**	**0.00**		**0.00**	**1.00**	**1.00**	**1.00**
Zorba														
Drorit				**0.00**	**0.00**	**0.00**	**0.50**				**0.11**	**0.92**	**0.66**	
Milky	**0.00**	**0.00**										**1.00**	**1.00**	
Zed	**0.00**	**0.00**		**0.00**			**1.00**	**0.00**		**0.00**	**0.00**		**0.00**	

Comparing the average MI of target behaviours for each monkey in the Gap phase (median=0) with that in the Poke phase (median = 0.1875) shows a significant difference (Wilcoxon test N=7 T = -2.032, p = 0.031) (see Table 7.6).

Table 7.6 Average MI of target behaviours for each monkey in the Gap phase and the Poke phase.

phase name	**Gap phase**	**Poke phase**	**Direction**
Duba	0.00	0.00	-
Shpigler	-	0.12	Increased
Seffie	0.00	0.44	Increased
Zorba	-	-	-
Drorit	0.00	0.27	Increased
Milky	0.00	0.25	Increased
Zed	0.00	0.12	Increased

Incomplete Target behaviours

Incomplete target behaviours of the Poke method (see Table 7.1) were frequently used during the Poke method phase (see Table 7.7).

Table 7.7 Percent of incomplete Poke method behaviours in the Gap phase (sessions 1-6) and the Poke method phase (sessions 7-14).

	Gap phase sessions						**Poke phase sessions**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Duba														22.58
Shpigler													16.67	73.33
Seffie			16.70					54.50	40.00					25.00
Zorba														
Drorit				8.30			76.90				11.53		85.40	
Milky								25.00					37.50	
Zed							50.00						35.90	

In the simpler Gap phase, this level of analysis could not be done as there was only one tool-use related behaviour, namely inserting the stick in the Gap. Instead, a comparison was made between the phases on target-behaviours combined with incomplete-target, showing a strong switch from the Gap method to the Poke method (see Table 7.8).

Table 7.8 MI for target + incomplete target behaviours in the Gap phase (sessions 1-6) and the Poke method phase (sessions 7-14). MI=0 (shaded green) indicates that the monkey only used Gap target + incomplete behaviours. MI=1 (shaded purple) indicates that the monkey only used Poke target + incomplete behaviours.

	Gap phase sessions						**Poke phase sessions**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Duba					**0.00**	**0.00**							**0.00**	**1.00**
Shpigler												**1.00**	**1.00**	**1.00**
Seffie			**0.50**	**0.00**	**0.00**	**0.00**		**0.80**	**0.80**		**0.00**	**1.00**	**1.00**	**1.00**
Zorba														
Drorit				**0.02**	**0.00**	**0.00**	**0.97**				**0.33**	**0.92**	**0.97**	
Milky	**0.00**	**0.00**						**1.00**				**1.00**	**1.00**	
Zed	**0.00**	**0.00**		**0.00**			**1.00**	**0.00**		**0.00**	**0.00**		**0.82**	

Comparing the average MI for target + incomplete target behaviours for each monkey in the Gap phase (median = 0.0) with that in the Poke phase (median = 0.375) showed a significant difference (Wilcoxon test N=7 T = -2.023 p = 0.031) (see Table 7.9).

Table 7.9 Average MI for target + incomplete target behaviours in the Gap phase and the Poke phase.

phase / name	**Gap phase**	**Poke phase**	**Direction**
Duba	0.000	0.125	Increased
Shpigler	-	0.375	Increased
Seffie	0.083	0.575	Increased
Zorba	-	-	-
Drorit	0.028	0.399	Increased
Milky	0.000	0.375	Increased
Zed	0.000	0.228	Increased

Target-aimed behaviours without a tool

Testing only target aimed behaviours without a tool shows that the move from one method to the other was mostly manifested in target aimed behaviours related to the Poke method (e.g. opening sliding door with finger and looking inside). Seffie showed Poke method non-tool behaviour in one session in the Gap phase but conformed to what the others were doing in the following sessions (see Table 7.10).

Table 7.10 MI for target -like behaviours without a tool in the Gap phase (sessions 1-6) and Poke phase (sessions 7-14). MI=0 (shaded green) indicates that the monkey only used Gap target – like behaviour. MI=1 (shaded purple) indicates that the monkey only used Poke target – like behaviours.

	Gap phase sessions						**Poke phase sessions**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Duba				**0.0**					**1.0**			**1.0**	**1.0**	
Shpigler									**1.0**		**0.0**	**1.0**		
Seffie			**1.0**						**1.0**					**1.0**
Zorba														
Drorit								**1.0**						
Milky								**1.0**				**1.0**	**1.0**	
Zed														

Comparing the average MI for this level of behaviour between the Gap phase (median = 0.0) and Poke phase (median =0.25) using a Wilcoxon test showed a significant difference (N=7 T = -2.032, p = 0.031) (see Table 7.11).

Table 7.11 Average MI for target-like behaviours without a tool in the Gap phase and the Poke phase.

phase name	Gap phase	Poke phase	Direction
Duba	0.000	0.375	Increased
Shpigler	-	0.250	Increased
Seffie	0.170	0.250	Increased
Zorba	-	-	-
Drorit	-	0.125	Increased
Milky	-	0.375	Increased
Zed	-	-	-

Target locus orientated behaviour

Comparing the average MI for target locus orientated behaviours in the Gap phase (median =0.0) and the Poke phase (median =0.13) showed no significant difference (Wilcoxon test N=7 T = -1.826, p = 0.063) (see Tables 7.12 and 7.13). Thus, this level of behaviour did not change between phases.

Table 7.12 MI for locus orientated behaviours without a tool in the Gap phase (sessions 1-6) and Poke phase (sessions 7-14). MI=0 (shaded green) indicates that the monkey only used Gap target- locus behaviours. MI=1 (shaded purple) indicates that the monkey only used Poke target – locus behaviours.

	Gap phase session						**Poke phase sessions**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Duba									1.00			1.00	1.00	
Shpigler									1.00		0.00	1.00		
Seffie			1.00						0.33					0.50
Zorba														
Drorit						0.00	0.00	1.00			0.00			
Milky						0.00		1.00				0.50	1.00	
Zed													0.00	

Table 7.13 Average MI for target locus orientated behaviour in the Gap phase and Poke phase**.**

phase / name	Gap phase	Poke phase	Direction
Duba	-	0.38	Increased
Shpigler	-	0.25	Increased
Seffie	0.17	0.10	Decreased
Zorba	-	-	-
Drorit	0.00	0.13	Increased
Milky	0.00	0.31	Increased
Zed	-	0.00	-

Behaviour with potential for social learning

a. Observing other monkeys solve the task

Two types of behaviours were recorded:

a. The percent of Cacao's demonstration each monkey watched. As a group, the monkeys watched an average of 78% of Cacao's demonstrations.

b. The number of instances monkeys watched their conspecifics manipulate the boxes. All the monkeys were seen closely watching a conspecific operate the box (see Table 7.14).

In this phase, as in the Gap phase, Zorba spent most of the time (75% of all his coded behaviours in this phase) watching others work, yet he did not solve the task himself.

b. Scrounging

Scrounging was hardly seen in this phase. Duba and Milky were each seen scrounging in two instances, and Zorba was seen doing this once.

Unrelated tool use behaviours

Seffie was seen poking the stick on the board on which the box was fixed. Five of the monkeys were seen going to bring a stick, returning with it but then leaving it without using it (Duba, Shpigler and Drorit once each, Seffie and Zorba twice each).The monkeys were also seen biting the stick, perhaps to modify it, but then dropping it and not using it (Duba, Seffie, Zorba once each, Drorit six times and

Zed three times).The monkeys were not seen probing sticks in other objects during the sessions.

Table 7.14 Attention towards models. In the top part of each row is the percent of Cacao's demonstrations each monkey watched. In the bottom part of each row in *italics* is the number of instances each monkey observed a conspecific manipulate the box. The last column indicates the percent of these behaviours out of all coded behaviours for the monkey during the Poke phase.

Session **Name**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Sum**	**% Of Total Behaviours**
Duba	60	60 *2*	80	60	0 *3*	60 *5*	100	80 *4*	***14***	**20**
Shpigler	100	80	100	60	60 *3*	0 *1*	0 *1*	80	***5***	**5.3**
Seffie	100	60 *2*	80	80	40	0	100	100 *2*	***4***	**3.7**
Zorba	100 *4*	100	100	100 *5* *(gap)	100 *5*	80 *3*	80 *4*	100	***21***	**75**
Drorit	100	100	100	100	60 *3*	100	100	80	***3***	**1.9**
Milky	100	80 *3*	80	100	100	100	100 *2*	60	***5***	**7.0**
Zed	100	100 *1*	0	80	100 *2*	80	80	80	***3***	**3.4**

* Zorba was watching a conspecific use the Gap method.

Phase Three: Baseline for the Complex Method

The monkeys had three additional sessions to manipulate the box, without watching a model, in order to see whether more time to manipulate the box would lead to discovery of the Complex method, or parts of it, on their own. The subjects did not show any behaviour related to the Complex method during these sessions. The MI for these sessions shows the monkeys primarily used the Poke method behaviours during the three sessions of this Baseline phase (see Table 7.15).

Table 7.15 MI for target + incomplete target behaviours in The Poke phase (sessions 1-8) and Baseline (sessions 9-11) MI=0 (shaded green) indicates that the monkey only used Gap target +incomplete target behaviours. MI=1 (shaded purple) indicates that the monkey only used Poke target +incomplete target behaviours.

	Poke phase sessions								**Baseline phase**		
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Duba								1.00			
Shpigler						1.00	1.00	1.00			
Seffie		0.80	0.80		0.00	1.00	1.00	1.00	0.80		
Zorba											
Drorit	0.97				0.33	0.92	0.97		1.00	0.85	1.00
Milky		1.00				1.00	1.00		1.00		1.00
Zed	1.00	0.00		0.00	0.00		0.82		1.00	1.00	1.00

A comparison of the MI for these levels of behaviours between the Poke phase (median =0.378) and Baseline phase (median = 0.46) using a Wilcoxon test showed no significant difference (N=7 T = -0.524 p = 0.344) (see Table 7.16)

Table 7.16 Average MI for target + incomplete target behaviours in the Poke phase and Baseline.

Phase name	**Poke phase**	**Baseline phase**	**Directions**
Duba	0.13	0.00	Reduced
Shpigler	0.37	0.00	Reduced
Seffie	0.57	0.27	Reduced
Zorba	-	-	-
Drorit	0.40	0.95	Increased
Milky	0.38	0.67	Increased
Zed	0.23	1.00	Increased

Phase Four: The Complex Method.

Once again Cacao was the demonstrator for the group. As in the Poke method demonstrations, she sat next to the observers' cage and demonstrated to the whole group, and then the box was put in their cage. There were 6 sessions in this phase lasting no more than 30 minutes each.

Results:

Although the monkeys had many opportunities to observe and learn, none of the Island group subjects performed the complete Complex method behaviours. However, behaviours related to the Complex method were used in this phase by four of the subjects: Zorba, Milky, Zed and Drorit even though this constituted a very small percentage of their overall behaviours.

Testing the different levels of behaviours used by the monkeys showed that most of these behaviours were Target-locus orientated (see Table 7.17) in which the monkeys touched, licked, or tried to look into the bolt hole.

Incomplete Complex behaviours included inserting the stick in the bolt hole but not continuing to do something with it, or trying to lever open the lid with the stick. Target aimed behaviours without a tool included trying to pull open the lid with the fingers.

Table 7.17 Average percent of the Complex method related behaviours out of the total behaviours coded during the Complex phase.

Behaviour / Names	Incomplete Target	Target Aimed No Tool	Target Locus Orientated
Duba	0.00	0.00	0.00
Shpigler	0.00	0.00	0.00
Seffie	0.00	0.00	0.00
Zorba	2.08	0.42	4.18
Drorit	0.00	0.00	1.85
Milky	3.42	0.43	19.48
Zed	1.85	0.00	3.52

A Friedman test was used to compare the average percent of the Complex method related behaviours in the Complex phase to the average percent of these behaviours in the Gap phase and Poke + Baseline phases. This comparison only revealed a significant difference for the incomplete Complex behaviours (Friedman test p = 0.05).

Thus, although the capuchins in this study did not show a shift from the Poke method to the complete Complex method they did indicate significant attempts (see Table 7.17).

Three explanations of the monkeys' difficulty to switch to the Complex method were then examined:

a. The bolt-hole on the side of the box could have been rather similar to the Gap the monkeys had previously used and this may have confused them. If this were so, we would expect to find more Gap method behaviours during the Complex method phase than during the Poke method phase and the Baseline phase that followed it.

A comparison between the average Gap behaviour for each monkey in the Poke phase + Baseline Phase (median= 4.33) with the Complex method phase (median= 1.04) did not show a significant difference (Wilcoxon test, N=7 T = -1.261 p = 0.125) (see Table 7.18). In fact, use of the Gap method declined in most monkeys. Thus lack of success cannot be ascribed to confusion with the Gap method.

Table 7.18 Average percent of Gap behaviour during Poke + Baseline phases and the Complex method phase.

phase **name**	**Poke + Baseline phases**	**Complex phase**	**Direction**
Duba	4.54	0.00	Reduced
Shpigler	0.00	0.00	Reduced
Seffie	9.83	0.00	Reduced
Zorba	0.00	4.54	Increased
Drorit	4.33	1.04	Reduced
Milky	0.00	1.75	Increased
Zed	20.66	4.37	Reduced

b. Second, it might have been too difficult for the monkeys to learn the function of pushing the bolt in the hole, as it was concealed. The monkeys might not have understood the effect of removing the bolt on opening the lid. However, the end result of the open lid could have been salient enough. Thus there should be more attempts to open the lid of the box in different ways in this phase. Behaviours in this direction were seen only in this phase yet they were very few (see Table 7.19).

Table 7.19 Incomplete lid opening behaviours. L= lever with stick P = pull with hand. These behaviours were only seen in the first, second and fifth sessions of the Complex method phase.

Session / Name	**1**	**2**	**5**
Duba			
Shpigler			
Seffie			
Zorba	1 (12.5%) L	2 (2.5%) p	
Drorit			
Milky			8 (20.5%) L, 1 (2.56%) p
Zed			

A comparison of the average incomplete lid opening behaviour in the Complex method phase with the Poke method phase using a Wilcoxon test was not significant ($N=7$ $T = -1.342$ $p = 0.250$).

Zorba started to manipulate the box only in this phase. He used the Gap method as well as the Poke method. He also exhibited a behaviour which the other monkeys did not; namely, pounding a stone on the box in two of the sessions (in session 4 he did this 23 times!). This was done perhaps to open the box as he would open a hard shelled fruit.

c. Since the monkeys could obtain a rather large amount of the reward using the Poke method, they might not have been motivated to switch to the Complex method. Therefore four additional sessions were given in which the reward was not jam, which was easily obtained by dipping the stick, but rather pieces of solid fruit. Dipping the stick in the box would get the taste of the fruit on the stick but only opening the box would enable the monkeys to actually eat it.

A comparison of the different levels of behaviour, between the first six sessions of the Complex method phase and the four sessions of the enhanced Complex method phase using a Wilcoxon test revealed no significant difference:

Incomplete target behaviours: $T = 0.0$ $p=1.0$
Target aimed no tool: $T = -1.342$ $p=0.180$
Target locus orientation: $T = -1.095$ $p=0.273$

Thus, partially blocking the Poke method in this way did not facilitate the performance of the Complex method.

Discussion

The current experiment showed that a behaviour naturally seeded in a group of capuchin monkeys could spread to other members of the group, as took place with the Gap method. It was also shown that when a new method, related to the same object, is introduced to the group it is possible for this behaviour to be socially learned and used by the group as shown by the introduction of the Poke method.

The second question asked at the beginning of this study was about the nature of change in traditions: can a new tradition introduced by an immigrant monkey overpower an old established one or does the old one continue to exist? If it does, does each monkey continue to use both methods or perhaps the two traditions are maintained in the group with different subgroups using them?

To prefer to use the more efficient method, the monkeys would have to appreciate its advantages; for example, a larger quantity of reward made available by using the method. Studies have shown that *Cebus* monkeys in experimental settings are capable of estimating a difference in quantity (Judge, Evans, & Vyas, 2005) as well as food value (Westergaard *et al* .2004). Thus the reason the monkeys did not abandon the Gap method immediately is probably not due to lack of perception of quantity.

Myowa-Yamakoshi & Matsuzawa (1999) showed that in imitation tasks chimpanzees made errors which showed "preservative repetition of previously instructed actions". Thus, the capuchin monkeys in this study that were using both the Gap method and the Poke method could have been following this principle especially as both are related to the same box and make use of the same tool. Over the course of 24 sessions the Gap method almost disappeared but it was still seen during the final sessions of this experiment

When the Complex method was introduced the monkeys failed to learn it. Explanations for this failure can be sought in two directions: the general aspects of how new behaviours spread in a group and the specific characteristics of the Complex method used in this study.

One possibility is again perseveration. With now two existing optional ways to manipulate the box, the difficulty of learning a third method perhaps increased. Although the reward was changed in the last sessions in order to partially block both the Gap method and the Poke method, the monkeys still did not learn the Complex method. Such perseveration is perhaps the obstacle impeding the ratchet effect characteristic of human culture (Boesch & Tomasello, 1998). Human culture evolves by adding new behaviours to previous ones, creating more complex traditions. The Complex method was an improvement on the earlier Poke method, making use of the same behaviour of opening the sliding door and inserting the stick, yet the monkeys were not able to add the needed actions to the basic behaviour.

Other possible explanations concern the actions of the Complex method. As mentioned earlier, it may be that the structure of the bolt, hidden on the side of the box made it very difficult for the monkeys to comprehend the connection between the bolt and success. Perhaps they thus considered placing the stick there as redundant.

In an unpublished MA thesis (Fredman, 1995) dealing with understanding of physical causality in capuchin monkeys, it was found that even after monkeys had witnessed hundreds of trials in which a ball rolled down a chute and disappeared into a box, and a second later “Jack in the box” popped out, at the end of the study the monkeys, when given the ball to make the puppet jump themselves, pulled the puppet by its hair and pushed the ball under it. The connection between the ball and puppet was perceived but not the necessity to roll the ball down the runway where the actual launching of the puppet was not seen. Perhaps something similar was happening here: inserting the stick into the hole without being able to see its result was not informative enough for the capuchin monkeys.

In order to test whether the failure to shift to the Complex method was due to the influence of perseveration of the Poke method or the difficulty of the Complex method, we would need to demonstrate the Complex method to a different group of monkeys, without demonstrating other methods beforehand. If these monkeys are not able to socially learn the Complex method in this condition, it would suggest that the structure of this method cannot be learned socially by capuchin monkeys. However, such a test was not possible in this study.

Social learning mechanisms

Although the monkeys did not learn to open the box using the Complex method, social influence was seen in the fact that one monkey inserted the stick to the bolt hole, which could imply a localized stimulus enhancement effect. Also, the fact that the monkeys tried in this phase, even though instances were few, to pull open the lid with their hand, or lever the lid open with the stick, could imply a form of object movement re -enactment or goal emulation.

Learning tool-use from observation

Monkeys in this study were able to socially learn a tool-using task whereas in the Coffee-Tin study (Chapter 6 in this thesis) the same monkeys did not socially learn to use the tool to open the lid and usually moved it away from the apparatus. Two factors might explain this difference:

Firstly, in this experiment the tools were natural sticks and twigs, whereas in the Coffee-Tin study it was a metal + plastic artificial tool. Monkeys in the Island group might be more familiar with sticks and twigs as potential tools, as they have them daily in their enclosures. Therefore they might have been able to learn more easily how to use them in a new situation.

Secondly, in order to obtain the reward in this experiment it was *necessary* to use a tool, whereas in the Coffee-Tin study it was possible to extract the reward without a tool.

In conclusion:

Capuchin monkeys in this study were able to socially learn to use a tool to solve a task. Further, this experiment showed that through social learning, one, apparently superior, tool use tradition can replace an earlier one.

Experiment 2: The Enculturated monkeys

The monkeys from the enculturated population were tested on the same Dipping-Box task.

Subjects

Four subjects were available: three males, Adam, Koko and Rusty, and one female, Hezda. Adam and Koko were housed together and Hezda and Rusty were housed together in a different enclosure. Cacao, familiar with all four subjects, served as the model in this experiment too (see Figure 7.3). Cacao was housed with Hezda and Rusty but spent time with the other two subjects as well, sometimes sleeping in their enclosure at night if she wanted to. Thus all four monkeys were accustomed to her.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

The experimental plan was the same as for Experiment 1. All sessions lasted no more than 30 minutes or were terminated if the monkey left the apparatus for more than 10 minutes.

Figure 7.3 Adam watching Cacao demonstrate how to open the Dipping-Box using the Complex method.

Results

Phase One: Baseline 1

One of the four subjects, Adam, solved the task during the second session of this phase. None of the monkeys used the Gap method observed in the Island group, although actions orientated towards the gap were seen. General behaviours related to the Poke method were seen as well.

The MI index was calculated in this experiment in the same way as it was used in Experiment 1 of this study. A score of MI > 0.5 indicates that the Poke method was dominant; MI<0.5 indicates the Gap method was dominant. Applying the MI for target-like behaviours of the Poke method and Gap behaviours showed that two of the monkeys, Hezda and Adam, tended to show more behaviours orientated to the Poke method, while the other two showed a trend of orientating their behaviour towards the Gap (Table 7.20).

Table 7.20 MI for incomplete and target aimed Gap and Poke actions during the Baseline-1 Phase. MI=0 (shaded green) indicates that the monkey only used Gap behaviours. MI=1 (shaded purple) indicates that the monkey only used Poke behaviours.

	Baseline-1 phase					
	1	**2**	**3**	**4**	**5**	**6**
Hezda	0.50	0.87		1.00	0.00	
Rusty	0.40	0.33		1.00	0.00	
Adam	-	0.60	1.00			
Koko	0.00		0.00		0.77	0.33

In the fifth and sixth sessions Koko showed orientated attention towards the bolt-hole (8.33% and 6.67% of his actions respectively) which is associated with the Complex method.

Phase Two: the Poke Method

The three monkeys who did not discover the Poke method during the Baseline sessions, Hezda, Rusty and Koko, observed Cacao demonstrate this method in Phase Two.

Results

All three monkeys learned the Poke method during this phase. Hezda and Koko solved the task on the second session, Rusty only on the fourth. However Koko stopped using it for two sessions. Once the monkey was observed using the Poke method in two consecutive sessions, s/he moved to the next stage.

Table 7.21 MI for target Gap and Poke behaviours in the Baseline (sessions 1-6) and the Poke method (sessions 7-12) phases. MI=0 (shaded green) indicates that the monkey only used Gap target behaviours. MI=1 (shaded purple) indicates that the monkey only was only using used Poke target behaviours.

	Baseline 1 phase						**Poke phase**					
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Hezda								1.00	1.00			
Rusty										1.00	1.00	
Adam		1.00	1.00		1.00							
Koko								1.00	0.17	0.00	1.00	1.00

Looking at the behaviours related to the Gap method and the Poke method reveals a less clear picture. The fact that Adam discovered the Poke method in the baseline phase left only 3 subjects for comparing the change in behaviour between the phases; however, a Wilcoxon test for only 3 subjects is meaningless. A descriptive comparison of all Poke related behaviours between the Baseline phase and the Poke method is presented in Figure 7.4.

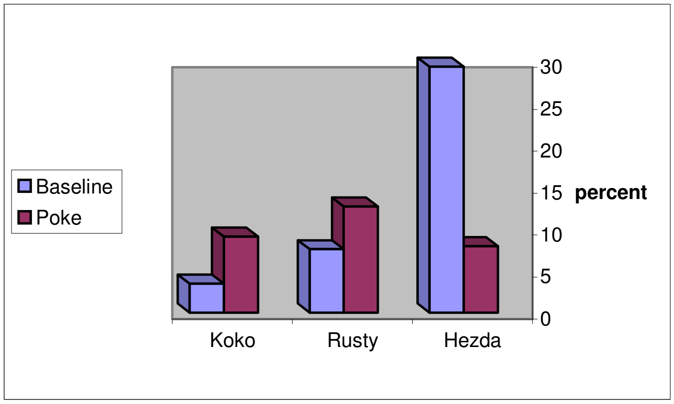


Figure 7.4 Incomplete Poke behaviours during the Baseline and the Poke method phases.

Phase Three -Baseline II

After having learned how to obtain the food in the box using the Poke method, all four subjects received six additional sessions to manipulate the box to see whether they would discover the Complex method on their own. None of the subjects did so during this baseline phase. All four monkeys continued using the Poke method behaviours.

As previously mentioned, the Island group only received three sessions in this baseline phase. However, the enculturated monkeys reached this stage having had many fewer sessions to manipulate the box. Thus, if they had received only three sessions in Baseline II it could have been argued that with more time they might have found the Complex method on their own.

Phase Four: The Complex Method

The monkeys were given six sessions in this phase as with the Island group. Hezda showed the first signs of using the Complex method in the fourth session and Adam in the fifth session.

As with the Island group, the monkeys were given four additional sessions in which a piece of fruit was placed in the box instead of jam in order to enhance the use of the Complex method by the monkeys who had not learned it.

Rusty started using the Complex method in the second session of the enhanced phase, and Koko in third. They both needed another session in order for a full switch to be made. Thus all four enculturated monkeys eventually learned to use the Complex method (see Table. 7.22).

Table 7.22 MI for target Poke and Complex behaviours during Phase Four. MI=1 indicated the monkeys only used the Complex method (shaded blue). MI=0 indicated they only used the Poke method (shaded purple).

	The Complex Method phase						**Enhanced Complex phase**			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Hezda	0.00	0.00	0.00	0.29	0.03	0.00	1.00	1.00	1.00	1.00
Rusty	0.00	0.00	0.00	0.00			0.00	0.27	0.70	1.00
Adam				0.05	0.60				1.00	1.00
Koko				0.00	0.00	0.00	0.00	0.00	0.24	1.00

Comparing the MI for Complex target behaviours (MI=Complex/Complex+ Poke) between the Complex phase and the Poke method phase shows a strong, but not significant trend (Wilcoxon test, N=4 T = 1.83, p = 0.063).

The switch to the complete Complex method was not a radical one, as it might seem when looking only at the target behaviours. The monkeys started to use Complex target-like behaviours already in earlier sessions of Phase 4 (see Table 7.23).

A comparison of the average MI for all related Poke and Complex behaviours (Complex method / Complex method + Poke method) between the Complex method phase (median 0.25) and the Enhanced Complex method phase (median =0.27) showed there was not a significant difference (Wilcoxon test, N=4 T = 0.0, p = 0.563).

Table 7.23 MI for all related Poke and Complex behaviours during the entire Complex phase. MI=1 indicated the monkeys only used the Complex method (shaded blue). MI=0 indicated they only used the Poke method (shaded purple).

	Complex method phase						**Enhanced Complex phase**			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Hezda	**0.18**	**0.56**	**0.00**	**0.60**	**0.50**	**0.39**	**0.53**			
Rusty	**0.00**	**0.00**	**0.00**	**0.35**			**1.00**		**0.59**	**1.00**
Adam				**1.00**	0.83					
Koko					**1.00**	**0.14**	**0.11**		**0.54**	**1.00**

Hezda for example spent a great deal of time in the second and fourth sessions examining the bolt-hole and the way it worked; poking her finger in it while trying to open the lid with the other hand or with a stick. At times she would do this while lying down, inspecting the bolt-hole intensively.

Island group versus enculturated group

A comparison between the groups has its limitations, one of which is the experimental setting. The Island monkeys were tested in a group whereas the enculturated monkeys were tested alone. Tested in a group setting can have an inhibiting effect on responding by the low ranking monkeys (Visalberghi, 1990).

Thus, at least for the dominant monkeys, for which a group setting may be less inhibiting, a comparison with singly tested subjects could be made with caution.

A comparison was made between the four enculturated monkeys and the four higher ranking monkeys in the Island group (Zed, Milky, Zorba and Drorit) on the average MI for target behaviours (Complex method/ Complex method +Poke method) in Phase Four. There was a significant difference between the mother-reared monkeys (median=0) and the enculturated monkeys (median=0.2399) (Mann Whitney test U=0.0 n_1=4, n_2=4, p=0.014).

However, as stated previously, the Island group monkeys showed some general Complex behaviours in this phase. Comparing the two groups on these general behaviours, using the Mann Whitney test, did not reveal a significant difference (see Table 7.24).

Table 7.24 A comparison between the four high ranking Island group monkeys and the Enculturated monkeys on general Complex method behaviours**.**

Incomplete target behaviours		**Target aimed- no tool**		**Target locus orientated**	
Enculturated median=2.740	Island median=1.389	Enculturated median=0.737	Island median=1.260	Enculturated median=1.247	Island median=3.86
1.114	1.250	15.824	0.253	2.349	4.173
2.124	0.000	1.212	0.000	2.657	1.111
3.356	8.485	0.263	0.256	0.145	12.542
4.034	1.528	0.000	0.000	2.727	3.540
U=6 n_1=4, n_2=4 p=0.343		U=3 n_1=4, n_2=4 p=0.1		U=3 n_1=4, n_2=4 p=0.1	

Discussion

Except for Adam, who found the Poke method on his own, the other three monkeys performed the complete Poke method only after watching the demonstration. However, this behaviour cannot be attributed to the demonstration alone as the monkeys showed behaviours related to the Poke method in the Baseline phase. Thus, watching the demonstrator apparently helped canalize their behaviour towards the complete Poke method. This cannot be said for the way the monkeys learned the Complex method.

The monkeys did not show signs of this method during the two baseline phases and the Poke method phase, except for two brief occasions in which Koko orientated his attention towards the bolt-hole during the first baseline and one instance of Hezda looking in the bolt-hole in the first session of the Complex method phase.

All four monkeys switched entirely to the Complex method. However several points must be mentioned.

1. It seems that these monkeys like the Island group monkeys, did not understand the effect poking the bolt had on opening the lid, as they mainly inserted the stick into the hole pulling it up as a lever. Nevertheless these monkeys copied the insertion of the stick to the hole, implying that they might have been imitating.

If the enculturated monkeys' behaviour was based on imitation it was not a perfect copy. The observing monkeys acted differently than Cacao in several ways. Cacao demonstrated poking the bolt when it was positioned on the right side of the box. The observers often preferred to sit in front of the box with the bolt hole at the far end to them. This is perhaps an easier way to hold and manipulate the stick in relation to the bolt-hole. Further, the stick was often poked in the bolt- hole and then with a levering action moved up and down, more as though they were trying to lever the lid open from that angle. Perhaps levering had a more obvious effect on the lid, as it moved a little with the levering.

Opening the box using the Complex method demanded that the monkeys use a fixed sequence: first unlocking the bolt and then opening the lid. However it was seen that the monkeys, after having opened the box using the Complex method, still tried at times to first open the lid and then insert the stick in the bolt-hole. This behaviour may also imply that they did not understand the effect unlocking the bolt had on opening the lid.

Not all the monkeys used the stick to open the lid. Some used their finger while others, Adam and Rusty, found an original way and after poking the bolt with the stick they inserted the stick in the door, brought a stone and hammered the stick until the lid opened. However they did not continue with this, maybe realising there was no advantage in using the stone (note they did not see each other do this action).

Thus the Complex method was transmitted socially between the monkeys, but they modified it.

This study responds positively to the question posed by Bering (2004) whether “enculturated” primates would show complex social learning abilities when viewing a monkey instead of a human model. However, attention to the monkey model was lower than seen towards the human model in the previous two studies (the Artificial

Fruit and the Coffee Tin studies) in which their attention to the model was almost perfect. If more monkeys were available for the study it would have been possible to address this question more directly and compare attention to human versus monkey models demonstrating the same task, as well as test the effect on latency to first success as a function of model type.

Mother reared versus Enculturated monkeys

It was clear that only the enculturated monkeys were able to fully switch from the Poke method to the more complex yet more advantageous Complex method. Four of the Island group monkeys nonetheless showed behaviours related to this method after observing the demonstrations. The fact that the Island group did not perform the complete Complex method could be a result of confounding factors.

Both groups showed they were able to undertake one switch between the different techniques. It is possible, as mentioned in Experiment 1, that the Island group did not manage to learn the Complex method as it demanded that they make a second switch. Thus, testing mother-reared monkeys having to make only one switch from the Poke method to the Complex method would eliminate this factor.

However, recent results with a similar task tested on eleven young chimpanzees found that these subjects, who only had to master one switch from a poking to a more complex probing method, were unable to do so (Marshall-Pescini & Whiten, 2008). These results with chimpanzees emphasise the positive results found in the enculturated capuchin monkeys.

The question of the enculturated monkeys' superior experience with objects still remains open. This appears most clearly in their lack of neophobia. It took six sessions for the Island group to stop threatening the box whereas the enculturated monkeys immediately approached the box and started to manipulate it. It cannot be ruled out that perhaps this experience with objects was the component missing for the Island group monkeys to acquire the complete Complex method.

One way to avoid the effect of the influence of experience with tools, which enculturated monkeys have, is to test the enculturated monkeys’ understanding of the abstract concept of imitation. Such understanding goes beyond mere experience with the affordance of tools and can be manifested in other domains such as actions without tools and gestures. The ability to understand this abstract concept of imitation will be dealt with in the next chapter.

Chapter 8

CAN “CEBUS SEE CEBUS DO”? - A PRELIMINARY STUDY

The current experiment explores the question of whether capuchin monkeys are able, through training, to learn the concept of imitation. An eight stage training strategy employing a “do as I do" paradigm was designed to facilitate teaching the monkeys the concept of imitation, that went from simple matching behaviours with objects to matching actions without objects.

Four enculturated monkeys participated in this preliminary study. All four monkeys responded above chance in the first stages of matching actions on objects. One monkey proceeded to the fifth stage in which he was required to match different actions on the same object. The study was stopped at that stage because of limitations of time.

The results show suggestive evidence for the ability of enculturated capuchin monkeys to learn the concept of imitation. Factors which may enhance the learning of the concept of imitation in capuchin monkeys are discussed.

The previous studies in this thesis have concentrated on the question: do capuchin monkeys learn by observing a model? testing this question from different angles.

The experiment described in this chapter tries to answer the question: *can* capuchin monkeys imitate? Or more specifically, can they learn the concept of imitation?

These are two different questions, the first of which (“do they?”) may be related to strategies of behaviours used by an animal, whereas the second (“can they?”) is related to the cognitive ability of the species to imitate. Primates confronted by a problem may employ different social learning strategies in different situations as has been seen with chimpanzees (Horner& Whiten, 2005). Re-enacting goals may take priority over imitating an action even if the action can be copied (see the short discussion on this topic in Chapter 5). Thus the lack of imitation may not always be a sign of inability.

The “Do-as-I-do” paradigm has been used to test whether a subject has the ability to learn the concept of imitation. This within - subject design involves a first phase of moulding and teaching the subject to reproduce actions it observes and then a test stage which requires the observer to perform a new action immediately after the demonstration. Once this has been established the subject can generalize the concept to new instances.

It has already been established that except for humans, only chimpanzees, orang-utans and dolphins are able to perform arbitrary actions on command and thus seem to be able to represent the concept of imitation (Hayes & Hayes, 1952; Herman, 2002; Custance *et al.* 1995; Miles *et al.* 1996; Harley *et al.* 1998).

Attempts to teach a macaque monkey (*Macaca fascicularis*) to imitate on command (to scratch a specific body part) failed, although the monkey did scratch in a general manner after seeing the demonstrator scratch (Mitchell & Anderson, 1993). Nevertheless, a different species of macaque monkey (*Macaca nemestrina)* was able to recognize being imitated (Paukner *et al.* 2005). However, the monkeys did not try to test this by changing their movements the way human infants and chimpanzees do (Nadel, 2002; Nielsen *et al.* 2005), thus showing, perhaps, only an implicit understanding of being imitated.

Accordingly, there may be two levels of the concept of imitation: the ability to recognize one is being imitated and the ability to transfer this into action. The production of the imitative action may be more difficult as it also demands planning and using the correct motor actions (Paukner *et al.* 2005).

This ability to entertain the concept of imitation may have implications for the emergence of culture as Whiten (2000) suggests:

> "…Knowing you are imitating is a step towards this, and is a kind of 'meta-representation' (mentally representing some mental process or representation) that may link it with other abilities to represent 'states of mind' " (p. 490).

Why test capuchin monkeys on this task?

The studies in this thesis have shown that the enculturated monkeys presented a higher ability to learn socially than the mother-reared monkeys. It has been argued here that one of the reasons for this difference is the high level of attention paid by these monkeys to the human caretaker who serves as demonstrator. Visalberghi & Fragaszy (2002), reflecting ten years after the publication of their paper "Do monkeys ape" conclude that:

> "In retrospect, we can see that intensive and prolonged interaction with humans (during early life, and in the course of extended training to respond to verbal commands issued by humans) does affect capuchins' visual attention to humans, and enhances their interest in objects a human touches, and these perceptual tendencies may enhance the monkeys' probability of matching object movement. However, such experience does not seem to lead to enhanced ability to match *action*, the signature feature of imitation" (p. 488-489).

This conclusion was based partially on the attempts to test capuchin monkeys on a spontaneous "Do-as-I- Do" test (see Chapter 2). However, no attempt has been made to *teach* capuchin monkeys to imitate.

In this study I will try to teach the monkeys the concept of imitation and suggest that there may be a way to overcome the apparent limitation of action - imitation. I intend to try teaching the enculturated monkeys the rule of imitation using objects as mediators between the demonstrator's actions and the observer's action.

This is based on the following principles:

1. Capuchin monkeys readily manipulate objects.
2. Chimpanzees have been found to be more successful in imitating actions which included objects. Myowa-Yamakoshi & Matsuzawa (1999) used objects in their "Do-as-I-Do" study. They found that chimpanzees perform differently when the action involves an object or only body movements. Adult chimpanzees performed better (including some first-trial imitations) on trials when one object was used on another than when the action was directed towards a single object or when an object was directed at the self. Both chimpanzees and orang-utan were found to "match aspects of actions on objects they had seen although they seem to have paid attention more to the object than to the model's actual action" (Myowa-Yamakoshi & Matsuzawa, 2000).
3. Enculturated monkeys show a high level of attention to a human model.

It is true that imitating actions with an object may be tapping different social learning mechanisms than the imitation of arbitrary gestures (see Chapter 2). However, even if the monkeys manage to learn the rule for this level, it will be a worthwhile achievement as being able to switch back and forth from one action on an object to the other constitutes the basic understanding of matching behaviour through imitation.

Starting from such matching behaviour in a systematic training schedule may provide the best conditions for making the transfer from imitating behaviour with an object to imitating the *same* behaviour without the object. Once this transfer is achieved it may be possible to generalize it to novel actions without an object.

Imitation in apes is not spontaneous as is found in children; thus there is no reason to presume it would be spontaneous in capuchin moneys either. Learning the concept of imitation would demand extensive training for the capuchin monkeys to succeed, just as found with chimpanzees (3 months, 5 days a week training: Custance *et al.* 1995). Further, other concept formation tasks carried out with capuchin monkeys require intensive training too (between 1000-1500 trials; Adams-Curtis, 1990).

This study could only be carried out after the other studies in this thesis had been completed, because trying to teach the monkeys the rule of imitation would have confounded the aims of the previous studies. Therefore, as the time limits of this thesis would not permit the entire training schedule to be covered, this study was considered a preliminary one, in preparation for the full-scale study to be continued once this thesis is submitted. Thus, the testing at the different stages described in the following section, did not continue until a high level of performance criterion had been met but rather 3-6 sessions were run regardless of the performance of the monkey.

The methodological plan for this study included eight main stages:

Stage 1. Training – in this stage the monkeys learn to respond after the command "Now you".

Stage 2. Simple matching: The monkeys are rewarded for choosing the same object combination as demonstrated, out of two options.

Stage 3. **Complex matching**: The monkeys are rewarded for choosing the same object combination as demonstrated, combining two objects out of three possible options.

Stage 4. Two-action games: The monkeys are rewarded for producing the same action on an object as demonstrated. Both actions are demonstrated in each session.

Stage 5. Pre movement imitation: The monkeys are rewarded for matching one of two movements using the same object (rubbing or pounding a small stone on a surface, with one hand).

Stage 6. Action on surface: The monkeys are rewarded for matching the same action demonstrated on the surface, using the same actions as in Stage 6 but without an object; rubbing or pounding the hand on the surface.

Stage 7. **Action with object on body**: The monkeys are rewarded for matching the same action as demonstrated using a small object on visible body parts:

(a) Rubbing a stone on arm or hand.

(b) Clapping or rubbing two small stones between two hands.

Stage 8. Action on body without object: Same as Stage 8 but without an object.

Two points were taken into consideration:

A. Behaviours in some of the stages of the current study will most probably demand moulding the hand of the monkey into the correct action (Custance *et a.l* 1995 1994, for chimpanzees). Such a procedure is possible with the enculturated monkeys and might assist the process of learning.

B. The physical differences between the human model and capuchin monkeys are immense and may be an obstacle for teaching action imitation. Nevertheless, it seems that these monkeys do have at least a rudimentary understanding of the similarity of function between human and monkey body parts. For example, these monkeys put an object in the human hand to "make it work". Understanding the similarity in function of the human mouth and the monkey mouth may be suggested from the following observation:

> Cheppy used to like having carrots, apples and some other food items chewed for him by humans. When once I refused to chew a carrot for him, closed my mouth and turned my face to the side, he went to Hezda, who was very young at that time, and pushed the carrot in her mouth. He then pushed his fingers in it to get the little pieces out.

Method

Subjects:

Four of the enculturated monkeys participated in this study: two females, Hezda and Cacao, and two males, Rusty and Adam (age range 11-18 years).

Procedure

The monkey sat opposite or next to the experimenter. Adam was tested in his cage. The other three monkeys were tested either in their cage or outside of it in an area where they played freely. In the first 5 trials of each stage, when the new task was introduced, the human model, myself, demonstrated the behaviour and then exclaimed an excited “good”. The monkey was then given a reward (small portion of jam, yogurt, raisons or nuts). This was done in order to indicate to the monkey that this was a positive outcome. Next, the monkey was told “now you”. The monkey was rewarded for acting in the same way as the demonstrator. After these initial trials, the action was demonstrated without “sharing” the reward with the monkey. Throughout the experiment the subjects were rewarded verbally (“good “) and with a small treat, for acting the same way as the demonstrator.

Results

Stage 1: Training

A pot and wooden block were used for the training session. The block was put in the pot and then the monkey was told “now you”. Adam, Rusty and Hezda had no problem responding from the first trial and did not need training. This was repeated ten times. Cacao was more hesitant and 10 trials were done co-acting together with the experimenter before she responded herself to additional 10 trials.

Stage 2: Simple matching

The apparatus in this stage consisted of two objects placed on either side of an up-side-down funnel fixed to a wooden board. The monkeys had to choose the same object as demonstrated and put it on the thin part of the funnel (see Fig. 9.1). Both monkey and demonstrator had the same set of objects. The monkeys were given 120 trials in three sessions. Hezda stopped responding in the middle of the sessions; thus she only totalled 60 trials. Applying a binomial test shows that all the monkeys responded above chance level.

In the test session at the end of this stage both objects were placed on one side of the funnel, thus checking that the monkeys were responding to the object chosen and not to the side it was moved from. Only Cacao responded correctly significantly above chance. Results are shown in Table 8.1.

Figure 8.1 The apparatus in Stage 2. The monkey and the demonstrator had identical sets of objects. The monkey had to put the same object on the funnel as demonstrated. In the picture: Cacao observing and choosing the correct object

Table 8.1 Correct responses in the matching task. n= number of correct trials.
N= total number of trials.

	Adam	**Rusty**	**Hezda**	**Cacao**
	n(N)	n(N)	n(N)	n(N)
Training	83(120) p<0.001	63(120) p=0.022	38(60) p=0.037	75(120) p=.0036
Test	12(20) p=0.503	14(20) p=.0115	12(20) p=0.503	16(20) p=0.012

Stage 3: Complex matching

In this stage the monkeys were presented with three out of four potential objects on each trial and had to choose the combination demonstrated to them out of three possible combinations. Thus the chance success rate was 33.3%. The objects included a wooden cube, a plastic circle, a funnel, and plastic cup. The sessions were shorter in this stage than in Stage 2 in order to better sustain the attention of the monkeys. In the fourth session a set of different objects was given to the monkeys to test for generalization of the task. A binomial test in which chance level was adjusted to 33.3% was used to assess the monkey's success. All monkeys performed above (33.3%) chance in the first 90 trials. In the fourth session with a new set of objects only Rusty did not respond above chance. Results are shown in Table 8.2

Table 8.2 Correct responses Stage 3. n = number of correct trials. N = total number of trials.

	Adam	**Rusty**	**Hezda**	**Cacao**
	n(N)	n(N)	n(N)	N(N)
Training	46 (90) p<0.001	45(90) p=0.001	49(70) p<0.001	48(90) p<0.001
Test	12(20) p=0.013	10(20) p=0.091	14(20) p=0.001	12(20) p=0.013

Discussion

The paradigm used in Stage 2 and Stage 3 of this experiment resembles the Match-To-Sample (MTS) paradigm used to test concept formation in non- human animals (e.g. Katz & Wright, 2006 for pigeons; Thompson et al 1997 for chimpanzees). In the MTS the subject is presented with a sample stimulus and then has to choose a matching stimulus from an array of stimuli presented simultaneously or delayed. The choice is based on understanding the relation between the sample stimulus and its match. After the first stage of acquisition, the generality of the learned relation between the stimuli is inferred from the subject's ability to match novel items in transfer tests.

Several studies have been carried out with capuchin monkeys showing they were able to learn abstract relations between stimuli such as the concept of identity and oddity (D'Amato et al., 1985). D'Amato & Colombo (1989) however claimed that this concept is limited in capuchin monkeys. They concluded this from the extended length of time it took the monkeys to learn the correct choice with novel stimuli. However, Wright et al (2003) showed that with closer control of different elements of the procedure (e.g. learning set size) capuchin monkeys showed a high level of concept formation. Spinozzi *et al.* (2004) found that capuchin monkeys were able to learn the abstract concept of "above" and "below" using the MTS paradigm. Thus, the MTS has been a powerful instrument to test concept formation in capuchin monkeys.

The paradigm used in the current study differs somewhat from the standard MTS. The main difference is that an agent, the demonstrator, was involved as an intermediary between the stimuli presented and the correct stimuli to choose. If, as I claim, these monkeys learn through enculturation to pay extra attention to the human caretaker, this should be a much easier task than the previously mentioned MTS experiments, as the monkeys can use an extra cue, the social cue, for the correct choice. The fact that the monkeys responded above chance in the test of Stage 2 after only 90 trials could imply that indeed the demonstrator's actions were used as a cue for choosing the correct objects.

On the other hand, in the standard MTS paradigm the subject indicates understanding of the concept by pointing to a stimulus which acts as the word "same" or "different" or in other experiments, pointing to the stimulus with the correct answer on it, in order to receive food reward. In the current study, the monkeys had to replicate the action they saw using the correct stimuli and not just *recognize* the same end result. From this point of view this paradigm is more complex than the standard MTS.

In the next stages replicating the action becomes the major factor for success as the stimulus remains constant.

Stage 4: Two-action games

In this stage the monkeys were presented with different games, which could be acted upon in two ways. In traditional two- action experiments each monkey or group of monkeys is shown only one way of acting on an apparatus. Here, the monkeys were asked to use each of the two ways according to what they saw. Further, the reward was not in the apparatus itself as in the different puzzle boxes experiment, but rather the monkey received the reward after acting the same way as the demonstrator.

The games included:

1. The Short Rod: A wooden rod (10 cm long, diameter 2 cm) was placed in a slot on the top of a wooden box (20x13x13 cm). By holding the top of the rod with one hand it could be either (a) moved in the slot along the top of the box in a sliding motion from one side of the box to the other or (b) pushed into the box. (See Figure 8.2 a, and b).

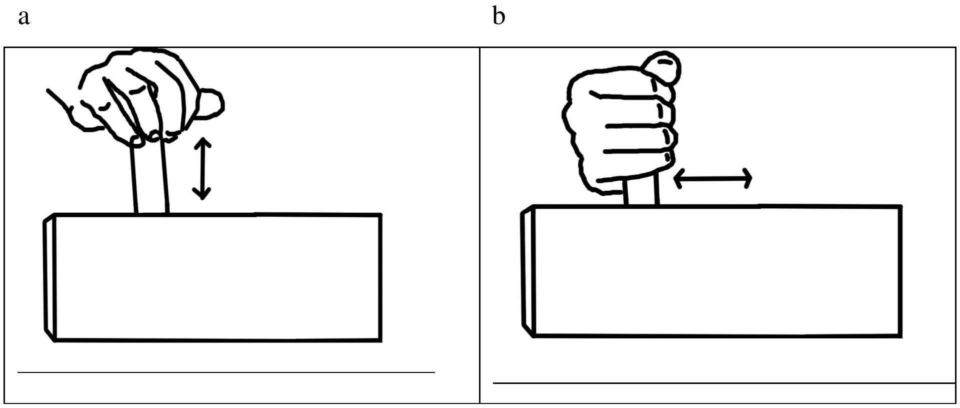


Figure 8.2. The Short Rod. (a) The rod is pushed down; (b) The rod is moved to the side.

2. The Long Rod: A wooden rod (10 cm long, diameter 2 cm) was placed in a slot on the side of a wooden box (16x17x12 cm). By holding the top of the rod with one hand it could either be (a) pushed up the slot to the top of the box or (b) pulled out of the box and extended a further 10 cm (see Figure 8.3 a and b)

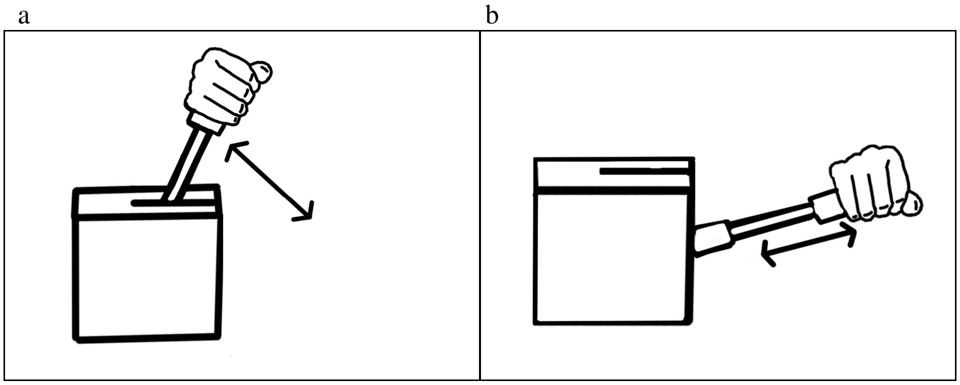


Figure 8.3. The Long Rod: (a) the rod is pushed up; (b) the rod is pulled out.

3. The Box Lid. The lid of a wooden box (12x8x10 cm) could be opened by holding the handle in the middle of the lid and either (a) sliding the lid to the side of the box or (b) pulling the lid upwards (See Figure 8.4 a and b).

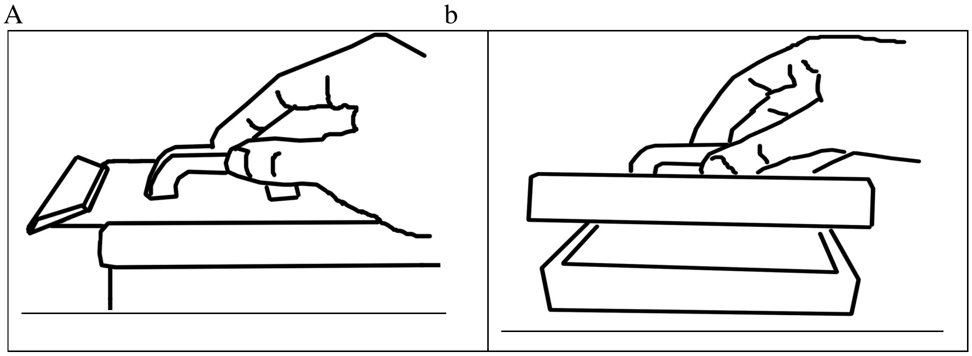


Figure 8.4. The box lid: (a) The lid is slid to the side; (b) The lid is pulled up.

4. The ring: A wooden ring (2.5 cm diameter) was placed on a rod (2 cm diameter 15 cm long) which was held by two wooden squares on the top and bottom of the rod (each square measuring 11x11 cm). Holding the ring with one hand it was possible to either (a) move it up the rod or (b) spin it round the bottom part of the rod (see Figure 8.5 a and b).

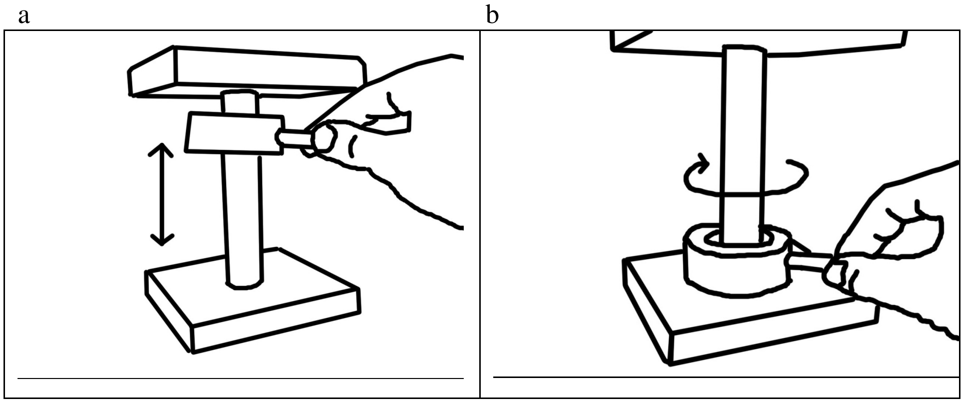


Figure 8.5. The Ring: (a) the ring is pulled up; (b) the ring is spun round.

There were two sessions of 24 trials each in which each morph of each game was presented three times. On the third and fourth sessions two new games were introduced together with 24 trials of the original four games. These games were:

1. The cardboard box – a square lid (10 x 10 cm) was placed on a cardboard box (10 x10x10 cm). The box could be opened by either (a) taking the lid off the box or (b) pushing the lid into the box (See Figure 8.6 a and b).

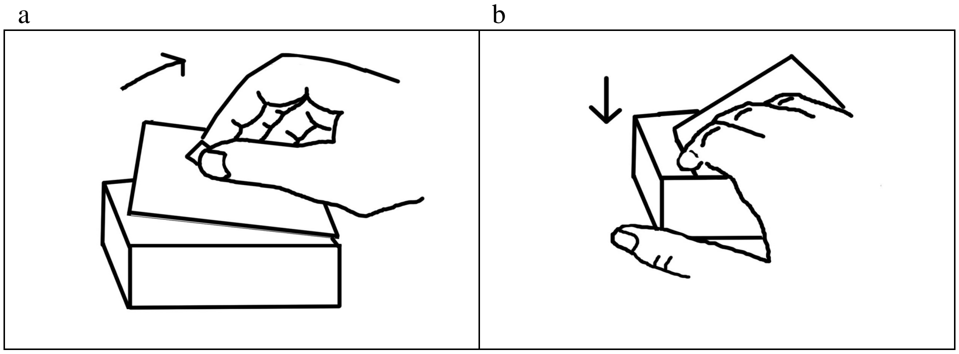


Figure 8.6 The Cardboard box: (a) taking the lid off the box; (b) pushing the lid into the box.

2. The pastry crimper: a pastry crimper was manipulated in two ways: (a) holding the crimper with the wheel facing downwards and rolling it on a surface as would be done on pastry or (b) holding the crimper with the disc upwards and spinning the disc with the other hand (see Figure 8.7 a and b).

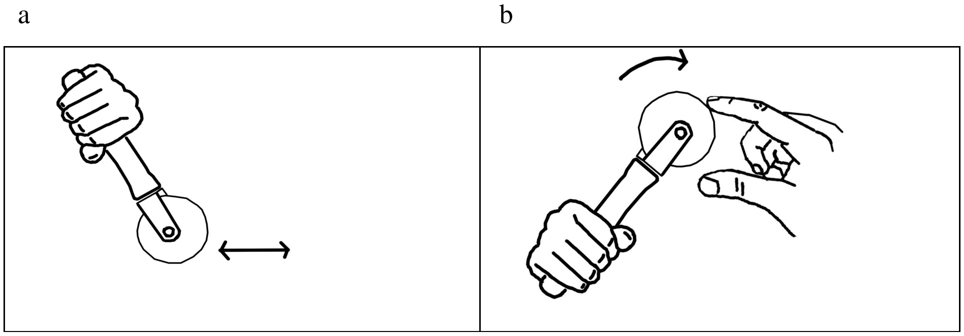


Figure 8.7 The Pastry crimper: (a) rolling the crimper on the surface; (b) spinning the wheel.

Results:

The overall percentage of correct responses in the 96 trials of the four base games was: 78.12 % (Adam), 69.79% (Rusty), 65.25% (Hezda) and 67.7% (Cacao). A two- tailed binomial test showed that the monkeys responded correctly above chance (see Table 8.3).

Table 8.3 Correct responses in Stage 4. n = number of correct trials. N = total number of trials in session. % = percent of correct responses in each session. p = binomial statistical significance of responding above chance.

	Adam	**Rusty**	**Hezda**	**Cacao**
n(N) %	75 (96) 78.12%	67(96) 69.79%	62(95*) 65.26%	65(96) 67.7%
P	P<0.001	P<0.001	p=0.004	P=0.001

* Hezda left one session before it was finished

A Friedman test, testing the correct response rate for each game (Table 8.4) showed there was not a significant difference between the games. (Friedman test p=0.537).

Table 8.4 Success rate of each monkey on each morph of the games. Numbers indicate the number of correct trials Number in brackets indicate the total number of trials that morph was demonstrated in the session. Bold numbers represent correct responses significantly above chance.

	Box Lid		**Ring**		**Short rod**		**Long rod**	
	Slide	Open	Up	Spin	Push	Slide	Up	Out
Adam	9(12) 75%	9(12) 75%	***12(12)*** 100%	4(12) 33.3%	6(12) 50%	***12(12)*** 100%	***11(12)*** 91.6%	***12(12)*** 100%
Rusty	***10(12)*** 83.3%	***10(12)*** 83.3%	5(12) 41.6%	8(12) 66.7%	6(12) 50%	***12(12)*** 100%	***11(12)*** 91.6%	5(12) 41.6%
Hezda	8(12) 66.7%	***12(12)*** 100%	8(12) 66.7%	7(12) 58.3%	9(12) 75%	7(12) 58.3%	5(12) 41.6%	6(11)* 54.5%
Cacao	9(12) 75%	***11(12)*** 91.6%	***10(12)*** 83.3%	4(12) 33.3%	***10(12)*** 83.3%	4(12) 33.3%	***11(12)*** 91.6%	6(12) 50%

* Only 11 trials for this action instead of 12.

<u>Introducing new games</u>

The Cardboard box was introduced in the third session. The two morphs of opening the box were demonstrated four times each, randomly between the 24 demonstrations of the four original games. Only Adam came close to responding successfully above chance on the test trials (see Table 8.5).

The pastry crimper apparently was difficult to operate. None of the monkeys managed to roll it on the surface except for one trial in which Hezda came close to rolling it. They did not try to respond using the second morph of spinning instead of rolling it, but rather rubbed the crimper on the surface, or banged it. It seemed then, that the actual action was not easy for them to produce and might require more opportunities for practice. Spinning the top was more successful, but the fact that the disc of the crimper was made of metal enabled monkeys to see themselves in it and distracted their attention. Results for the test trials can be seen in Table 8.5.

Table 8.5 Results for the test trials with the Cardboard box and Crimper: n= number of correct trials. N= numbers of trials the morph was demonstrated. In the Total column is the total number of successful trials.

	Cardboard box			**Crimper**		
	Lid in n(N)	Lid off n(N)	Total n(N)	Roll n(N)	Spin n(N)	Total n(N)
Adam	4(4)	3(4)	7(8) P=0.07	0(4)	3(4)	3(8) P>0.05
Rusty	3(4)	2(4)	5(8) P>0.05	0(4)	2(4)	2(8) P>0.05
Hezda	4(4)	2(4)	6(8) P>0.05	1(4)	2(4)	3(8) P>0.05
Cacao	2(4)	3(4)	5(8) P>0.05	0(4)	2(4)	2(8)P>0.05

Stage 5. Pre-movement imitation

Only Adam participated in this stage as he had done better than the other monkeys on the previous stages and seemed to be more motivated. The aim of this stage was to teach Adam to move a small stone on a surface as a function of what he observed: rub or pound. This stage was a preparation for teaching the monkey to move his hand on the surface without an object.

In the first session the two behaviours were established. At first, Adam mainly rubbed the stone on the surface in response to the demonstrations of both actions.

It was then decided to use a second object as a mediator to achieve the required action of pounding. Adam was shown “pound” while pounding the stone on a pip. He immediately did that and after 5 trials the pip was removed and Adam was shown “pound” on the surface to which he responded correctly.

This is a good example of how an object may serve as a mediator to show an action to the monkey and once removed the action may be repeated without the object. This is the basis for the rationale of later Stages 7-9, which aim to show generalization of a movement with a very small object to the same movement without an object.

After the first session in which the two behaviours were established, three additional sessions of 50 trials each were carried out. Adam showed progress through the sessions. By the fourth session the number of correct responses came close to being significantly above chance (see Table 8.6).

Table 8.6 Adam's correct responses in Stage 5. n=number of correct trials. N= total number of trials in session. %= percent of correct responses in each session. P= binomial statistical significance of responding above chance.

	Session 1	**Session 2**	**Session3**	**Session 4**
n(N) %	20(50) 40%	29(50) 58%	30(50) 62%	32(50) 64%
P	p=0.203	P=0.322	P=0.203	P= 0.066

For time reasons, the preliminary study was halted at this stage. It is planned to be continued.

Discussion

There were two aims to this preliminary study. The first was to investigate the methodological features of the "do-as- I -do" procedure in order to maximize the ability to teach capuchin monkeys the rule of imitation. The second was to assess the success rate of the monkeys in a "do- as -I -do" procedure bearing in mind that the number of learning sessions given to the monkeys in this study might not be sufficient to achieve a high success rate.

Methodology

The monkeys in this study were able to sit through most of the "do- as- I- do" sessions. However, in some sessions they showed signs of frustration manifested by leaving the session, lying down next to the apparatus, looking backwards at an unseen target, and on two occasions, stressful vocalizations (Rusty). Capuchin monkeys can spend a long time trying to open puzzle boxes without success (Fragaszy *et al.* 2004) but in this study the monkeys appeared to be more frustrated when not succeeding. This may indicate that they were not as sure of what was expected from them. Perhaps the goal, the food item, which the monkeys could see placed in the puzzle boxes, sustained their efforts. In the "do- as- I- do" type of task, the end result of their action is not in the apparatus itself.

Two solutions were used when the monkeys seemed to be frustrated:

a. Stopping and going back to a simple task (e.g. placing one object on the other). Such actions were also used to end a session if the last trial was unsuccessful.
b. Doing a task together – holding the monkey's hand and co-acting.

Success rate

The monkeys showed higher success rates in the two-action games in Stage 4 than in the matching choice behaviour in Stage 2. This could be attributed to the practice they had with the "do-as- I-do" procedure by the time they reached Stage 4, thus gaining more understanding of the concept of imitation.

However, it may also be attributed to the difference in the *type* of actions they were asked to perform in the two stages. In Stage 4 the two actions in a given game resulted in different end states of the apparatus (e.g. lid of the box was either up or moved to the side in order to open the box) whereas in Stage 2 the end state of both options was much the same – the funnel had an object on it (although it was either object A or B).

If capuchin monkeys, as some claim for chimpanzees, are more attuned to results, they might find Stage 4 easier than Stage 2 which was thought initially to be an easier simple choice-matching task. In order to test this, naive monkeys should be tested on Stage 4 without going through Stage 2, to determine whether their success rate differs from the results found in this study.

Action centred imitation

Stage 5 is the beginning of training for action imitation. Only 4 sessions were given with improvement from 40% success on the first session to around 60 % on the next 3 sessions. It is thought that perhaps more exemplars for the rule in each session are needed for a better understanding to occur (Oden ,Thompson, Premack, 1988; Rosch, 1978). Such actions could include scratching a surface with a small twig versus poking with it, as well as actions with two hands; e.g. banging two discs with two hands on a surface versus clapping them together.

Human- monkey interaction

a. Visual attention

Individual differences were seen in this study. Hezda, who seemed to be the best social learner in the previous studies, lost interest very early in this study, and would sometimes walk away at the beginning of a session. These sessions were omitted from the statistical analysis. Adam showed the longest attention span during the sessions. This might have been due to the fact that the other three monkeys spent much time socializing with the experimenter beyond the sessions whereas Adam, at that time, mainly spent time with the experimenter during the experimental sessions.

Attention to demonstration was lower in this study (average 83.7%) than in the previous studies using a human model (Artificial Fruit study, Chapter 3 and Coffee-Tin study, Chapter 5) in which attention reached almost 100% of the time.

This is most probably due to the longer sessions, which included up to 50 demonstrations as opposed to a maximum of 6 demonstrations in the previous studies. As attention seems to be a dominant factor in succeeding to learn socially, this problem needs to be approached before further testing. One way to sustain attention may be using a larger variety of objects and tasks in each session. This could be complemented by shortening the sessions as well.

b. Coactions

In some of the trials the monkeys put their hand on the experimenter's hand while the experimenter was demonstrating. Such behaviour, referred to as 'coaction' by Fragaszy & Visalberghi (1989), has been considered a powerful means of learning novel skills. Visalberghi & Fragaszy (1990a) claim that "coaction of a skilled model and a learner, in which the model allows the learner to participate intimately in its actions, is probably the most effective setting for learning a novel motor skill in nonhuman primates" (p. 267).

c. Requesting help

In the previous studies the enculturated monkeys were observed asking for help from the demonstrator, either by taking her hand or by putting the object in her hand. In this experiment as well this behaviour was seen in Stage 4, with actions on the crimper which seemed to be difficult for the monkeys to produce. I will further discuss the nature of this type of communication and its implications for social learning in Chapter 9- General Discussion.

Conclusion

The preliminary test of the "do- as- I- do" paradigm shows there is a potential for teaching these monkeys the rule of imitation, given that they are allowed enough trials to enable learning of the concept. Further, in order to sustain their attention, sessions should not exceed 20-25 trials and should contain several exemplars of the rule being taught.

Chapter 9

GENERAL DISCUSSION

Long term observations of groups of capuchin monkeys have suggested that these monkeys have traditions in nature showing group contrasts in feeding techniques and hunting, as well as in social conventions (Perry *et al.* 2003). Yet it is mainly suggestive information, such as high tolerance and close observation of conspecifics, which is interpreted as reflecting the influence of social learning in acquisition of these behaviours. The fact that laboratory experiments have not been able to simulate this in experimental studies (Visalberghi & Fragaszy, 1990a) is puzzling and may be due to methodological flaws (see Chapter 2) and not necessarily to capuchin inability.

The studies described in this thesis, carried out with groups of mother-reared as well as enculturated capuchin monkeys, have shown strong social learning influences on the acquisition of behaviour patterns by these monkeys, allowing us to draw some conclusions which may be helpful in understanding capuchin cultural behaviour in nature, as well as having implications for other related cognitive abilities.

High fidelity imitation was not seen in the groups of monkeys studied. However complex social learning, which allows for the creation of two distinct modes of behaviour, clearly took place. This strengthens the notion that the behaviours observed by Perry *et al.* (2003) were indeed transmitted socially.

There is still a need for long term observations to determine whether such learned behaviours can be sustained in the group for longer periods of time, creating local traditions. In order for traditions to be sustained, there is a need for conformity to the norms of the group. Whiten *et al.* (2005) define such conformity as behaving in accordance to the group's norm, even if through exploration or chance a different method of behaving towards the same stimulus is discovered. For conformity to take place the monkey may have to know when s/he is imitating. Whiten & van Schaik (2007) claim such conforming behaviour has only been found in humans and chimpanzees. However, some possible implications for a basic level of this understanding may be found in the current experiments in Chapter 6, in the way one of the enculturated monkeys tried to repeatedly copy the action she had seen the demonstrator do even though she had found another way to get the reward. Further, the preliminary results of the "do-as- I- do" experiment in this thesis, in which Adam, after a relative short training period, showed signs of matching the movement he saw with the stone, may imply some rudimentary understanding of this sort .

However, conformity to a norm may also be achieved without relying on a high level of understanding of the concept of imitation, and may be strengthened by social rewards. The importance of a social reward was discussed in detail in Anderson (1998) and is seen in practice in the fact that capuchin monkeys maintain social traditions in nature (Perry *et al.* 2003). Experimental studies are needed in order to further assess the extent of conformity in capuchin monkeys.

The function of social learning

Scholars have claimed that social learning has an important role in acquiring behaviours related to all aspects of an animal's life, behaviours which may be dangerous or difficult to acquire through individual learning (Avital & Jablonka, 2000; Galaf, 1995; Visalberghi & Fragaszy, 1990). Others question the adaptive function of social learning, limiting its benefits to specific conditions (Boyd & Richerson, 1988; Laland, 1996, 2004). The experiment dealing with cumulative social learning (Chapter 7) may provide some insights into this issue. Monkeys were able, through social learning, to switch from one established way of gaining a reward from a puzzle box to a more advantageous method. This was limited by the fact that a second switch to an even more rewarding method did not occur in the mother-reared monkeys.

Social learning in the opposite direction still has to be tested in primates. Namely, would monkeys copy a new *less* efficient way? Boesch (1996) suggested that if an inefficient behaviour is found in a group it would imply this behaviour was a cultural tradition since ‘we would expect individuals to test the possibilities and choose the best ecological solution they find’ (p.259).

In this thesis I added a control group to the experimental design, which was lacking in previous studies. In the Coffee Tin experiment this was a control group which had not observed a demonstrator. In the cumulative learning study this was a within -subjects control in which the subjects had time to manipulate the target before observation. Employing such control groups allows for further evaluation of the benefits of social learning. Mother-reared monkeys in the control group of the Coffee

Tin experiment were slower in opening the box, implying a benefit for social learning over individual learning, whereas the enculturated monkeys in the control group were not slower than the experimental subjects, even though the latter exhibited higher fidelity copying than mother-reared monkeys. Thus, the tendency to copy faithfully may be costly at times, where emulation would be more beneficial. The fact the enculturated monkeys behaved this way strengthens the notion that these monkeys show a higher fidelity capability for imitation than has been observed in previous experiments (see Visalberghi & .Fragaszy, 1990, 2002).

Social learning mechanisms

At the outset of this thesis I inquired what capuchin monkeys are tuned to when watching a human or conspecific act. The merit of carrying out experiments as described in this thesis lies not only in showing the influence of social learning but also trying to respond to this "how" question, which is usually impossible to answer in natural environments.

Fragaszy & Visalberghi (1996) originally claimed that capuchin monkeys have only been seen to attend to the general stimuli a conspecific was manipulating, thus showing social learning based on stimulus enhancement. Almost ten years later, with the accumulation of more data, Fragaszy, Visalberghi & Fadigan (2004) concluded that “Watching another monkey solve a problem promotes the observing monkey’s interest in the places and objects where the other worked or is working. However watching others is not sufficient for a capuchin to learn a sequence of actions or to produce specific relations between objects" (p. 259).

The studies in this thesis produced different results, showing low fidelity copying, object movement re-enactment and very localized stimulus enhancement in the mother- reared-monkeys. This shows more complex social learning than has been demonstrated in a laboratory setting up to now. These results may shed light on the process of transmitting knowledge in a natural environment. For example, a *Cebus apella* monkey in Surinam watching a conspecific process a hard husked fruit such as capsules of *Phenakospermum guyannese* (Boinski *et al.* 2003) may learn through very localized stimulus enhancement the precise locus of the fruit, the apex, to which to orientate his pounding behaviour or other pressure, as well as learning through object movement re-enactment how to open the husk after it cracks from the pounding. With canalization of the monkey’s behaviour, as found in the studies of his thesis, as well as needed practice, the fruit would be opened in a similar way to that observed.

The social conventions found in capuchin monkeys in nature (Perry *et al*. 2003) cannot be interpreted by such mechanisms. The results of the enculturated monkeys may help better understand this domain of social traditions. The enculturated monkeys showed higher fidelity copying than the mother-reared monkeys, which might indicate a simple form of action-centred imitation that is important for transmitting social conventions. Nevertheless, to further understand whether the enculturated monkeys were extracting information about action, experiments in which the monkeys only see the attempts of the model to operate the apparatus without the actual movement of the object would be of interest. Such studies have been carried out on chimpanzees and children (Call, Carpenter & Tomasello, 2005)

Further, all experiments targeted to test social learning in capuchin monkeys have dealt with tasks in the material domain. However, high fidelity copying may be more important in the social realm than in the ecological one. This is in line with theories claiming that primate cognitive abilities had evolved first and foremost through selective pressures of the social environment (Humphrey, 1976; Byrne & Whiten, 1988). Experiments simulating social conventions with capuchin monkeys, although methodologically difficult to produce, would provide more insights into the role of imitation in the social domain (see Bonnie *et al*. 2007, for an attempt to test this with chimpanzees).

The importance of practice

Experiments designed to test for imitation have usually analysed only the first few responses of the subjects to the apparatus, after having seen the observation (e.g. Whiten & Custance, 1996; Custance, Whiten & Fredman, 1999). This is logical, as after the initial attempts to manipulate an object some individual learning may be involved.

However, for simple such as bidirectional actions, it may be sufficient to solve the task in one or two trials. More complex actions may not be possible to master in such a short time and may demand practice. These perhaps abnormal testing conditions, in which only a few demonstrations are given, as well as only a few trials to perform in, can result in underestimation of complex social learning and imitative abilities of chimpanzees (McGrew, 1992) and perhaps capuchin monkeys as well. The

Dipping-Box experiment approached this problem by allowing more time for the monkeys to integrate the information they observed with practice, and thus was a more ecologically valid test. The results showed how, with time, monkeys canalized their behaviours towards the observed action. This suggests that for more complex behaviours, more time may be needed for the observer to faithfully reproduce the action. The fact that practice is needed even in a species as highly imitative as humans was shown in Teleki's (1974) attempt to learn how to fish for termites by imitating chimpanzees. Although he was consciously trying to imitate, it took much more than just observation for him to obtain a termite.

The effect of enculturation

The enculturated capuchin monkeys in the studies in this thesis appeared to show higher fidelity copying than the mother-reared monkeys. They were able to copy the tool use behaviour they observed and even when realizing the task could be done without a tool still tried to do so in the way it had been modelled to them (Coffee-Tin experiment). They also showed the ability to learn the Complex method of opening the Dipping-Box as opposed to the mother-reared monkeys.

The fact that the second complex method of opening the Dipping Box was an elaboration of the first method may imply that these monkeys are capable of cumulative learning. Further experiments designed to directly test this basic cumulative learning hypothesis should be carried out.

At least one of the enculturated monkeys showed signs of potentially being able to understand the meaning of imitating, which he manifested by switching from one movement with an object to another as a function of the movement he saw demonstrated. What factors in the history of these monkeys can explain the difference in performance between the enculturated and non-enculturated monkeys on social learning tasks? There are several possible options:

1. Experience with objects

The idea that the enculturated monkeys have had more experience with objects and therefore watching a demonstrator only serves as a prime for performing a known response, tends to be the default explanation for the monkeys' performance. It is true that finding something totally novel for these monkeys to imitate is not an easy task. Previous experience with objects can perhaps explain their lack of neophobia but not the fact that they switch from one morph of acting on a game to the other as a function of watching a human do so (do-as-I-do, Chapter 9).

2. Attention

It has been claimed that attention to the model is an important factor in social learning (Kumashiro *et al*. 2003). The enculturated monkeys were seen to closely observe the human model. However mother-reared capuchins in everyday settings have also been observed watching others very closely (Boinski *et al*. 2003); sometimes their heads and hands are almost under the pounding stone of their group mate (personal observations). Thus, it may be more than just paying attention to the demonstration that makes the difference. Rather, the information these monkeys extract from the demonstration may be different, through perhaps paying some attention to the action of the model as well.

3. Intentional communication

In all the experiments involving the enculturated monkeys the subjects occasionally made two types of actions involving the human demonstrator.

1. They took the demonstrator's hand, moving it towards the apparatus.
2. They tried to give the tool or object to the demonstrator. This was seen when monkeys handed the screwdriver in the Coffee-Tin study or the crimper in the Do-as- I-Do study to the demonstrator.

Similar behaviours have been seen in apes. Kohler (1927) described how in his classic experiment, in which chimpanzees had to stack boxes in order to reach an out-of-reach banana, one of the chimpanzees took the human’s hand and brought him close to the banana then tried to climb on the human to get the reward. Kohler claimed this was an instance of “using a human as an instrument”.

Gomez (1990) found similar behaviours with a young hand-reared gorilla that was tested on different out-of-reach tasks. He described two strategies involving humans which the gorilla employed in order to reach the reward:

1. Intentional manipulation - using a human as a tool e.g. climbing on a human to reach the reward.

2. Intentional communication- requesting help from the human.

I have observed enculturated capuchin monkeys using a human as a tool in different free play occasions. For example, the monkeys sometimes moved the human's foot, placed a nut under the shoe of a human and then pulled his/her foot down using force to crack open the nut, or wait for the cooperative human to break the nut this way.

The capuchin monkeys' behaviour in the experiments in this thesis fit into the second category of intentional communication, in that they both took the human's hand and gave the object to the human. Gomez concludes that "the only possible reason why the gorilla includes the human in her schemes is that she considers the human as a subject capable of carrying out by himself the action of opening the door's latch" (p. 345). Gomez claims that such behaviour represents a basic form of intentional communication. The onset of intentional communication in humans is seen between the ages of 9-12 months when human babies start to engage in gestures and vocalizations to request help from humans (Sugarman, 1984).

Figure 9.1 Cacao requesting help in the Coffee –Tin Study.

Can we, through homology, claim that the enculturated capuchin monkeys behave like the human infants and the gorilla? It may very well be the case although such conclusions may at times be misleading. For example Huffman & Hirata (2004) suggested that the use of medicinal plants by chimpanzees is partially transmitted socially. Capuchin monkeys also use plants for self-medicating purposes. They use plants and worms to rub on their fur as an insect repellent (Baker, 1998). Young monkeys closely watch older monkeys while behaving this way and may scrounge parts of the garlic or orange peels they are using for this purpose (personal observation). However the enculturated monkeys, who were separated from their mothers at about the age of 6 weeks and most probably never saw their group mates acting in this way, immediately rub onions on their fur when it is given to them.

Nevertheless I believe that intentional communication as discussed above does take place in enculturated monkeys. The nature of the interaction between human and monkey in the help request context is important for the emergence of such communication. If a monkey were to hand over a nut to a more proficient nutcracker, he would most probably never get it back. The monkey-human relationship, similar to the human mother–infant relationship, is based on the fact that the human has the intention to help and teach. The monkey learns not only that the human can solve the task, but also that she will do so for him and thus will hand over very important items he would most probably never hand over to a conspecific - exactly those items which are important for him to learn how to manipulate.

This active behaviour of requesting help when confronted with a difficult task is what Vygotsky (1978) claims to be the basis for cultural learning in humans. Requesting help can only emerge when the complementary process of teaching and scaffolding exists, as in these dyads of human mother-infant and human-enculturated monkey/ape. These two processes may explain the more complex social learning found in enculturated primates.

Such handing over of objects for manipulation in the mother-reared monkeys (Island group or Enclosure group) has not been seen. Interestingly, although rare, such instances between the enculturated monkeys themselves were observed (see Cheppy using Hezda to chew carrots for him described in Chapter 8) implying that these monkeys might have tried to generalize such aiding interactions to other enculturated monkeys in their group.

Another aspect of intentional communication is making eye contact during requests to make sure that the focus of the receiver is on the request. Making eye contact was seen only in some of the cases of requesting help by the capuchin monkeys in the studies described in this thesis. The role of making eye contact by the enculturated capuchin monkeys still needs to be further examined.

What does all this say about the cognitive representational ability of the enculturated monkeys? By actively requesting help, monkeys may be trying to influence what the human thinks, namely “the monkey needs help,” implying a second- order intentional system (Denett, 1988). Nevertheless it may be more parsimonious at this stage to conclude from the data available that the monkey is trying to influence the human’s behaviour (first order intentional system).Through experience s/he may have learned that requesting help gets the problem solved. There is still need for more controlled experiments in this domain.

Individual differences

Cebus apella monkeys are known to show definite individual difference in tool use abilities (Boinski *et al*. 2003). Social learning is considered by some to be part of general a-social learning (Fragaszy & Perry, 2003). Thus we might expect to find individual differences in the strategies monkeys employ while watching a conspecific. The fact that most experiments with capuchin monkeys have tested only a small number of subjects highlights the personal differences and may obscure what may be a “general characteristic capuchin behaviour”. Recent experiments with chimpanzees have employed a great number of subjects and have been able to show significant social influence. I suggest that if we want to better understand capuchin monkeys’ social learning abilities subjects in different experimental locations need to be tested using the same tasks as an attempt to override individual difference (bearing in mind the differential influence of housing and settings on results).

Practical implications of the results

Understanding the way social behaviour may be transmitted socially has practical value when attempting to rehabilitate monkeys who were raised in isolation from members of their species. In the Israeli Primate Sanctuary (IPSF), where the Island group and enculturated monkeys live, an effort is made to reintroduce confiscated monkeys and ex-laboratory monkeys to social groups. Many of these monkeys did not have the chance to learn social behaviour norms during their childhood, as group- raised monkeys would (Walters, 1987). Thus it is hoped that the monkeys can learn some of the social codes of behaviour, through observation, and not have to undergo slow trial and error learning which at times can be distressing for them. Further, the question raised above as to whether a monkey could socially learn a maladaptive behaviour from his new group mates (such as self-biting seen in some ex-laboratory and ex-pet newcomers) has important implications when contemplating which monkeys to introduce to each other in the sanctuary. Some indications that abnormal behaviours are socially transmitted in chimpanzees have been found (Nash *et al*. 1999).

General Conclusions

The battery of experiments in this thesis has provided new information about the social learning abilities of capuchin monkeys. Two methodological issues which were addressed in these experiments, and were lacking in previous studies, contributed to the findings:

1. Employing a control groups which emphasises the difference between social learning and individual learning.
2. Carrying out a detailed analysis of the sublevels of the observers' actions, such as target behaviour, target-like behaviour etc., which emphasises the fact that imitation is not an "all or nothing" phenomenon.

The results have enhanced our understanding of the role and function of social learning in capuchin monkeys. It has been shown that:

1. Mother reared capuchin monkeys *can* socially transmit information to the extent that two groups will show two different behaviours dealing with the same stimuli as a result of viewing a model (See behaviours towards the coffee tin)
2. Social learning has been found beneficial in terms of

a. latency

b. switching to more advantageous techniques.

Both demonstrate the role of social learning in maximizing a monkey's position in relation to its environment.

3. The mechanism of canalization, as well as perhaps low fidelity imitation, has been shown to underlie this process in mother- reared monkeys.
4. Enculturated monkeys show higher fidelity imitation, which was manifested in:
    a. Learning a new method to use a tool from a model.
    b. Showing signs of conforming, in their persistence to try to copy the model even when the monkey discovered a different way to solve the task on its own.
    c. Exhibiting the basic ability to understand the concept of imitation which up to now was thought to exist only in apes and dolphins.

5. The main role of enculturation as regards to social learning appears to be the development of very basic understanding of intentional communication in the human monkey dyad.

Suggestion for further research

In addition to the various suggestions for further research mentioned above, two issues still need to be addressed:

1. Piaget (1962) claimed that deferred imitation was more cognitively demanding as it depends on the ability for mental representation. At nine months, human infants are capable of deferred imitation, a Piagetian Stage 6 achievement. Mathieu & Bergeron (1981) and Mignault (1985) found chimpanzees are also able to display deferred imitation. However, there has not been any systematic experiment on deferred imitation in monkeys. This is crucial with the capuchin monkeys, because using deferred imitation as an experimental design would serve to rule out criticism claiming that the findings could be attributed to response facilitation (e.g. see Byrne, 2005 for a criticism of the results of the artificial fruit study with the capuchin monkeys, discussed in chapter 3, and other two-method experiments). In other words, incorporating a delay between observation and production, would show that such a facilitating influence cannot play a role in the behaviour of the observer.

2. Research on imitation in monkeys has mainly focused on looking for evidence of action imitation. However, research needs to go one step backwards and establish how monkeys perceive similarity and differences between actions. One appropriate possibility is to use a variant of the match- to-sample paradigm, as implemented in the training phases of the Do- as- I- Do study in this thesis, in order to test the nature and limits of the same/different concept regarding action stimuli in capuchin monkeys. The subject would be presented with an action stimulus (video clip) and would have to match it to one of two action stimuli on the screen. Different levels of similarity could be used, accelerating the abstractness of the concept from same action on the same stimulus to the same action on different stimuli, in order to avoid classification on the basis of information on the object or the end result on the original object.

Results from such an experiment could help pinpoint the shortcomings of action imitation in the subjects and will be useful in designing experiments which aim to better elicit the production of action imitation.

Ethical end note

The enculturated monkeys tested in the studies described in this thesis used to belong to a “Helping-Hands” program in Israel, which aimed to teach capuchin monkeys to be helpers for quadriplegics. This program was closed down mainly because it was decided that the socialization of monkeys into the human world, away from other conspecifics, was not warranted. Given advances in technology, many actions in the household that were done by the monkey can now be achieved technically. The emotional contribution of the monkey to the quadriplegic can be found by using guide dogs instead. With the closure of the Helping Hands project, the monkeys who participated in it were introduced to each other, allowing them to live in social groups.

The results of the experiments carried out with these monkeys are intriguing and pose questions for further research. However it is my great hope that it will not encourage enculturating new monkeys.

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