CAUSAL INFORMATION AND SOCIAL LEARNING IN CHIMPANZEES (PAN TROGLODYTES) AND CHILDREN (HOMO SAPIENS)

Victoria Kate Horner

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**

2004

Causal Information and Social Learning in Chimpanzees *(Pan troglodytes)* and Children *(Homo sapiens)*

Victoria Kate Horner

Thesis submitted to the University of St Andrews for the degree of Doctor of Philosophy

September 2003

ABSTRACT

Many of the tool-using activities of both chimpanzees and children involve a complex mixture of interconnected causal relationships between a tool and a reward, and much of this tool-use is thought to be acquired, at least in part, by social learning. However, despite the considerable research effort focused on both causal understanding and social learning, few studies have directly addressed the potential interaction between these areas. It seems likely that the way in which an individual learns to use a tool through observation will be significantly influenced by its understanding of the causal relationships that it observes. This thesis presents a series of nine experiments with 3- to 7-year-old chimpanzees and 3- 6-year-old children, designed to investigate whether causal information is involved in determining which social learning strategy they employ. The first set of experiments demonstrated that chimpanzees could be influence to switch between imitation and emulation to solve the same task, by altering the availability of causal information. When causal information was available, by presenting a tool-use task in a transparent condition, chimpanzees were found to reproduce only the results of a model's behaviour, consistent with emulation. However, when the availability of causal information was restricted, by presenting the same task in an opaque condition, the chimpanzees included a greater proportion of the model's behaviour, consistent with imitation. The second set of experiments revealed that chimpanzees could learn specific causal information by observation, such as the significance of tool-reward contact. However, they may be overwhelmed by observing multiple causal relationships, or those involving unobservable causal principles, such as gravity or force. The common view that the widespread evidence for emulation in chimpanzee social learning studies indicates a deficit of imitative capacity may therefore be misleading. The results of this thesis suggest more generally that when causal information is available, chimpanzees tend to use emulation. They are also able to imitate, but do so mainly in situations were emulation is not possible. Thus, the availability of causal information plays an important role in chimpanzee social learning, by determining which learning strategy is employed, and ultimately the degree of behavioural fidelity that is achieved. In contrast, the studies with children revealed that they imitate the actions that they observe without appearing to consider the causal efficiency of their behaviour. This may be due to a greater focus on the actions of a demonstrator rather than the results or goals of their behaviour, and a greater tendency to interpret those actions as intentional.

DECLARATIONS

I, Victoria Kate Horner, hereby certify that this thesis, which is approximately 45 000 words in length has been written by me, that it is a record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date. 10th March 2004...... Signature of Candidate. ...

I was admitted to the University of St Andrews as a candidate for the degree of Doctor of Philosophy in 2000. The higher study for which this is a record was conducted between 2000 and 2003.

Date. 10th. March. 2004...... Signature of Candidate... ....

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date. 22 March 2004.. Signature of Supervisor.

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and abstract will be published, and that a copy of the work may be made and supplied to any *bona fide* library or research worker.

Date... 10th March 2004...... Signature of Candidate.. ..

TABLE OF CONTENTS

CHAPTER 5: STUDY SITE, PARTICIPANTS AND GENERAL METHODOLOGY

CHAPTER 6: EXPERIMENT 1: IMITATION & EMULATION SWITCHING IN CHIMPANZEES

LIST OF FIGURES

SUMMARY OF CHAPTER 1

Many definitions of culture exist, however most agree that culture can be broadly determined by identifying differences in the behaviour of two or more populations of the same species. These differences must not result from genetic variation between the populations, or ecological differences between the habitats. Using this criterion, claims for culture have been made for many phylogenetically diverse taxa, including birds, fish, marine-mammals, rodents and primates. However, of all these species, the cultural repertoire of chimpanzees is by far the greatest. Thirty-nine cultural variants, which are present at some sites, and yet absent at others, have been reported at long-term study-sites throughout Africa. Nevertheless, the acceptance of chimpanzee culture remains controversial. A number of authors argue that observational data alone cannot adequately exclude ecological or genetic explanations for the observed population differences. Instead, it has been argued that the acceptance of chimpanzee culture should hinge on the social learning mechanism by which behaviours are transmitted throughout a population.

CHAPTER 1

THE ORIGINS OF CULTURE

1.1 A history of cultural theory

For most of human history, it has been assumed that we are the only species with the capacity for culture. Although Darwin had suggested that there might be a continuum between the mental abilities of humans and other animals almost a century before, many scientists still believed that the capacity for culture was uniquely human, and was what set us apart from other animals. The concept that non-human species may have culture was first introduced by Imanishi (1952), who suggested that Japanese macaques *(Macaca fuscata)* may develop population-specific behavioural differences as a result of social, rather than genetic variation. However, these reports initially fell on deaf ears, and it was not until the 1960's, when reports of the sweet-potato washing behaviour of Japanese Macaques from Koshima Island spread, that the scientific community was forced to acknowledge the potential for culture in non-human species.

1.1.1 *Sweet-potato washing by Japanese macaques*

In 1953, Imo, a young female macaque from Koshima Island, began washing pieces of provisioned potato in a nearby stream in order to remove sand before eating them. Over the course of the next two years, potato washing spread throughout her community, spreading first to her mother and close associates, then later to all but the adult male members of her community (Kawamura, 1959; Kawai, 1965; Itani & Nishimura, 1973). Many reports of this phenomenon concluded that the behaviour spread from one individual to the next because they learned from each other and hence, this was the first evidence for cultural transmission in a non-human animal (Nishida, 1987).

With the benefit of hindsight, it seems that these conclusions were premature. More recent studies have revealed that food washing has arisen spontaneously in other macaque populations (Hirata, Watanabe, & Kawai, 2001), and under different conditions (Suzuki, 1965). Potato washing might therefore have developed spontaneously and spread throughout the Koshima Island community because monkeys that displayed some food washing behaviour were preferentially provisioning by human caregivers, and not because the behaviour was passed between individuals by cultural transmission (Galef, 1992; Green, 1975). Nevertheless, although Imo's achievements may have been more modest than originally thought, her behaviour was responsible for an increase in both interest and acceptance of the study of non-human culture.

1.1.2 *Definitions of culture*

Even today, the acceptance of non-human culture remains a controversial issue (Whiten, Horner, & Marshall-Pescini, 2003). Disagreements stem partly from variations in the definitions of culture used by different groups of researchers (McGrew, 1998). In order to understand the evolutionary conditions that may have favoured the development of culture in humans, it is widely accepted that many phylogenetically distant species must be studied. However, definitions that are too broad or too restrictive are not useful from a comparative point of view. For example, many definitions typically from anthropology, state that culture relies on language and beliefs, and often include the words 'man' or 'human', hence eliminating other animals *a priori*. At the other extreme, less discriminatory definitions, which grant culture to all species that acquire behaviour through any means other than genetic inheritance, tell us nothing of comparative interest. Behavioural scientists have therefore attempted to create definitions that fall between the two extremes. Although a great number of these definitions now exist, most share the same central features.

All definitions acknowledge that cultural behaviours must be acquired, at least in part, by social learning (Boesch & Tomasello, 1998; Fragaszy, 2003; McGrew, 1992; Whiten et al., 1999). In other words, cultural behaviours must be *learned* by passing information between the members of the population. Most also agree that cultures can be identified by differences in the behaviour of two or more populations of the same species than cannot be explained by genetic variation between the populations, or ecological differences between the habitats.

Population differences that arise through genetic variation cannot be considered as cultural because the behaviour of each individual is pre-programmed, for example comb building in bees (*Apis* spp). The genes that code this behaviour are inherited once per lifetime (Ridley, 1996), and therefore population differences can only arise in the same species due to genetic mutation and genetic transmission leading to local spread of the behaviour. The differences do not result from *learning* and are therefore not cultural.

Individuals may acquire behaviours during their lifetime by individual learning. For example, an organism may learn to adapt to its environment by modifying its behaviour through its own experience. However, like genetic inheritance, individual learning cannot lead to culture. If the members of two populations are exposed to two different habitats, the members of each population may exhibit different behaviours because they converge on different optimal responses. However, these behaviours cannot be considered as cultural because they were learned by individual experience, and not from other members of the population. By defining culture in this way, based on the exclusion of ecological and genetic variables, cultures have been identified in a wide range of species[1].

1.2 The phylogenetic distribution of culture

Claims for culture have been made for many phylogenetically diverse taxa, including birds, fish, marine mammals, rodents and primates. Regional song dialects have been reported in several species of songbird (Catchpole & Slater, 1995; Marler & Tamura, 1964; Slater, 1986). Pod-specific differences have been reported in the vocalisations of Sperm Whales *(Physeter macrocephalus)*(Rendell & Whitehead, 2001), and humpbacked whales *(Megatera novaeangliae)* (Noad, Cato, Bryden, Jenner, & Jenner, 2000). Killer Whale pods *(Orcinus orca)* display variations in both the vocalisations and feeding behaviours that they use (Rendell & Whitehead, 2001). Group-typical behaviours have been reported in the feeding behaviour of black rats *(Rattus rattus)* (Terkel, 1996), and Californian sea otters *(Enhydra lutrus)*(Bonner, 1980). Population specific differences have been reported in reef

[1] It was originally suggested that group-typical behaviours of animals should be viewed as analogous, and not homologous to human culture, and that therefore the word 'culture' should be reserved for humans, and 'tradition' used for other animals (Galef, 1992). However, many authors use both words synonymously in the literature, and hence this will be the case for the remainder of this thesis.

fish, including migration routes, schooling-sites and feeding behaviours (Helfman & Schultz, 1984; Warner, 1988; Bshary, Wickler, & Fricke, 2002; Laland & Hoppitt, 2003). Capuchin monkeys *(Cebus* spp*)* have been found to differ between communities in both food choice and food processing behaviours (Panger et al., 2002; Perry & Manson, 2003; Perry et al., In press).

However, many of these reports refer to only one or two behaviours, and therefore the cultural repertoire of these species is relatively limited (Whiten et al., 2003). In contrast, studies of ape populations have revealed a great richness in the number and diversity of behavioural variation reported. Twenty-four population specific behaviours have been reported in Orangutans *(Pongo pygmaeus),* including tool-use and social signals (van Schaik et al., 2003). However, studies of chimpanzee behaviour *(Pan troglodytes)* indicate that they have a diverse cultural repertoire that exceeds all other animals with the exception of humans (McGrew, 1992; Boesch, 1996b; Boesch & Tomasello, 1998; Whiten et al., 1999; Whiten et al., 2001).

1.3 Chimpanzee cultures

Chimpanzee behaviour has been the focus of research attention for over a century (Whiten & Ham, 1992). Researchers have been drawn to chimpanzees for many reasons, the first of which is their phylogenetic proximity to humans (Morin et al., 1994 Byrne, 1996; Krings, 1997). During the last century much has been learned about the phenotypic evolution of humans by studying fossil evidence from ancestral hominids. However, our knowledge of cognitive evolution remains limited. Many researchers believe that as our closest living relative, chimpanzees can be used as a 'referential model' for human evolution, providing both physical and behavioural data. This data can then be used to infer the characteristics of the common ancestor from which chimpanzees and humans diverged approximately 4-6 million years ago, and therefore the conditions which may have driven the evolution of our own cognitive abilities (Gibson, 1993; McGrew, 1993).

Another reason for this interest stems from the sheer diversity and flexibility of chimpanzee behaviour that is demonstrated by both wild and captive populations (McGrew, 1993, 1994). In 1973, Jane Goodall reported 21 behavioural traits, including tool-using and social interactions that she believed represented cultural variations between chimpanzees at her study site in Gombe and other African populations (Goodall, 1973). In 1992, McGrew listed 19 tool-using behaviours that differed between communities, and in 1998, Boesch and Tomasello reported 25 differences that could represent culturally specific behaviour. The most recent surveys have reported as many as 39 population specific behaviours that are customary at some sites, and yet absent at others (Whiten et al., 1999; Whiten et al., 2001). In this study, researchers pooled the data collected from six long-term study sites throughout Africa. At these sites, chimpanzees have been observed for between 10 and 40 years, and hence the majority of behavioural variants have been recorded. Sixty-five potential variants were originally put forward, indicating the flexibility of chimpanzee behaviour. From this list, those differences that may have ecological or genetic explanations were excluded, leaving 39 behaviours that include courtship, grooming and tool-use (see Fig. 1.1).

One of the best known examples of chimpanzee culture is nut-cracking, which is performed by chimpanzees at Bossou and Taï (Boesch & Boesch-Acherman, 2000). The chimpanzees crack nuts (*Coula edulis* and *Panda oleosa*) on solid anvils, such as surface roots and loose stones, with hammers made of stone or wood. These nuts are a valuable source of energy, providing a proficient adult nut-cracker with up to 3000 calories per day (Boesch, 1993). While the same nut species are present at other study sites throughout the evergreen belt, nut-cracking is conspicuously absent from these sites (Boesch, 1996a; McGrew, Ham, White, Tutin, & Fernandez, 1997). McGrew (1997) was able to systematically show that at Lopé, Gabon, where nut-cracking is absent, chimpanzees have adequate access to suitable nut species, as well as suitable hammers and anvils with which to perform nut-cracking. He also showed that the lack of nut-cracking behaviour was not the result of availability of alternative high-energy food sources, or a lack of material intelligence. Instead, he concluded that the chimpanzees of Lopé did not crack nuts simply because it was not part of their culture. Similar arguments have been made for the other cultural variants shown in Figure 1.1, that are present at some sites, yet absent at others (Boesch, 2003; Whiten et al., 2003).

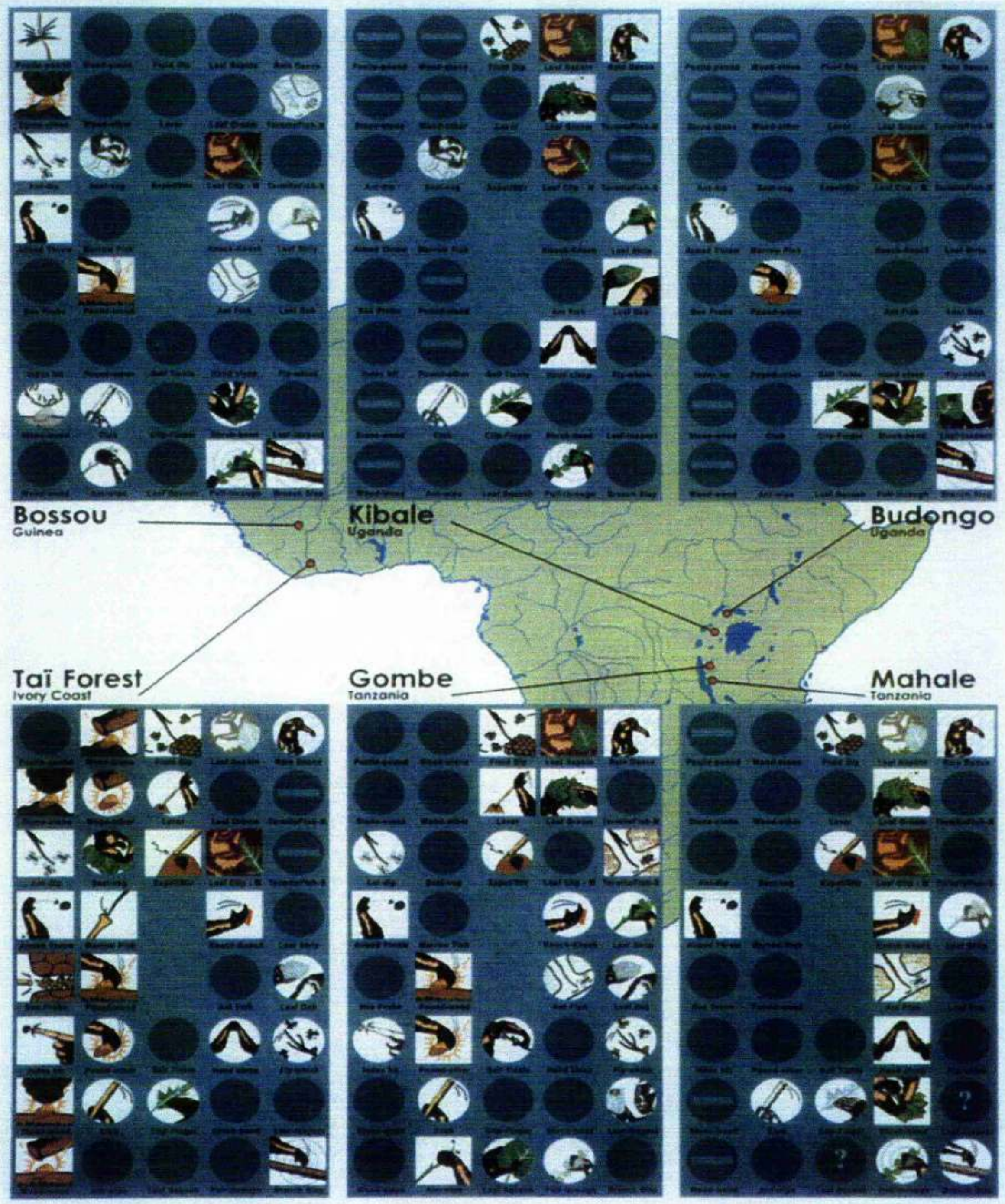


Figure 1.1 Taken with permission from (Whiten et al., 1999) page 684. Population specific behaviour patterns found at the six long-term study-sites in Africa. Squares = customary behaviours, circles = habitual behaviours, monochrome = behaviours that are present, plain grey = behaviours that are absent without ecological explanation, and horizontal bar = absence with ecological explanation.

1.4 Chimpanzee and human cultures

It is not just the scale of behavioural variation shown by chimpanzees that is of interest from a comparative perspective. Several authors have proposed chimpanzee and human culture may be similar in more fundamental ways:

1.4.1 *Community differences*

Chimpanzee and human communities each have a distinct cultural profile which makes it possible to assign an individual to its home community on the basis of its behaviour alone (Whiten et al., 2003).

1.4.2 *Shared meaning*

Many human cultural traits involve arbitrary behaviours that have a shared meaning. This can be seen most clearly in gestures. For example, extending a hand towards an individual upon meeting is regarded by many communities as a sign of welcome. In most cases the recipient of this gesture will respond by taking the person's hand and shaking it up and down. Both the gesture and the response provide no information about the meaning of the act, yet the meaning is shared by both individuals. Similarly, there are a number of examples of shared meaning in chimpanzee cultures (Boesch, 2003).

'Leaf-clipping' is the practice whereby chimpanzees rip leaves apart with their mouths in order to generate a loud tearing sound, but do not ingest any part of the leaf. Male chimpanzees from Taï regularly leaf-clip before drumming on tree trunks (Boesch, 1996b). At Bossou, leaf-clipping is performed to elicit play (Sugiyama, 1981). At Mahale however, males leaf-clip in order to attract oestrus females (Nishida, 1987). Chimpanzees from each site have never been observed to leaf-clip in a culturally atypical context, and at each site, recipients of this arbitrary gesture will always respond in the correct cultural way. At Bossou the recipient will initiate play with the performer, whereas at Mahale females will react to leaf-clipping by presenting to the performer (Boesch, 1996b).

Interestingly, male chimpanzees at Taï attract females by knocking their knuckles on tree trunks, and not by leaf-clipping (Boesch, 1996b). Other members of the Taï community will always react to the knuckle-knock by presenting, regardless of the sexual state of the recipient, or the gaze direction of the actor. This indicates that all members of the population recognise the meaning of the gesture, and react accordingly (Boesch, 1996b). A similar argument has been made for ectoparasite removal (see Boesch 2003).

1.4.3 *Collections of related ideas*

Many anthropological definitions of culture state that culture is more than a list of behaviours, it is a collection of related ideas (LeVine, 1984). There are two possible examples of this from chimpanzee cultures. Chimpanzees from Taï forest in West Africa have been observed to use 20 different tools, including complex behaviours such as nut-cracking and tool modification. Chimpanzees may modify the same tool in up to three different ways, and often without trial and error (Boesch & Boesch, 1990). In contrast, chimpanzees from Budongo and Kibale in East Africa, use only five and six tools respectively, and these are often more rudimentary than those of Taï. This variation has no obvious ecological or genetic explanation, and it may suggest that Taï chimpanzees have a collection of shared ideas about the application of tools to a wide variety of problems that is not common to other populations (Boesch, 2003; Whiten et al., 2003).

Similarly, while Central African communities employ modified 'brush-sticks' to collect termites (*Macrotermes* spp) and nesting ants *(Dorylus gerstaecheri* and *D. nigricanus)* (Sugiyama & Koman, 1979; Sugiyama, 1985; S. Suzuki, Kuroda, & Nishihara, 1995), communities from East Africa use unmodified sticks as probes for the same tasks (Goodall, 1986). It is possible that Central and East African populations have a different collection of ideas about the appropriate configuration of tools.

1.4.4 *Cumulative cultural evolution*

Cumulative cultural evolution refers to additive, incremental improvement upon an original behaviour, such that the resulting behaviour could not be invented from scratch with each new generation. This process is also known as 'the ratchet effect' (Tomasello, Kruger, & Ratner, 1993). It is easy to find examples of cumulative culture in modern Western human society. Everyday technologies such as mobile phones, computers and cars have reached their present designs through a series of incremental improvements on earlier models. Although the technological achievements of chimpanzees are a far cry from cars and telephones, there are several potential candidates for cumulative culture. In a recent study that was designed to investigate the history of chimpanzee nut-cracking using traditional archaeological analysis, it was found that this behaviour may date back 900 years (Mercader, Pagner, & Boesch, 2002). Unfortunately, chimpanzee populations have only been observed scientifically for 40 years, therefore it is unlikely that researchers will be able to witness ratcheting first-hand. Nevertheless, if chimpanzee populations have been cracking nuts for the better part of a millennium, it is possible that ratcheting may have occurred in this behaviour. Indeed, the complex form of nut-cracking found at Taï and Bossou in West Africa may well be an elaboration of a simpler ancestral behaviour common in many chimpanzee communities. In its simplest form, hard-shelled nuts are opened by hitting them with the hand or against tree trunks and roots (Boesch, 2003). This behaviour may have been elaborated in West Africa to incorporate a hammer and anvil, and in one case an additional stone to level the anvil (Matsuzawa & Yamakoshi, 1996). It has also been suggested that the practice of leaf-sponging, in which leaves are chewed in the mouth, removed and used to absorb water from inaccessible sources such as tree hollows, may have originated from an ancestral behaviour of well digging (Matsuzawa & Yamakoshi, 1996). When looking at the development of chimpanzee culture, it is important to consider that in early pre-agricultural human history, there was very little evidence for ratcheting in stone technology for almost a million years (Boesch & Tomasello, 1998; McGrew, 1998).

1.4.5 *The distribution of cultural variants*

Human culture varies in many ways, and it is often possible to track the distribution of a particular cultural variant or group of variants from an origin. A second collaborative study, which pooled records from long-term chimpanzee study sites throughout Africa, was aimed to assess whether patterns of behavioural diffusion could be found in chimpanzee cultures (Whiten et al., 2001). It was found that the distribution of several of the 39 cultural variants previously identified (Whiten et al., 1999) could be traced between populations back to one or multiple origins. For example, 'leaf grooming' (whereby an individual picks a leaf and while inspecting it closely starts to groom it) appears to have started from a unitary source and extended to a large, but defined region of East Africa (Whiten et al., 2001).

Chimpanzee and human populations are therefore qualitatively similar not only in the degree of behavioural variation, but also in some of the subtler characteristics of their culture.

1.5 Criticisms of the claim of chimpanzee cultures

There are a number of potential shortcomings associated with assigning culture to chimpanzees based upon observational data. For example, high-resolution comparisons of habitat ecology are not abundant in the literature. Ecological differences that may be critical to behavioural expression in chimpanzees may be indistinguishable to a human observer (Tomasello, 1990). In addition, even if environmental uniformity is assumed, past ecological conditions, which may have driven behavioural differentiation cannot be determined (Call & Tomasello, 1998). The number of population specific behaviour patterns that result from ecological differences may therefore be underestimated.

The degree of habituation, and therefore the probability of observing behavioural variants differs between sites (McGrew, 1992, 1994). The status and number of individuals involved may influence the probability of observing a specific behaviour. For example, behaviours that are performed by high-ranking conspicuous individuals, or that convey an obvious adaptive advantage, may be more noticeable than subtle behaviours of a subordinate (Visalberghi & Fragaszy, 1994). The number of variants that have been identified because they are present at one site, yet absent at others, may therefore be overestimated.

As a result, it has been suggested that ecological and genetic variables can only truly be excluded by performing translocation experiments, such as those that have been successfully carried out with reef fish (Laland & Hoppitt, 2003). If individuals from population A are translocated to population B, and adopt the behaviour of B, then the differences between A and B cannot be genetic. Similarly, if the whole population A is relocated to the habitat of population B, and does not adopt B's behaviour, then the differences between groups A and B cannot be related to ecology (Laland & Hoppitt, 2003). However, such experiments are practically and ethically difficult with chimpanzees.

It has therefore been argued that the acceptance of chimpanzee culture should hinge upon evidence that the behaviours are learned socially, by passing information from one individual to the next in a population by any social learning process (Whiten & Ham, 1992; Russon & Galdikas, 1995; Boesch, 1996b). However, others have specified that cultures can only be acquired by particular social learning processes such as imitation and teaching (Nagell, Olgin, & Tomasello, 1993; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh, & Kruger, 1993). The following chapter will therefore focus on the study of social learning processes in chimpanzees.

SUMMARY OF CHAPTER 2

Social learning can be defined as learning that results from observation of, or interaction with another individual or its products. Social learning is distinct from non-social learning in that the observer acquires a *new* behaviour as a result of this interaction, and it is not merely influenced to perform behaviours that already exist in its repertoire. Social learning can be broadly divided into four categories (observational conditioning, emulation, imitation and teaching), each varying with the fidelity with which the observer reproduces the actions of the model. Some authors are willing to accept any form of social learning as a mechanism for cultural transmission. However, others maintain that only imitation can guarantee that behaviours are transmitted with enough fidelity between individuals for discrete cultural variants to be maintained.

Experimental studies of chimpanzee social learning have found evidence for imitation in the context of non tool-use tasks. These studies have shown that chimpanzees can imitate novel manual and facial gestures, object manipulations and the sequential and hierarchical structure of observed actions. They are also able to imitate gestures that involve out-of-sight body parts, and imitate object manipulations after a substantial delay.

However, in contrast, tool-use tasks have typically failed to find evidence for imitation. Instead it seems that chimpanzees employ non-imitative social learning strategies, specifically emulation to solve these tasks. It therefore appears that chimpanzees use difference social learning strategies to solve different types of problems. However, this trend may be related to the amount of causal information that is available in each task, rather than the task domain *per se*.

CHAPTER 2

SOCIAL LEARNING

2.1 The requirements of culture

Due to the potential uncertainty of determining culture using only observational data (see section 1.5), some authors have suggested that culture should be determined by the cognitive processes through which behaviours are passed between the individuals of a population. In other words, culture must be determined by the social learning mechanism by which behaviours are transmitted (Nagell et al., 1993; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993).

2.1.1 *A history of social learning*

Historically, it was believed that most behaviours were transmitted by imitation, which was thought to be a relatively simple process that was widespread throughout the animal kingdom, and common in primates. However, the increased interest in studies of animal culture and social learning has lead to a fundamental change in this assumption. The study of Israeli black rats *(Rattus rattus)* provides a good example. These rats have developed an efficient way to extract seeds from pine-cones by removing the scales from the bottom of a cone and following the natural spiral of the scales to the top. Alternative methods, such as biting through each scale, burn more energy than the seeds provide. This behaviour was initially though to result from complex social learning, as only young rats that were raised with their mothers learned this efficient technique. Young rats that were cross-fostered with mothers who did not strip scales, did not discover this efficient technique on their own. However, it was found that young rats could learn the efficient technique if they were given cones that had been started in the appropriate way (either by a conspecific or a human). Young rats could therefore learn the efficient strategy if their attention was draw to the relevant part of the problem (Aisner & Terkel, 1992). Hence, complex behaviours need not be the result of complex social learning (Galef, 1988). Studies like these have lead to a reappraisal of the existence, distribution and significance of imitation. Subsequently, a more sophisticated concept of social learning has been developed (Whiten & Ham, 1992; see

Figure 2.1). However, before social learning can be discussed in more detail, a distinction should be made between social and non-social processes.

2.2 Non-social processes

Members of a population may behave in similar ways as a result of either genetically controlled behaviour or individual learning. Behaviours that are under genetic control may be similar between individuals because of convergent evolution, common ancestry or Batesian or Mullerian mimicry (Ridley, 1996). Individual learning may lead to behavioural similarity between members of a population if they are exposed to the same environments and therefore converge on the same optimal, individually learned strategies (Whiten & Ham, 1992). Behavioural similarities that arise through non-social processes are executed under genetic control, or are learned through an individual's own interaction with its environment. They are therefore not involved in cultural transmission.

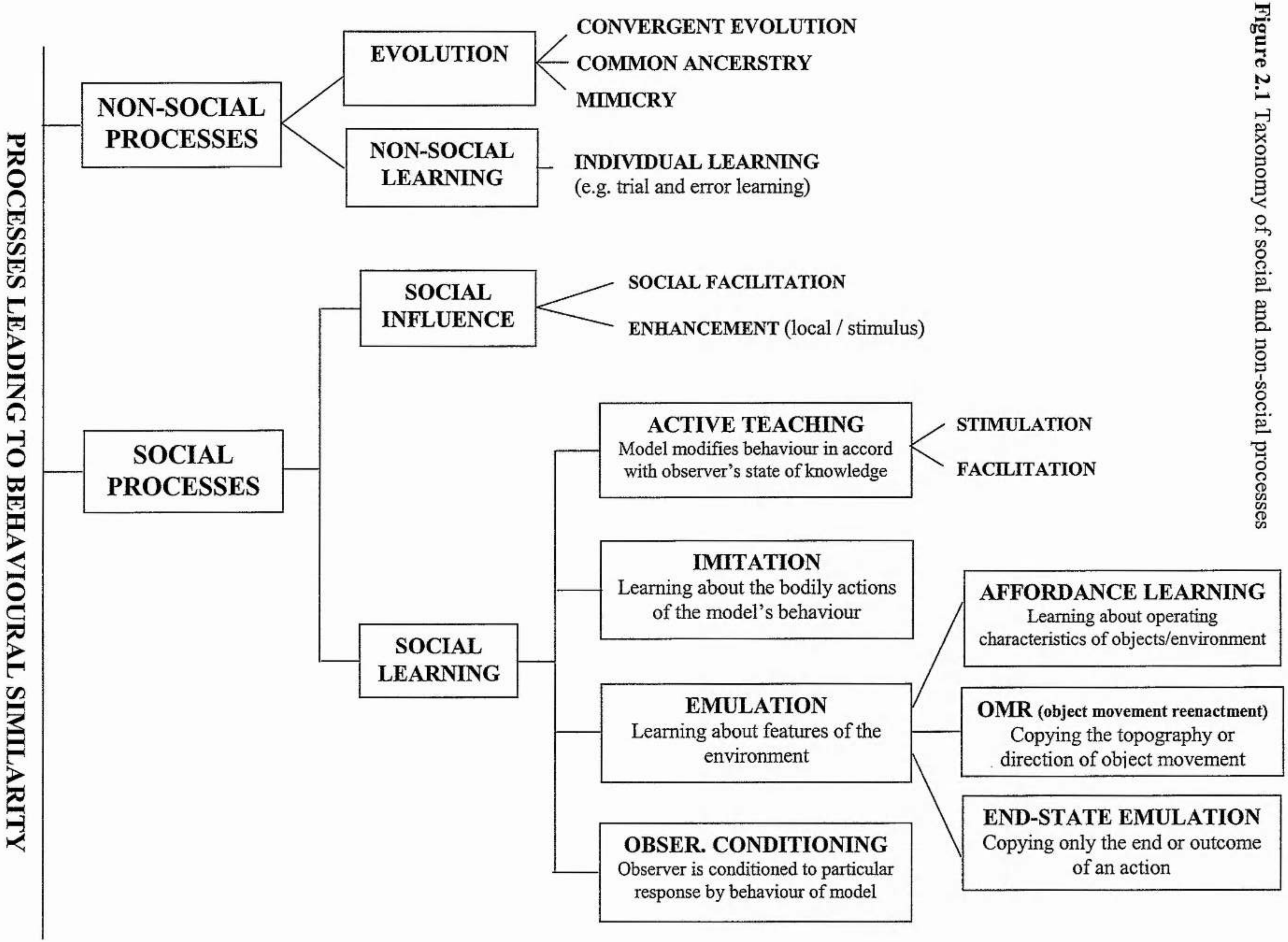
2.3 Social processes

Behaviours that result from social processes arise from observation of, or interaction with another organisms or its products (Heyes, 1994). Social processes can be broadly divided into behaviours resulting from social influence, and behaviours resulting from social learning.

2.3.1 *Social influence*

Behavioural similarities may arise between members of a population because the behaviour of one individual is influenced by either the presence of another individual or its products. However, the first individual *does not learn* a new behaviour through this interaction. For example, 'enhancement' occurs when an observer's attention is draw to a particular object, or location in the environment by the actions of a model (Thorpe, 1956). The observer may then converge on the same behaviour as the model because their individual exploration is constrained by the limited responses possible at that location or with that particular object (Thorpe, 1956; Whiten & Ham, 1992; Heyes, 1994).

Figure 2.1 Taxonomy of social and non-social processes



2.3.2 *Social learning*

Social learning is distinct from social influence in that the observer actual *learns a new behaviour* by observing another individual. Social learning encompasses several different learning mechanisms, each varying with respect to the fidelity of the match between the actions of the model and the actions of the observer (Whiten & Ham, 1992; see Fig. 2.1).

(i) Teaching

The demonstrator modifies their behaviour in accordance with the observer's state of knowledge (Boesch, 1991; Caro & Hauser, 1992).

(ii) Observational conditioning

An observer associates the behaviour of a model (e.g. fear) with a particular stimulus. When the observer is then exposed to the stimulus they respond with the same behaviour as the model (Whiten & Ham, 1992).

(iii) Emulation

An observer learns about the results of a model's actions, but not about the details of the behaviour required to bring about that result (Tomasello, Davis-Dasilva, Camak, & Bard, 1987). For example, an individual may learn to use a tool by observing the effect of the tool in gaining a reward, and seek to reproduce this outcome using their own efficacious actions, such as manipulating the tool with a different hand or arm movement. The critical characteristic of emulation is that the observer learns about essential features of the environment, rather than about the behavioural processes involved in task solution (Tomasello, 1998a).

The possibility that an individual may learn about results by observation, was first highlighted by (Tomasello et al., 1987) to differentiate a level of social learning more sophisticated than enhancement (see above), but without the behavioural fidelity required for imitation. This learning mechanism was later named 'emulation' (Tomasello, 1990). As a term, 'emulation' has been used divergently within the literature to describe a wide range of social learning processes. Firstly it was used to describe copying only the results of a model

(Tomasello, 1990), then later to describe copying the affordances and causal relationships of a task (Tomasello, 1996; Want & Harris, 2001, 2002). Others have sub-divided emulation into several different categories (Byrne, 1998; Custance, Whiten, & Fredman, 1999).

One of these sub-categories is object-movement re-enactment. This occurs when an observer recreates the movements of objects that are manipulated by the demonstrator, but not the body actions of the demonstrator that produced the movement (Custance et al., 1999). For example, an observer would recreate the direction in which a bolt was pushed or pulled, but would not use the same behaviour that they observed. The distinction between imitating the body movements of the demonstrator, and re-enacting the object movements of their actions therefore lies only at the junction between the body and the object (Whiten, In press). In this respect object movement re-enactment could be considered to overlap somewhat with imitation. However, object re-enactment involves learning about aspects of the environment rather than bodily behaviour, and for this reason it is classified under emulation.

Throughout this thesis, the term emulation will be used in a general way to describe learning about the affordances, end-states, or object movements of a task. In other words, emulation will be used to describe learning about the environmental features of a task, rather than the details of the observed bodily behaviour.

(iv) Imitation

By contrast, imitation occurs when an observer learns some specific aspect(s) of the intrinsic form of an act from the observation of a model (Whiten & Ham, 1992). An observer would therefore produce a recognisable (if not accurate) copy of the original behaviour required to bring about the same result as the model. For example, an individual may learn to use a tool by observing the effect of the tool in gaining a reward, and then seek to reproduce the same effect by using the same behaviour, such as the same hand or arm movement as the model. Imitation is distinct from other forms of social learning in that the behavioural technique of the model is attended to, and therefore the observer reproduces a more complete copy of the model's original behaviour .

Byrne & Russon (1998) have suggested the category (or subcategory) of programme level imitation, whereby the observer copies the overall structure of the model's actions, but not at a detailed level. However, this hypothesis has not been backed-up with empirical data, and hence many authors have discounted it (Matheson & Fragaszy, 1998; Tomasello, 1998a; Want & Harris, 1998; Whiten, 1998a; Whiten, 1999; Whiten, 2000).

As the number of social learning studies increases, the terminology that is created to distinguish different processes becomes increasingly complex. Call & Carpenter (2002) and Carpenter & Call (2002) have therefore suggested that instead of creating more terms, researchers should classify the type of information that an observer learns in terms of actions, results and goals. Different combinations of these three types of information could be used to describe emulation (results and goals) and imitation (actions). However, a great number of different combinations would be required to distinguish all the terms that are currently in use. Therefore, although this approach may be useful in some situations, it will not necessarily decrease the number of different processes that are described.

2.3.3 *The requirements of cultural transmission*

Some authors consider any form of social learning to be sufficient for cultural transmission in chimpanzees (Whiten & Ham, 1992; Russon & Galdikas, 1995; Boesch, 1996b), arguing that if the same level of behavioural variation between two populations was described in humans, anthropologists would not hesitate to grant culture (McGrew, 1992; Boesch, 1993; McGrew, 1993; Boesch, 1996b; Boesch, 1998; McGrew, 1998). However, others are more particular.

(i) Teaching

Some authors have suggested that in order for a species to have culture, it must show evidence of active teaching (Galef, 1988, 1992; Premack & Premack, 1999). However, active teaching seems rare in chimpanzees. There are only two reports of this behaviour, both involving mothers from Taï apparently teaching their offspring to nut-crack. On one occasion a mother was observed to correct the position of her son's nuts on the anvil. On the other occasion a mother was seen to demonstrate the correct hammer grip to her daughter (for more details see Boesch, 1991). Nevertheless, active teaching is only one form of pedagogy, and more commonly mothers are seen to 'stimulate' or 'facilitate' the acquisition of nut-cracking by their offspring, by leaving appropriate hammers and anvils for them to use, and intact nuts on the anvil (Boesch, 1996a). Active teaching may be rarer because at the age when young chimpanzees start to interact with nut-cracking apparatus (approximately 2-years-old) teaching would be conceptually difficult, and it may be more efficient for mothers so shape their offspring's individual efforts (Boesch, 1996a).

It is easy to assume that all human cultures depend heavily on active teaching. However, this view overlooks many societies, such as those of hunter-gatherer communities, where children learn mainly by observation and eavesdropping (Rogoff, Chavajay, & Matusov, 1993; McGrew, 1993). The evidence from chimpanzee studies suggests that they may have the cognitive capacity for active teaching, but that the rarity of reports makes this a poor criterion for culture.

(ii) Imitation

Instead, it has been suggested that culture should be determined by the presence of imitation, as this is the only social learning mechanism that can guarantee that behaviours are transmitted accurately enough for a cultural variant to be maintained. It is argued that other forms of social learning are too inaccurate for variants to remain distinct over time (Galef, 1992; Heyes, 1993; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993). Therefore much research interest has focused on identifying those species that have the capacity for imitation.

2.4 Identifying imitation

Many researchers believe that although observations of wild populations are essential for identifying particular behaviours which may result from cultural transmission, only controlled experimental studies are able to adequately isolate the particular learning mechanism which may be involved (Visalberghi & Fragaszy, 1994). Because of the potential importance of imitation as a requirement for culture, many experimental studies have focused on documenting the phylogenetic distribution of imitation in non-human species. Thus, experiments are often designed primarily to look for imitation, describing alternative non-imitative mechanisms only when it is not found. The increased focus of research on imitation has attracted attention from a number of different disciplines, including child development (Want & Harris, 2002; Whiten, 2002b), artificial intelligence and robotics (Dautenhahn & Nehaniv, 2002) as well as neurophysiology (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Miklosi, 1999) and neuropsychology (Meltzoff & Prinz, 2002; Hurley & Chater, In press). The literature on imitation is therefore rich and scattered.

2.4.1 *The two-action method*

As the literature increases, the task of excluding alternative, non-imitative social learning processes becomes increasingly cumbersome. However, it is generally accepted that the strongest evidence for imitation comes from studies that employ a two-action design (Shettleworth, 1998). The two-action method was initially used by Thorndike (1911; cited in Shettleworth, 1998), then later by Dawson & Foss (1965), to control for non-imitative processes such as enhancement. Two-action designs involve an instrumental task that can be solved equally in two different ways. For example, obtaining a food reward by pushing a handle (behaviour A), or pulling the same handle (behaviour B). One group of individuals observes a model solve the task using behaviour A, the other group observes the model use behaviour B. Since the model acts on the same object, in the same part of the environment in each case, this controls for enhancement. When subjects from each group are then given the opportunity to interact with the apparatus, if they use the same technique that they observed to solve the task (A or B), this is a good indicator of imitation (Dawson & Foss, 1965; Galef, 1988).

However, although the two-action method is a good measure for imitation in theory, in practice researchers often do not apply the necessary controls. For example, it is possible that one of the two-action alternatives (behaviour A or B) is easier, or closer to behaviours already in an individual's repertoire than the other. In addition, if subjects from each group observe parts of the apparatus being moved in two different directions, it is possible to use object movement re-enactment to solve the task (see section 2.3.2) giving the illusion of imitation (Dorrance & Zentall, 2001; Zentall, 2001). In order to control for this, it has been suggested that the model must act on the same object, manipulating it in the same direction, and that the two-action method is incorporated by using different body parts. For example, a lever is moved to the left using either the beak (behaviour A) or the foot (behaviour B) (Dorrance & Zentall, 2001; Zentall, 2001). Some authors have claimed that only this methodology can be used to identify 'true imitation' (Voelkl & Huber, 2000).

2.4.2 *The problem of novelty*

Others have criticised imitation studies because the behaviour of the model is not completely novel to the observer (Byrne & Russon, 1998). However, this criticism has lead to further disagreements about definitions of novelty. Is it sufficient to ascertain that the behaviour is novel in the context of the study (Zentall, 2001), or can actions that involve the recombination of existing behaviours into a novel sequence be accepted? (Whiten, 1998b). It seems impractical to insist that behaviours are completely novel, since this restricts studies of species with a limited repertoire (Galef, In press), and overlooks the fact that new behaviours are assimilated into existing knowledge, and do not erase and replace old behaviours (Huber, 1998). It would therefore be more practical to determine that a behaviour has a low probability of being produced in the context of a task, by incorporating a control condition (Zentall, 2001).

2.4.3 *The role of intentions*

Another line of disagreement stems from the possible role of intentions in imitation. Tomasello, Kruger et al., (1993) have argued that imitation requires an observer to represent the intentions behind the demonstrator's actions. However, others have argued that imitation requires the observer only to represent what the demonstrator did, not what they thought or desired (Heyes, 1998). An individual's understanding of other's intentions can never be measured directly. Thus arguments about intentions are not productive, and according to some, are best avoided (Zentall, 2001).

2.4.4 *Removing environmental variables*

In order to get round all the potential disagreements listed above, it has been suggested that the strongest evidence for imitation comes from gestural imitation, where there is no environmental component. Arguments about emulation, imitation and enhancement are therefore avoided (Heyes, 1998; Russon, 1998).

2.5 Evidence for imitation in chimpanzees

2.5.1 *Early studies of imitation*

Imitation was originally thought to be a relatively simple cognitive process that was common in primates. Indeed, the phrase 'to ape' has become synonymous with 'to copy' in common language. This view dates back to early studies of chimpanzee social learning which claimed that home-raised chimpanzees were able to imitate many everyday actions of their human caregivers, such as sewing (Sheak, 1917; cited in Custance, Whiten, & Bard, 1995), smoking a pipe (Kearton, 1925), applying lip-stick (Hayes & Hayes, 1952), and painting a wall (Kohler, 1927). These reports were later backed-up with evidence from experimental studies. Hayes & Hayes (1952) trained their home-raised chimpanzee, Viki, to reproduce actions using the command 'Do-as-I-do!' They reported that she was able to imitate a number of novel object manipulations and arbitrary manual and facial gestures. The imitative abilities of chimpanzees therefore seemed clear.

However, these early conclusions were brought into question following a study by Tomasello et al., (1987). Chimpanzees observed a conspecific model use a rake to obtain out of reach food. It was found that chimpanzees who observed the model using the tool performed significantly better that chimpanzees who observed the model manipulate the tool in a non-functional manner. Nevertheless, the successful chimpanzees did not imitate the same technique as the model. Instead, it appeared that they had learned that the rake could function as a tool, but they did not learn the specific details of the model's behaviour. This study lead to the first description of emulation (see section 2.3.2), and suggested that, like Imo the Japanese macaque (see section 1.1.1), and the pine-cone stripping rats of Israel (see section 2.1.1), seemingly imitative behaviours may also result from alternative non-imitative processes in chimpanzees (Tomasello, 1990; Galef, 1992). This lead to a renewed interest in chimpanzee social learning and a new era of controlled experimental studies. Table 2.1 lists all the studies to date that have found evidence for imitation in chimpanzees.

EVIDENCE FOR IMITATION			
Author	**Task**	**Domain**	**Cognitive Process**
(Custance et al., 1995)	Gestures	Non tool-use	Imitation
(Myowa, 1996)	Gestures	Non tool-use	Imitation
(Tomasello, et al., 1993)	Object manip.	Non tool-use	Imitation
(Bering, et al,. 2000)	Object manip.	Non tool-use	Imitation
(Bjorklund, et al,. 2000)	Object manip.	Non tool-use	Imitation
(Bjorklund, et al,. 2002)	Object manip.	Non tool-use	Imitation
(Whiten, et al,. 1996)	Obj manip. Feeding	Non tool-use	Imitation
(Whiten, 1998b)	Obj manip. Feeding	Non tool-use	Imitation of sequence
(Marshall-Pescini, 2002)	Obj manip. Feeding	Non tool-use	Imitation of hierarchy

Table 2.1 Experimental studies of chimpanzee social learning that have found evidence for imitation.

2.5.2 *Gestural imitation*

The early study by Hayes & Hayes (1952) was later repeated by Custance et al., (1995) under more controlled experimental conditions. They found that, like Viki, their chimpanzees were also able to imitate novel arbitrary gestures, including some which involved out of sight body parts, such as touching the back of one's head. These gestures are thought to provide particularly convincing evidence for imitation, as the imitator cannot see what they are doing. In order to match the actions of the model they must be able to represent how the actions look from another individual's perspective (Piaget, 1952; Heyes & Ray, 2000). Myowa (1996) and Bard & Russell (1999) have shown that chimpanzee neonates are able to reproduce observed facial gestures, including tongue protrusion and mouth opening. These studies therefore corroborate earlier evidence that chimpanzees can imitate novel actions that have no environmental component.

2.5.3 *Object manipulation*

Experimental studies have also shown that chimpanzees can imitate actions with objects. For example, Tomasello, Savage-Rumbaugh et al., (1993) used the 'Do-as-I-do!' technique to show that human raised chimpanzees could imitate 16 simple and complex novel object manipulations. Similar results were later reported (Bering et al., 2000; Bjorklund et al., 2000; Bjorklund et al., 2002). These studies were of additional interest because they involved deferred imitation. The authors found that young chimpanzees were able to imitate observed objet actions following a 10-minute delay. Piaget (1952) suggested that imitating actions after a delay of this length was cognitively demanding because it involved symbolic representation of the actions in long-term-memory.

Studies which have employed the two-action method, such as the 'artificial fruit' employed by Whiten et al., (1996), have shown that chimpanzees can imitate object actions that are related to food processing. The artificial fruit is a box containing food, that is designed to mimic a naturally defended fruit. The box can only be opened by removing a number of external defences, such as bolts and pins. Subjects observe a demonstrator open the fruit in one of two ways, which are designed to control for stimulus enhancement. The use of the same technique by both the observer and the demonstrator can be taken as an indicator of imitation. Additional modifications of the original 'artificial fruit' design have demonstrated that chimpanzees can imitate at the level of the sequential and hierarchical structure of the model's actions (Whiten, 1998b; Marshall-Pescini, 2002).

2.5.4 *Enculturation*

One of the major concerns with investigations of ape social learning is that the rearing history of an individual may affect its performance in experimental tasks. Some authors have argued that extensive human contact (known as enculturation Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993), can lead to a fundamental change in the socio-cognitive development of great apes (Premack, 1983; Call & Tomasello, 1998). It has been proposed that enculturation increases a broad band of socio-cognitive skills due to increased exposure to objects with specific functions, increased observation of human models, attention focusing through training, and being treated as an intentional individual (Call & Tomasello, 1998; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993). This possibility was highlighted by Tomasello, Savage-Rumbaugh et al., (1993), who found that enculturated chimpanzees and human children were significantly better at imitating novel object actions than mother raised chimpanzees, leading to the assumption that only enculturated chimpanzees could imitate (Nagell et al., 1993; Call & Tomasello, 1998). However, many accounts of the achievements of enculturated chimpanzees are anecdotal. Imitative behaviours are more likely to be recorded in a home environment due to a far greater opportunity to observe novel behaviours in comparison to a few hours of experimental data. There is also little control over the extent or age at which enculturation occurs (Call & Tomasello, 1998).

It seems unlikely that evolution has favoured a dormant imitative capacity that is not expressed under natural conditions. Instead, chimpanzees are likely to demonstrate the apex of their abilities in the natural conditions in which the behaviour evolved. Exposure to human culture may therefore only replace the rich social and physical environment that would be experienced in the wild (Boesch, 1993; de Waal, 1998; Whiten, 2000). Captive studies that yield negative evidence for imitation might therefore result from impoverished social and physical conditions that lead to the retardation of development. The importance of the relationship between a model and an observer has been recognised in recent years (Coussi-Korbel & Fragaszy, 1995; Caldwell, Whiten, & Morris, 1999). Enculturation may therefore not transform cognitive abilities, but increases the willingness of the subject to imitate because they have an affiliative bond with the model (de Waal, 1998). Furthermore, studies which have found evidence for imitation did not involve chimpanzees with extensive human contact (Custance et al., 1995; Myowa, 1996; Whiten et al., 1996; Whiten, 1998b; Marshall-Pescini, 2002).

In summery, the literature suggests that investigations of chimpanzee social learning have come full circle. The strict experimental procedures of recent studies have demonstrated that chimpanzees can indeed imitate. They are able to imitate novel manual and facial gestures, actions with objects, deferred actions, and the sequential and hierarchical structure of an observed behaviour. After almost a century of research, even the most sceptical authors are prepared to review their opinions and concede that apes ape after all (Galef, In press).

2.6 The function of imitation

Now that the imitative ability of chimpanzees has been established, what is of interest is the evolutionary function of imitation. In other words, under what conditions is imitation employed? (Miklosi, 1998). This question can be best addressed by looking at the conditions under which chimpanzees do *not* employ imitation. What is immediately obvious is that all studies that have failed to find imitation have involved tool-use (see Table 2.2). In contrast, Table 2.1 shows that studies that have found evidence for imitation have involved non tool-use tasks. There therefore seems to be a relationship between the task domain and the social learning mechanism that chimpanzees employ to solve it.

NO EVIDENCE FOR IMITATION			
Author	**Task**	**Domain**	**Cognitive process**
(Hannah & McGrew, 1987)	Nut-cracking	Tool-use	Social learning (not specified)
(Sumita, et al,. 1985)	Nut-cracking	Tool-use	Social learning (not specified)
(Tonooka, et al,. 1997)	Probing	Tool-use	Social learning (not specified)
(Hirata & Morimura, 2000)	Probing	Tool-use	Social learning (not specified)
(Bard, et al,. 1995)	Probing	Tool-use	Social learning (not specified)
(Paquette, 1992)	Probing	Tool-use	Social learning / Trial & error
(Celli & Tomonaga, 2001)	Probing	Tool-use	Social learning / Trial & error
(Tomasello et al., 1987)	Raking	Tool-use	Emulation
(Nagell et al., 1993)	Raking	Tool-use	Emulation
(Myowa & Matsuzawa, 2000)	Open box	Tool-use	Emulation

Table 2.2 Experimental studies of chimpanzee social learning that have failed to find evidence for imitation. Where the cognitive process is defined as 'social learning' the authors were unable to identify which social learning process was in action.

Rather than argue that the relationship lies in a strict distinction between tool-use and non-tool use, it could be that there are other differences between to the two domains that produce this dichotomy. Whiten, Horner, & Marshall-Pescini, (In press) have identified a number of variables which may influence an individual's tendency to imitate, one of which is the availability of causal information.

Studies that have found evidence for emulation have typically involved tool-use, and thus have involved causal relationships between objects, such as a tool and a reward. In these situations, chimpanzees may employ emulation because they have access to information about the causal relationships of the objects involved. Chimpanzees may preferentially employ emulation because extracting rules of action from the causal relationships involved in a task can allow social learned behaviours to be generalised to different conditions (Tomasello et al., 1987; Visalberghi & Fragaszy, 1994; Want & Harris, 2001, 2002).

In contrast, studies that have found evidence for imitation, such as the 'Do-as-I-do!' paradigm used by Hayes & Hayes (1952) and Custance et al., (1995), have no environmental component, and thus no available causal information. Similarly, in studies that have involved object manipulation, such as the 'artificial fruit' used by (Whiten et al., 1996; Whiten, 1999; Marshall-Pescini, 2002), the tasks involved manipulation of a single object with the hands, and did not involve causal relationships between objects. Causal information was therefore either unavailable or difficult to infer, and the chimpanzees may have employed imitation to solve each task because emulation was not possible. Thus, the trend for imitation in non tool-use tasks, and emulation in tool-use tasks may be related to the availability of causal information, and not the task domain *per se*.

However, this will be discussed in more detail in Chapter 6. The following chapter will review the literature on chimpanzee causal knowledge to assess whether chimpanzees have sufficient knowledge of the physical world to warrant a likely involvement in determining which social learning strategy chimpanzees employ.

SUMMARY OF CHAPTER 3

Chapter 2 indicated that chimpanzees may use different social learning strategies to solve different types of tasks. One potential variable that may determine which strategy chimpanzees employ is the availability of causal information. This chapter investigates whether the causal knowledge of chimpanzees is sufficient to warrant a likely involvement in social leaning.

Studies of chimpanzee causal knowledge have mainly been conducted in the context of tool-use. Observations of wild populations suggest that they are able to select tools that have appropriate configurations for the requirements of a task, such as termite-fishing or ant-dipping. When an appropriate configuration is unavailable, they are able to manufacture tools by destructive modification of raw materials. Wild chimpanzees use tool-sets of up to four different types of tool. They are able to manufacture tools in advance of use, and flexibly employ tool-use skills in different situations. Observational studies therefore suggest that chimpanzees have a relatively sophisticated understanding of causality.

However, controlled experimental studies have revealed that chimpanzee causal knowledge is based solely upon observable aspects of the environment. For example, as long as two objects are in contact, a chimpanzee will view the objects as attached together and treat them as a whole. Chimpanzees do not seem to interpret the world in terms of unobservable phenomena, such as gravity or force that bind a cause and an effect. Instead, much of their knowledge seems to be gained by forming associations between reliable patterns of regularity in the environment, such as event A is always followed by event B. These rules can be used to reliably predict the outcome of an event, and can be employed in different situations. However, chimpanzees do not seem to understand causality in the same sense as an adult human (see Chapter 4). Nevertheless, the causal knowledge of chimpanzees, however basic, is all that is required to identify many causal features of the world. Chimpanzee causal knowledge is therefore sufficient to potentially be involved in social learning.

CHAPTER 3

CHIMPANZEE CAUSAL KNOWLEDGE

The previous chapter indicated that chimpanzees appear to use different social learning strategies to solve different types of task. Specifically, they use imitation to solve non tool-use tasks, and emulation to solve tool-use tasks. One potential factor that may influence chimpanzee's tendency to employ imitation or emulation is the availability of causal information. However, before this can be discussed in more detail, it is necessary to determine whether the causal knowledge of chimpanzees is sufficient to warrant a likely involvement in social learning.

3.1 Observations from wild populations

Causal knowledge can be divided into two domains; knowledge of physical causality and knowledge of social causality. The focus of this thesis does not allow for social causal knowledge to be discussed in any detail. However, for a review see Visalberghi & Tomasello (1998). Knowledge of physical causality has mainly been investigated in the context of tool-use.

3.1.1 *Selection of raw materials*

Wild chimpanzees have been reported to use tools with highly specialised functions, and they appear able to select suitable raw materials on the basis of shape, strength and flexibility. For example, tools that are used to collect nesting ants *(Dorylus gerstaecheri* and *D. nigricanus)* must be inserted into the nest cavity, and removed once the ants have swarmed halfway up the tool. If tools are too long they will be difficult to control, but if they are too short, they will not collect a sufficient number of ants before the tool must be withdrawn, as ants can deliver a painful bite. Similarly, if a tool has too many side branches it cannot be swept through the hand or mouth, however if it is too thin it will easily break. In comparison, tools that are used for termite fishing are usually longer and more pliable as they must be inserted into thin and winding tunnels within the termite mound (Goodall, 1986; Tomasello et al., 1987; Boesch & Boesch, 1990; Suzuki et al., 1995). Chimpanzees may spend time choosing a tool, picking up and discarding several pieces of vegetation before an appropriate configuration in selected. Several tools may be selected at once, and stored in the lap or placed on the ground nearby so that replacements are available should one tool become damaged (Goodall, 1986). However, vegetation with the appropriate configuration may not always be available, and tools must therefore be manufactured from raw materials.

3.1.2 *Tool manufacture*

Tools can be manufactured by modifying raw materials using four basic categories (Beck, 1980):

(i) Detach – sever from substratum or separate from main plant
(ii) Subtract – remove obstructive parts, such as leaves or side branches
(iii) Reshape – sharpen or blunt point, bend or straighten
(iv) Combine – construct a tool from two or more separate parts

Chimpanzee tool modification is mainly destructive, and therefore involves only categories (i) to (iii). Chimpanzees have been reported to modify tools using more than one of these categories. For example, chimpanzees from Taï Forest were reported to modify tools using up to three categories in 93.4% of observed cases (Boesch & Boesch, 1990). Similarly, chimpanzees in Guinea have been reported to manufacture 'brush-sticks' to collect termites by biting or crushing the tip of the tool with a rock. This behaviour involves detaching, subtracting and reshaping the tool to create a greater surface area on which termites can become attached, and hence increase tool efficiency (Sugiyama & Koman, 1979; Sugiyama, 1985).

3.1.3 *Tool-sets*

Chimpanzees in the Ndoki Forest, Congo, have been reported to use brush-sticks in combination with perforating sticks, which are used to puncture deeper into the subterranean section of a termite mound and therefore access more termites (Suzuki et al., 1995). Tool-sets have been reported in Gambia, where chimpanzees were found to use four different tool configurations to obtain honey. The chimpanzees used large and small 'chisel-sticks' to break the crust and widen the resulting hole, a 'bodkin-stick' to puncture the nest seal, and a 'dipping-stick' to retrieve the honey. Each tool was manufactured appropriately for its specific function (Brewer & McGrew, 1990).

3.1.3 *Planning ahead*

Boesch & Boesch (1990) reported that many of the tools manufactured by chimpanzees in Taï Forest were modified prior to use with no trial and error. Chimpanzees at Gombe have been reported to select an appropriate tool for termite fishing up to 100m away from, and out of sight of the nearest termite mound (Goodall, 1986). Chimpanzees at Taï who crack nuts *(Coula edulis* and *Panda oleosa)*, have been shown to memorise the location of up to five stone tool sites, and therefore to minimise the transport distance of nuts to the nearest anvil (Boesch & Boesch, 1984).

3.1.4 *Flexibility of tool-use*

Chimpanzees demonstrate an ability to flexibly deploy their tool using skills when required. For example, when stone anvils were no longer available for nut-cracking, chimpanzees from Taï Forest switched to using fallen tree stumps (Sakura & Matsuzawa, 1991). Chimpanzees at Gombe were reported to generalise adaptive tool behaviour to lever open food storage boxes with sticks (Goodall, 1986).

Observational studies therefore indicate that wild chimpanzees are able to select and modify tools to specific requirements, suggesting that they appreciate the physical properties of objects that allow them to function as tools. However, observational data typically lacks descriptions of an individual's experience prior to the reported event. It is therefore not possible to determine the depth at which chimpanzees understand the causality of their actions. Hence, experimental studies have been employed to study chimpanzee causal knowledge under controlled conditions.

3.2 Experimental studies of causal knowledge

3.2.1 *Early studies of causal knowledge*

Chimpanzee causal knowledge has been the focus of experimental research for almost a century. Köhler (1927) performed a series of experiments with seven chimpanzees at the Anthropoid Station, Tenerife between 1913 and 1917. One of Köhler's initial experiments, which required chimpanzees to use a box as a step to retrieve an out-of-reach banana, yielded very positive results. Unfortunately, often only Köhler's preliminary work is cited in the literature, leading to a biased interpretation of his results (Povinelli, 2000). When the task changed so that the chimpanzees were required to use two boxes to reach a banana that was suspended even higher from the ceiling, the chimpanzees revealed striking conceptual shortcomings. For example, they tried to 'stick' the box to the wall and climb up it, followed by an array of behaviours that demonstrated a lack of appreciation for the type, or quantity of contact that was required to make an object stable. Köhler's subsequent experiments reported the same conflict between seemingly insightful problem solving, and behaviours that suggested a lack of appreciation of basic causal principles. Accordingly, Köhler concluded that chimpanzees' understanding of the world appeared to be tied to observable phenomena. For example, he noted that as long as two objects are in contact, a chimpanzee will view the objects as attached together and treat them as a whole, with no appreciation of physical connection (Köhler, 1927).

3.2.2 *Recent studies of causal knowledge*

However, later studies appeared to show chimpanzees in a more favourable light. Nevertheless, many of the conclusions that were drawn from these studies have now been brought into question. For example, Dohl (1968 cited in Suddendorf & Whiten, 2001) reported that his home-raised chimpanzee Julia could use five different keys to open five different nested boxes in the correct order, without trial and error. However, the report does not give adequate details about the control conditions, or the level of Julia's previous experience.

Premack (1976) used picture cards to investigate causal knowledge in a language-trained chimpanzee, Sarah. The chimpanzee was shown a picture of an object (such as an apple), and an effect (cut apple) and asked to choose a picture that represented the correct cause (a knife). Although Sarah could pair up the correct cause and effect on the majority of trials, it is possible that her previous experience with these objects enabled her to learn associations about the scenes that were presented. For example, Sarah may have selected the 'knife' card simply because she has seen a knife with an apple more than the alternative combinations. She may therefore have had no understanding that the knife represented a cause, and would not need to understand the purpose of the task to succeed (Tomasello & Call, 1997).

Mathieu, Daudelin, Dagenais, & Decarie (1980), studied chimpanzees' knowledge of contact. Chimpanzees were shown two cloths, one with a desirable object lying on it, and the other with an object next to it. One of the two chimpanzees was able to pull the correct cloth in order to retrieve the object significantly more than chance. However, it is unclear what controls were taken for associative learning.

Premack & Premack (1994) investigated causal knowledge in adult chimpanzees and 3 to 4-year-old children. Both groups observed a human demonstrator place an apple under an opaque container and a banana under another container. The subjects were then distracted for two minutes, after which time the demonstrator reappeared eating either an apple or a banana. The subjects were then allowed to search under one of the containers for fruit. If the demonstrator was eating a banana, all the children and some of the chimpanzees successfully chose to search the container holding the apple, and vice versa, implying that they understood there were only two pieces of fruit and therefore only one left under the containers.

3.2.3 *Tube tasks*

In 1989, Visalberghi and Trinka published the first in a series of experiments that were designed to investigate causal knowledge in capuchin monkeys *(Cebus apella)* and great apes, in tool-use tasks (Visalberghi & Trinca, 1989). Subjects were required to modify tools in order to push a food reward out of a clear plastic tube (see Figure 3.1).

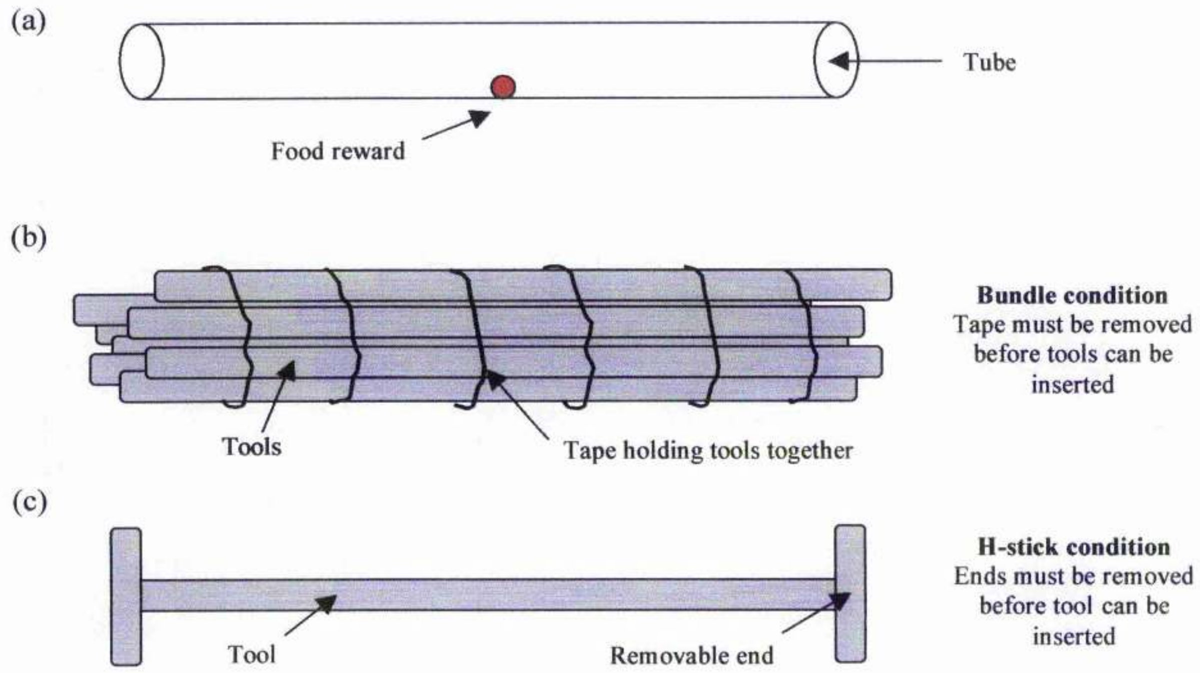


Figure 3.1. (a) Clear plastic tube containing food reward, (b) Bundle: the outside tape must be removed before one of the tools can be used to dislodge the food reward, (c) H-stick: the obstructive ends must be removed before the stick can be inserted into the tube to dislodge the reward.

Capuchin monkeys were able to solve the task in every trial, but errors persisted throughout the experiment and did not decrease over time. For example, the monkeys often inserted the tape that they had removed from the tools in the bundle condition, or the obstructive ends from the H-stick condition. Therefore the solution was only achieved by trying all possible alternatives (Visalberghi & Trinca, 1989; Visalberghi & Limongelli, 1994). In contrast, when chimpanzees, bonobos *(Pan paniscus)* and orangutans *(Pongo pygmaeus)* were exposed to the same task, errors were few and deceased rapidly across trials (Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995). As a result, the apes were thought to have a deeper understanding of the relevant causal features of the task (Visalberghi & Limongelli, 1998).

Monkeys and apes were then tested using a tube with a trap in the middle (trap-tube), with food placed on one side of the trapping hole (see Fig. 3.2). Subjects were required to insert a tool in the correct end of the tube so as to remove the food without pushing it into the trap. The correct end of tool insertion was therefore dependent on the position of the food relative to the trap.

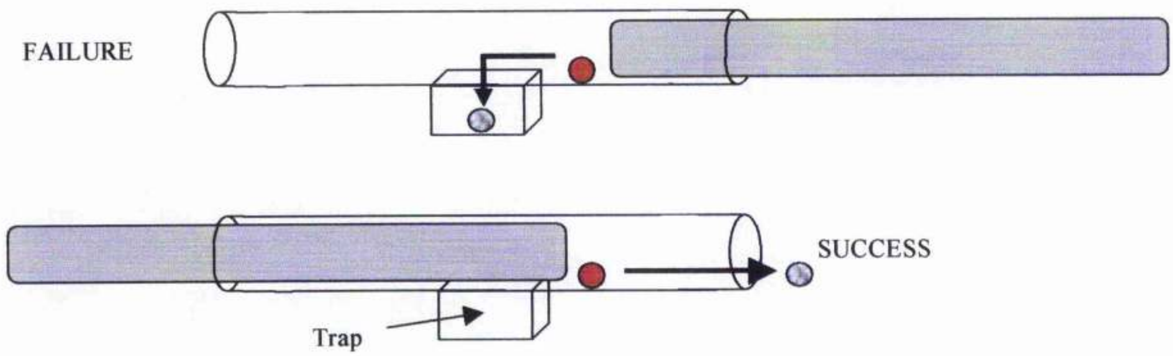


Figure 3.2 Trap-tube apparatus with trap in middle, used by (Visalberghi & Limongelli, 1994; Visalberghi et al., 1995).

One of the four capuchin monkeys obtained the reward significantly more than would be expected by chance. However, altering the position of the trap (see Fig. 3.3), revealed that this monkey had developed an inflexible rule-based strategy, centred on the distance between the food and the end if the tube. This strategy could not be generalised to new experimental conditions (Visalberghi & Limongelli, 1994). When the investigation was extended to chimpanzees, 2 of the 5 succeeded above chance. In contrast to the monkeys, the chimpanzees therefore seemed to have a better understanding of the causal features of the task that allowed them to generalise to new situations (Visalberghi et al., 1995).

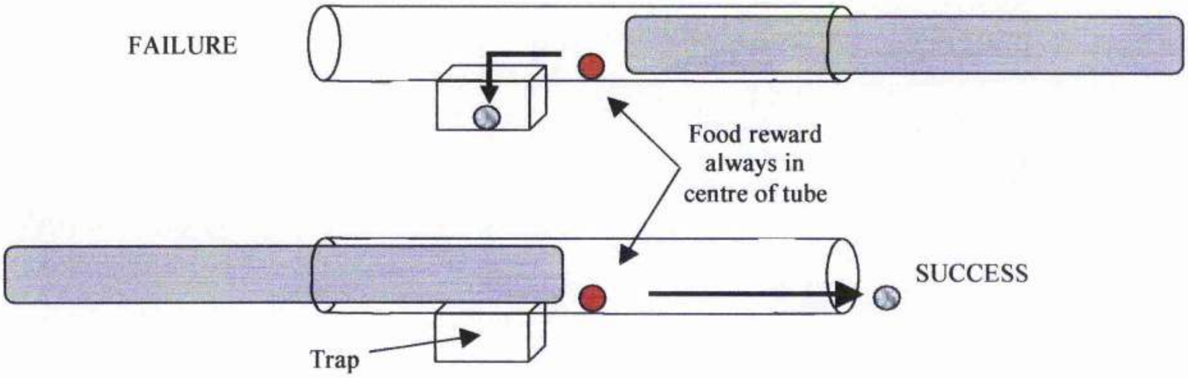


Figure 3.3 The altered position of the trap. A distance-based rule cannot be used to solve the task, as the food reward is always placed in the centre of the tube.

However, Povinelli & Reaux (2000) have argued that moving the position of the trap excluded only one of several associations that the chimpanzees could use. By inverting the trap and rendering it ineffective, Povinelli, et al., found that Megan, the only chimpanzee to perform significantly better than chance, continued to avoid the trap. She did this even when continuation of this strategy was penalised by placing the tool on the side closest to the trap, so that she had to pick up the tool and walk to the other side of the tube in order to continue using her rule. The authors concluded that her success was based on a complex set of associative rules that could be applied in different conditions. It was argued that chimpanzees may out-perform monkeys in the trap-tube task not because they have superior causal knowledge, but because they have a more sophisticated ability to extract observable patterns of regularity by association (Visalberghi & Tomasello, 1998; Povinelli, 2000). This ability may have enabled them to discover that insertion of the tool closest to the trap always resulted in success.

3.2.4 *Chimpanzee causal knowledge*

In summary, observational studies of wild chimpanzees suggest that they have sophisticated knowledge of physical causality, which allows them to select and modify tools in advance, and to the specific requirements of a task. However, when chimpanzee causal knowledge is investigated under controlled experimental conditions, it seems that much of their causal knowledge is based upon observable aspects of the environment. Chimpanzees do not seem to interpret the world in terms of unobservable phenomena, such as gravity or force that bind a cause and an effect. Instead, much of their knowledge seems to be gained by forming associations between reliable patterns of regularity in the environment, such as event A is always followed by event B. These rules can be used to reliably predict the outcome of an event, and can be employed in different situations. Nevertheless, the causal knowledge of chimpanzees, however basic, is all that is required to identify many causal features of the world. Chimpanzee causal knowledge is therefore sufficient to potentially be involved in social learning.

SUMMARY OF CHAPTER 4

Psychological studies of chimpanzees have mainly been conducted from an evolutionary perspective, in order to make comparisons between the mental abilities of chimpanzees and humans. Comparative studies, which have tested human children with similar tasks to chimpanzees, have found that, like chimpanzees, children are able to imitate novel gestures, and object manipulations after a delay, as well as the sequential and hierarchical structure of observed actions. However, children tend to imitate actions with greater fidelity than chimpanzees, and employ imitation in situations where chimpanzees have been found to emulate. Children may predominantly employ imitation because it is a highly adaptive strategy that plays an important part in many aspects of their development. However, like chimpanzees, the role of intentions in imitation is unclear.

Both chimpanzees and children pass through the same stages of development, but it seems that children have a more sophisticated understanding of causality than chimpanzees. They actively seek causal explanations for observed events, and are able to infer unobservable mediating forces such as gravity and force. In contrast, the literature suggests that chimpanzee causal knowledge is based on observable features of the environment. Nevertheless, the causal knowledge of both chimpanzees and children is sufficient to identify the relevant aspects of a demonstration, and therefore to be involved in social learning.

CHAPTER 4

COMPARATIVE STUDIES WITH HUMAN CHILDREN

4.1 Comparative studies of social learning

Psychological studies of chimpanzees have primarily been undertaken in order to compare their cognitive abilities with those of humans. A number of authors have therefore conducted comparative studies with chimpanzees and children under very similar conditions. Nagell et al., (1993) repeated the raking study of Tomasello et al., (1987) with 2-year-old children (see section 2.5.1). They found that unlike the chimpanzees, children imitated the actions of the model with high fidelity, although emulation would have lead to a more efficient solution. Similarly, Whiten et al., (1996) found that 2- to 4-year-old children opened an artificial fruit by reproducing the exact form of the actions they had witnessed, and were therefore *less* efficient than chimpanzees. It seems that chimpanzees and children use different social learning strategies to solve the same tasks. Specifically, it appears that children employ imitation in the same situations whereby chimpanzees tend to emulate.

4.1.1 *The predominance of imitation in children*

The prevalence of imitation in young children is well documented. Imitation is known to play an important role in early language acquisition (Meltzoff, 1988) and object knowledge (Abravanel & Gingold, 1985; Barr, Dowden, & Hayne, 1996). Neonates are able to imitate novel manual and facial gestures after only a few hours of life, indicating that the capacity for imitation may be present from birth (Meltzoff & Moore, 1977, 1983, 1989, 1994). Indeed, it has been suggested that imitation may be such an adaptive learning strategy in child development that it is routinely employed in situations where alternative learning strategies would be more efficient (Whiten et al., 1996).

4.2 Similarities between chimpanzees and children

4.2.1 *Comparative studies*

Chapter 2 indicated that chimpanzees do imitate in some situations, and there are some similarities between the imitative capacities of chimpanzees and children. For example, human infants as young as 9-months-old are able to reproduce novel actions following a week-long delay, indicating that, like chimpanzees, the representation of actions in long-term memory is involved in imitation (Meltzoff, 1988a, 1988b). Both human and chimpanzee neonates are able to imitate novel facial gestures, such as tongue protrusion and mouth opening (Meltzoff & Moore, 1977; Myowa, 1996; Bard & Russell, 1999). In addition, like chimpanzees, 3- and 4-year-old children are able to imitate details of the sequential and hierarchical structure of observed actions (Whiten, 2002a).

4.2.2 *The imitation game*

A number of authors have pointed out that the predominance of imitation in children may be due, in part, to early developmental experiences. Human mothers from all cultures imitate the vocalisations and gestures of their babies. Hence, children have months of early experience with face-to-face turn taking in which they can learn the 'rules' of the imitation game, and in most cases, care-giver imitation comes before imitation by the infant (Jones, 2003). In contrast, chimpanzees do not typically have the opportunity to learn about imitation in the sense of taking turns to copying the actions of a demonstrator. However, chimpanzees who are raised in a home environment do typically have this early experience with their human care-givers, and hence they may show imitation more readily, not because they have special 'enculturated' abilities, but because they have early experience with the imitation game (Bard, 1998). It seems that when care-givers encourage early imitation, both chimpanzee and human neonates are capable of gestural imitation. Adult chimpanzees have also shown evidence of gestural imitation in situations where they have been explicitly taught the turn taking procedure inherent in the 'Do this!' paradigm (see sections 2.5.1 and 2.5.2; Custance et al., 1995; Bard, 1998).

4.2.3 *Intention in imitation*

The fidelity with which children imitate can be determined by their perception of the model's goal. For example, after watching a model touch their right ear with the right hand, children will often touch their left ear with their left hand. However, the fidelity of imitation increases if they observe the model cross their arms and touch both ears with opposite hands. In the first case, children perceive the goal of the model to simply be touching an ear.

However, in the second case the goal of the model is clearer, and children copy with greater fidelity (Bekkering, Wohlschlager, & Gattis, 2000; Gattis, 2002).

If children observe a model attempt, but fail to perform an action (such as pulling apart a dumb-bell shaped toy), they are able to complete the action although they did not observe the final result (Meltzoff, 1995). This has been interpreted as evidence that the children understand the intention of the model. However, Huang, Heyes, & Charman (2001) and Charman & Huang (2002) have suggested that the completion of a failed attempt may be explained by alternative non-imitative processes. For example, children may pull apart the dumb-bell toy simply because their attention has been drawn to it, and they subsequently converge on the same behaviour through individual exploration because the number of potential actions is very limited.

Gergely, Bekkering, & Kiraly (2002) found that infants would copy the 'strange' behaviour of an adult model, as long as they perceived the adult's actions as intentional. Children who observed an adult turn on a light switch with their head whilst their hands were occupied by holding an object, would turn the light on with their hands. However, if the model's hands were free, the children would also push the switch with their head. The authors interpreted this as evidence that the children imitated because they perceived the actions of the adult to be intentional, as there was no other reason to use their head, if their hands were free.

Carpenter, Akhtar, & Tomasello (1998) found that 14- to 18-month-old children reproduced the behaviour of a model significantly more when it was followed by the model saying 'There!' than when it was followed by 'Whoops!'. However, it may simply be that children are able to learn by association that actions followed by 'There!' have more desirable outcomes (Heyes & Ray, 2002).

Few studies of intention reading have been conducted with chimpanzees. Povinelli, Perilloux, Reaux, & Bierschwale (1998) found that chimpanzees could not differentiate between a human caregiver who accidentally spilled a glass of juice, and one who purposefully poured it on the floor. However, the chimpanzee did not receive the reward in either case and therefore their lack of preference for a particular caregiver may not be surprising. In contrast, Call & Tomasello (1998) found that chimpanzees were able to preferentially search under a container on top of which a human had purposefully placed a maker, instead of a container where a marked had been accidentally dropped. However, the effect of this result was small, and decreased over subsequent trails. The role of intentions in chimpanzee social learning therefore remains unclear.

The literature therefore suggest that children copy observed behaviours with greater fidelity than chimpanzees, and that they use imitation in situations were alternative strategies would be more efficient. There is some evidence that children are sensitive to the intentions of the model, but this is not entirely clear.

4.3 Comparative studies of causal knowledge

4.3.1 *Seeking causal explanations*

Studies of human children suggest that they have a more sophisticated understanding of causality than chimpanzees, seeking causal explanations for observed effects (Tomasello, 1998b; Povinelli, 2000). For example, Povinelli & Dunphy-Lelii (2001) presented chimpanzees and 3- to 5- year old children with a block of wood that could be balanced on one edge in order to obtain a reward. From time to time, the block was replaced with a 'sham' block that did not balance because it had rounded edges, or was weighted at the top. The children, but not the chimpanzees, were seen to visually inspect the sham block following failure.

4.3.2 *Knowledge of unobservable forces*

Children as young as 4- to 6-months-old are sensitive to unobservable causal principles such as gravity. They are able to use this knowledge to solve tasks that appear difficult for adult chimpanzees, such as the contact and gravity problems set by Köhler. For example, infants look longer at objects that are not properly supported, thereby violating their expectations of the physical world. Unlike chimpanzees, they seem to appreciate the type and quantity of contact that is required to make two objects stable (Baillargeon, Needham, & DeVos, 1992; Needham & Baillargeon, 1993a, 1993b; see Fig. 4.1).

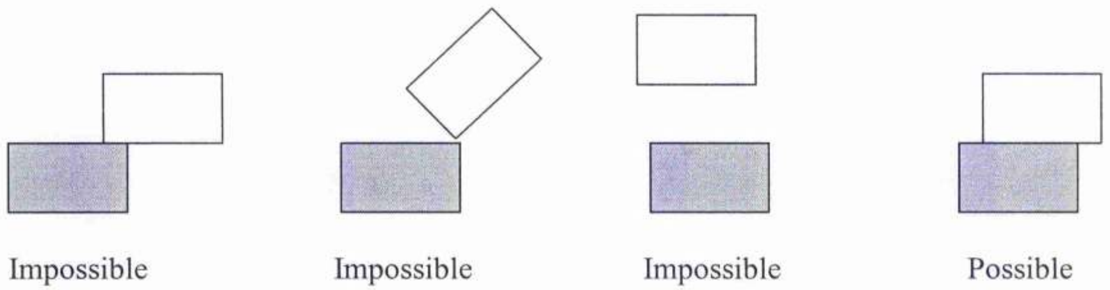


Figure 4.1 Object relations shown to 4 to 6-month-old infants in the preferential looking paradigm used by Baillargeon et al. Children were found to look longer at the first three configurations.

However, studies such as these with very young infants assume that they look longer at some events because they understand that they are causally impossible (Baillargeon & Graber, 1988). This is often interpreted as evidence that infants understand principles such as gravity and inertia (Spelke, Phillips, & Woodward, 1995). An alternative explanation may be that infants look longer at impossible events because they are, by definition, novel. Therefore looking time would not necessarily imply that the children have understood the causal principles, only that what they see is *unusual*. Experiments using this methodology may therefore give an artificially early age of the development of causal knowledge in humans compared to non-human primates.

Nevertheless, by the age of 3-years-old, children are able to combine different forms of causal knowledge to correctly predict the outcome of causal events. For example, Bullock, Gelman, & Baillargeon (1982) presented children with a series of domino-like blocks that could be toppled over so that the last block hit a lever which ejected a toy rabbit from a platform into a toy bed. Children were able to predict from visual inspection, that pushing the first block would cause the rabbit to fall into bed. They were also able to distinguish between changes to the apparatus that were causally relevant or irrelevant to the fate of the rabbit. The ability to predict outcomes in advance implies that, unlike the looking-time studies, children were not simply responding to novelty. It seems that by 3-years-old children do have a relatively sophisticated understanding of the physical world.

Many other aspects of causal knowledge have been found in children, including:

Gravity (Hood, 1995)

Contact (Bates, Carlson-Lunden, & Bretherton, 1980)

Force (von Hofsten, Vishton, Spelke, Feng, & Rosander, 1998)

Causal chains - understanding that if a chain of events has the order A>B>C, A causes C via a causal mediator B, (Bullock et al., 1982; Shultz, Pardo, & Altmann, 1982)

Temporal contiguity - the knowledge that a cause must precede an event (Bullock & Gelman, 1979; Shultz et al., 1982)

Logical searching - the ability to restrict the search for an object or person on the basis of where they were first and last seen (Wellman, Somerville, & Haake, 1979; Somerville & Capuani-Shumaker, 1984)

Predictive action - the ability to predict the trajectory of falling or moving objects (Krist, Fieberg, & Wilkening, 1993)

However, the developmental mechanism of children's causal knowledge is a subject of contention. Some authors argue that humans are born with an innate system of 'core knowledge' around which causal understanding is built (Spelke, Katz, Purcell, Ehrlich, & Breinlinger, 1994). This knowledge develops in accord with three causal principles (cohesion, continuity, and contact), with each having specific constraints on the motion of objects (Spelke et al., 1995; In-Kyeong & Spelke, 1999).

Others claim that humans are not born with innate knowledge, but with a learning bias that constrains and guides the acquisition of causal knowledge (Baillargeon, Kotovsy, & Needham, 1995; Goswami, 1998).

In contrast, Piaget (1952) argues that humans are born with neither knowledge nor biases, but that all causal knowledge is acquired through experience with objects. The development of causal knowledge is constrained only by maturation processes such as autoregulation, and therefore must be broken down into stages (Piaget, 1952, 2000). Piaget described four categories of sensory motor development in humans. One of which was the development of causal knowledge, which was divided into 6 stages:

Stage 1 – Reflexes

Stage 2 – Acts directed at own body

Stage 3 – Reproduction of interesting effects on external entities

Stage 4 – Hierarchical organisation of Stage 3 (e.g. moving one object to gain access to another)

Stage 5 – Relating objects to one another

Stage 6 – Mental representation of object relations

Piaget maintained that by the age of 12-15 months, children were capable of Stage 5 object knowledge, and Stage 6 mental manipulations by the age of 18 months. Comparative studies have shown that chimpanzees and humans pass through a similar developmental sequence (Mathieu et al., 1980; Bard & Russell, 1999). Within the first year of life chimpanzees are able to reproduce interesting effects on external objects (stage 3), and organise these actions hierarchically (stage 4) (Mathieu & Bergeron, 1981; Poti & Spinozzi, 1994). Vauclair & Bard (1983), investigated object manipulation in two chimpanzees, a bonobo and a human child in the first year of life. They observed that all subjects were capable of stage 4 manipulations, but that human infants reproduced and organised their object actions far more frequently than the other ape species.

4.3.3 *Cautionary note*

It is important to note that very few relevant experimental studies have been performed with non-human primates. Many of the tasks that have been presented to chimpanzees address very specific causal problems, often with tenuous analogies to natural behaviours. This sort of experimental paradigm may not be ethologically or motivationally appropriate to demonstrate the apex of their ability. In addition, the seemingly impressive abilities of very young human infants may be biased by the methodology, which has not been systematically used to study non-human primates of the same age.

4.3.4 *Comparative conclusions*

In summary, the literature suggest that, like chimpanzees, children are able to imitate novel manual and facial gestures, in some situations after a delay, and can imitate the hierarchical and sequential structure of observed actions. However, it seems that children copy observed behaviours with greater fidelity than chimpanzees and that they use imitation in situations were alternative strategies would be more efficient. Both chimpanzees and children pass through the same stages of causal knowledge development. However, it appears that the major difference between species is that children actively seek explanations for observed effects, and are able to implicate unobservable mediating forces, such as gravity. There is little evidence to date that chimpanzees do so, although no systematic studies have been carried out (Tomasello & Call, 1997; Visalberghi & Tomasello, 1998). Instead, the experimental literature suggests that chimpanzee causal knowledge is based upon an ability to identify regularities by association and generalising these to different environmental conditions. Nevertheless, the causal knowledge of both chimpanzees and children is sufficient to identify causal regularities and hence may be important in social learning to identify the relevant features of a demonstration.

SUMMARY OF CHAPTER 5

All the experiments with chimpanzees were conducted at Ngamba Island Chimpanzee Sanctuary, Uganda. The chimpanzee subjects were mainly bush-meat orphans, who were confiscated from traders in the Democratic Republic of the Congo at border towns near Uganda. With the exception of a three-month quarantine period, the chimpanzees have very little one-on-one contact with humans. Great care is taken to interact with the chimpanzees using species-typical vocalisations and gestures were possible. The chimpanzees do not receive any form of training, or demonstrations about how to interact with objects or each other. They spend the majority of time in a peer group, but have daily access to a species-typical forest environment and interactions with adult conspecifics. Therefore the chimpanzees who participated in this series of studies cannot be considered as 'enculturated' in the typical sense used in the literature.

All experiments with children were conducted at nursery and primary schools in Dundee and St Andrews, UK. The children were recruited from schools with a wide ethnic and demographic range of pupils. Experiments with children were undertaken from a comparative perspective, and therefore care was taken to keep the methodologies of the chimpanzee and child studies as similar as possible. The children were given very little verbal information about each task. Both children and chimpanzee observed the demonstrations from the same perspective, were allowed to move freely around the apparatus, and were not prevented from interacting with it during demonstrations.

CHAPTER 5

STUDY SITE, PARTICIPANTS AND GENERAL METHODOLOGY

5.1 Study site: Chimpanzees

5.1.2 *The Chimpanzee Sanctuary and Conservation Wildlife Trust*

Data collection for all the experiments with chimpanzees took place at Ngamba Island Chimpanzee sanctuary, Uganda. Ngamba is situated in Lake Victoria, 23 km from mainland Uganda (see Fig. 5.1). The sanctuary is run by the Chimpanzee Sanctuary and Conservation Wildlife Trust (CSWCT), and receives funding from the Uganda Wildlife Education Centre (UWEC), the Zoological Parks Board of New South Wales - Australia, Born Free – UK, The Jane Goodall Institute – Germany, and the International Foundation for Animal Welfare. CSWCT is also responsible for an educational out-reach project for local schools and communities, a snare removal project throughout the national parks of Uganda, and a chimpanzee habituation project at Kibale National Park.

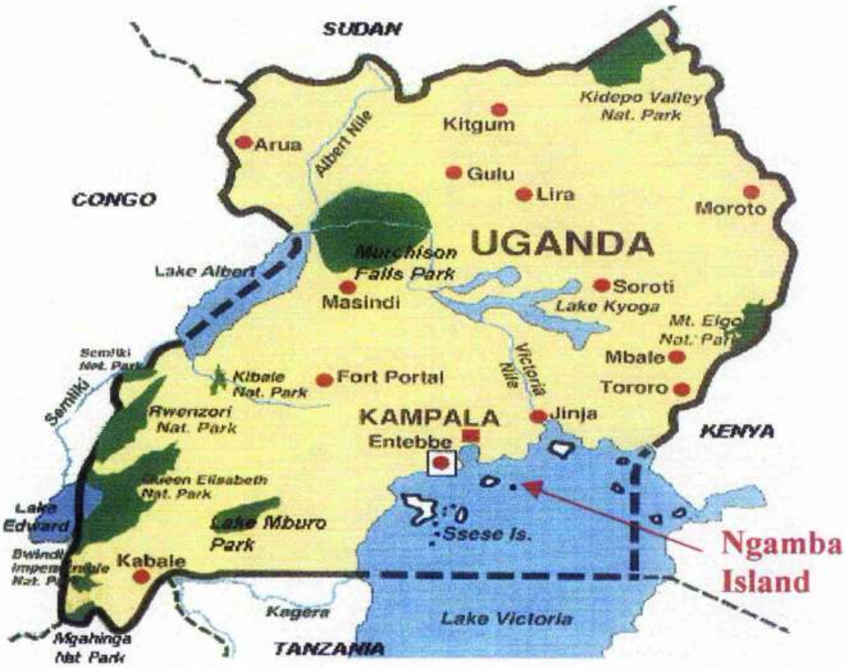


Figure 5.1 Location of Ngamba Island in Lake Victoria, Uganda.

5.1.2 *Ngamba Island*

Ngamba Island has an area of approximately 100 acres, of which 98 acres are covered by forest. The remaining two acres make up the human camp, which consists of three small accommodation buildings for staff and researchers, and a kitchen/store building. The camp and the forest are separated by an electric fence (see Fig. 5.2). The north section of the forest is flat with open grass areas covering approximately 10%, but the southern section is more hilly. Until 1997, the island was inhabited by a fishing community, as is typical of many of the small islands in Lake Victoria. The community logged many of the large trees in the forest, and much of the open grassland is the result of human clearing. When the sanctuary was first set up in 1998, a group of volunteers cut a series of trails through the forest, running from North to South, and from East to West at 50m intervals. These trails are still the main travel route used by both chimpanzees and humans.

CSWCT employs 10 members of staff who work on a 10 day rotation schedule. Therefore at any given point there are between three and six staff living and working on the island (see Fig. 5.3). The staff are responsible for all aspects of island life, including: feeding/cleaning/caring for the chimpanzees, looking after visitors and giving public presentations to tourists, cooking and cleaning, and helping the researchers when time permits. Researchers and staff live side-by-side and depend on a strong relationship to perform the daily activities on the island. As Ngamba is not primarily a research station, flexibility is essential. There are often days when, due to the number of visitors, or alternative activities, it is simply not possible to conduct experiments.

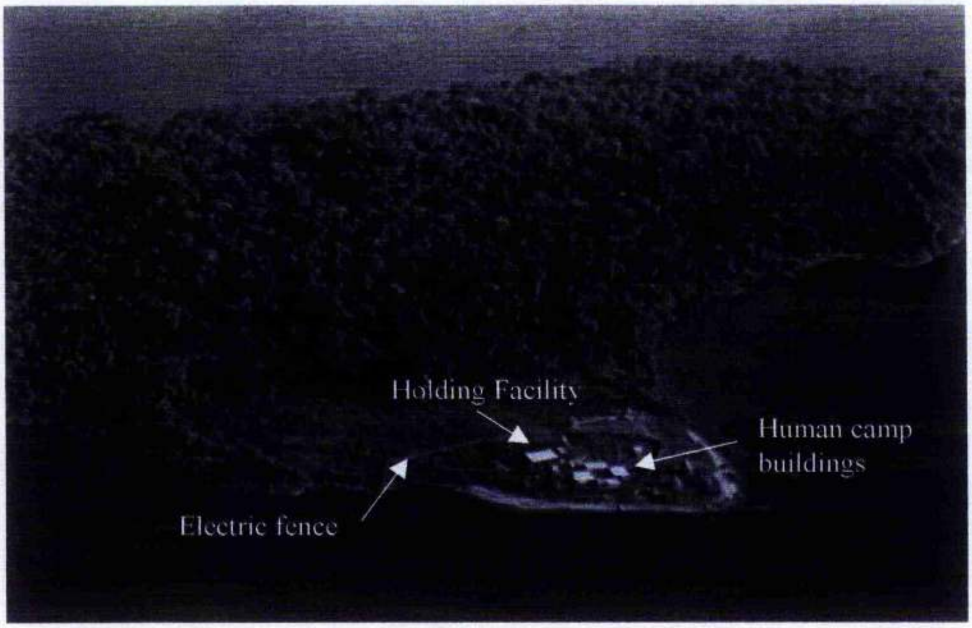


Figure 5.2 Arial photograph of Ngamba Island. The human camp can be seen at the bottom of the photograph.

Figure 5.3 Five members of staff from Ngamba Island. From left to right: Minani Gregoire, Isaac Mujaasi (Education Officer), Stany Nyandwi (Head Keeper), Robert Okello and Francis Lukwiya.

5.2 Participants: Chimpanzees

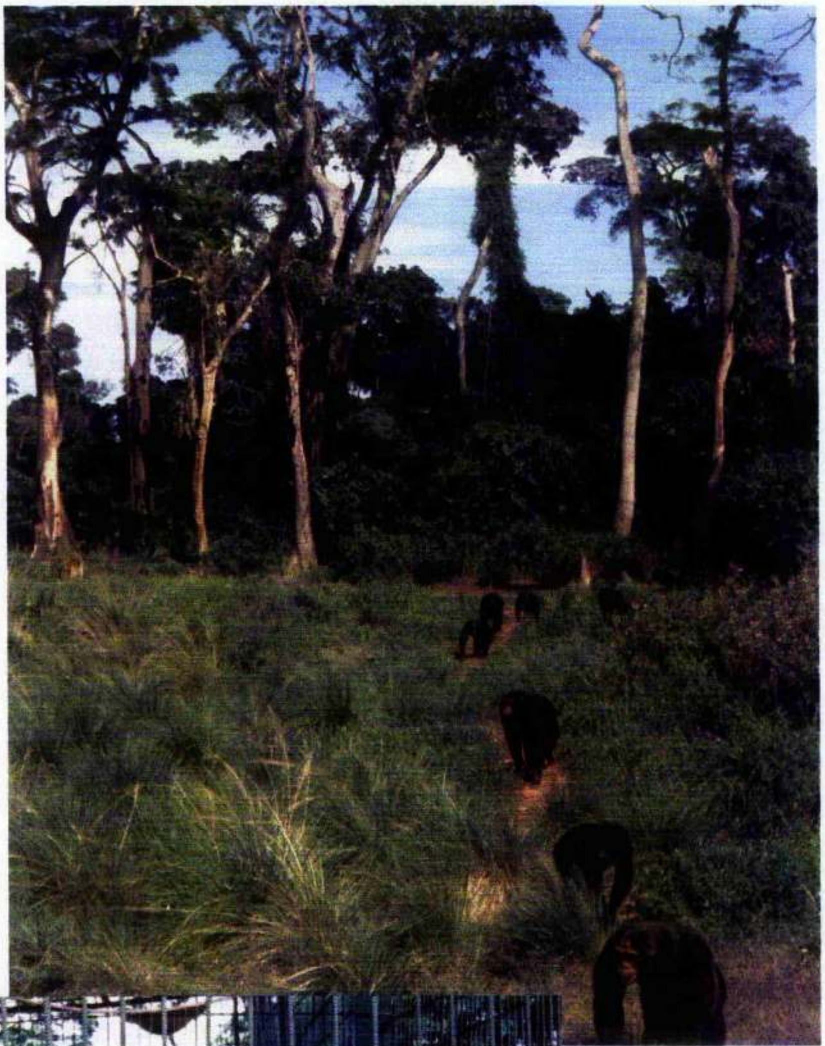
5.2.1 *The chimpanzees of Ngamba Island*

In 1998, CSWCT was founded to move chimpanzees living in overcrowded conditions at Entebbe Zoo (UWEC) to Ngamba Island. These individuals were all rescued by the Uganda Wildlife Authority as orphans of the bush-meat trade and live animal trade from Uganda and surrounding countries, and make up the adult group at the sanctuary. Since this first group was moved to the island, many more orphans have been rescued. Most of the arrivals since 1998 have been young chimpanzees from the Democratic Republic of the Congo, who were confiscated at border towns around Uganda. These individuals are mostly under 8-years-old, and make up the juvenile group at the sanctuary. This group is housed separately from the adults due to prior complications with integration attempts. All the chimpanzees on Ngamba are from the subspecies *Pan troglodytes schweinfurthii*. The age of each individual was estimated upon arrival to the sanctuary on the basis of dental eruption, size, weight and motor co-ordination. Unfortunately little is known about the history of each chimpanzee before they came to Ngamba (see Appendix A).

Before being integrated into the Ngamba community, new arrivals must spend three months in quarantine on the mainland. During this period the chimpanzees are cared for by a human surrogate parent. All 'chimp parents' are trained to use chimpanzee-typical gestures and vocalisations, such as the pant-hoot greeting, food grunts, fear calls, play faces and how to tickle and groom effectively. Great emphasis is placed upon using these behaviours in order to facilitate the young chimpanzee's integration into the sanctuary groups once the quarantine period has been completed.

5.2.2 *The chimpanzees' daily routine*

On the island the adult group spends all day in the forest. Whilst in the forest they are able to play, forage, nest build and perform many of the activities of a wild chimpanzee community. However, the endemic vegetation of the island is not sufficient to support the community, so they are provisioned five times per day with a variety of fruit and vegetables as well as seeds, nuts, eggs and porridge (see Figure 5.4a).



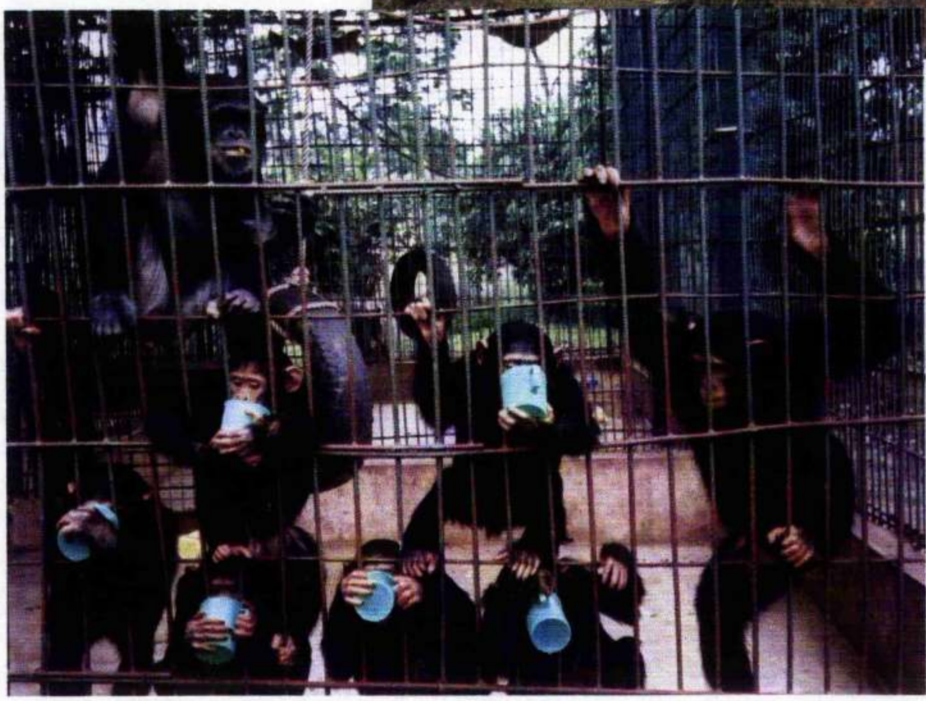


Figure 5.4 (a) Top picture - Members of the adult group spend the majority of each day in the forest. They are provisioned five times each day, and come out of the forest to the electric fence, where staff throw food from a viewing platform that runs across the top of the fence.

(b) Bottom picture - Members of the juvenile group remain in the holding facility while the adults are in the forest. Young chimpanzees receive milk in cups, as well as the usual food items each day.

The juvenile group spends the majority of each day in the holding facility while the adults are in the forest (see Fig. 5.4b). The holding facility consists of six rooms of varying size that are interconnected via a series of raceways and sliding doors (see Fig. 5.5). Chimpanzees enter and leave the holding facility though a tunnel that leads out into the forest. The tunnel entrance is locked each day while the adults are in the forest. Whilst in the holding facility, the juvenile group receives many behavioural enrichment activities in the form of simulated foraging tasks, and novel objects.

Figure 5.5 The holding facility at Ngamba Island. The research room is located at the far left of the picture. The hammocks in which the chimpanzees sleep at night can be seen hanging from the roof.

At night the adult group returns from the forest, and all the chimpanzees sleep in hammocks inside the holding facility (see Fig. 5.5). The chimpanzees choose to return each night, as the facility provides much needed protection from the frequent tropical storms that hit the island. This system enables the juvenile group to have access to the forest before the adults leave the facility in the morning, and after they have returned in the evening. During these trips into the forest the youngsters are often accompanied by adult female chimpanzees, who in many respects take over the role of a surrogate mother. Like the adult group, the young chimpanzees are free to perform many of the natural activities of a wild community.

5.2.3 *The issue of enculturation*

A number of authors have argued that extensive human contact can lead to a fundamental change in an individual's socio-cognitive development through increased exposure to objects with specific functions, increased opportunity to observe human demonstrations, attention focusing through training, and being treated intentionally (Premack, 1983; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993; Call & Tomasello, 1998). General arguments against this view were discussed in section 2.5.4. Nevertheless, it might be suggested that the chimpanzees of Ngamba Island are enculturated, and therefore that the findings of this thesis cannot be generalised to chimpanzees as a whole.

However, the chimpanzees of Ngamba Island experience very few 'human' objects with specific functions. Any objects that are introduced act as a form of enrichment and chimpanzees do not receive demonstrations or training about how the objects should be manipulated. The chimpanzees spend the majority of time in a peer group with daily excursions into the forest with adult female conspecifics, and are rarely one-on-one with humans (with the exception of the three-month quarantine period). However, great care is taken to interact with the chimpanzees using chimpanzee-typical gestures and vocalisations. When in contact with humans, the chimpanzees *are* treated as intentional individuals, but the influence of this interaction is less intense than would be experienced by a home-raised ape. Therefore the chimpanzees of Ngamba cannot be considered as 'enculturated' in the same sense as some studied by other researchers (Tomasello, Savage-Rumbaugh et al., 1993; Bering et al., 2000; Bjorklund et al., 2000; Bjorklund et al., 2002). Instead, the stimulation that is received on Ngamba Island could be viewed as a replacement for the rich social and physical environment that would be experienced in the wild.

The rearing history of the Ngamba chimpanzees, and in particular the juvenile group, can be seen as a mixture of nursery housing, coupled with the daily opportunity to interact with adult conspecifics in a species-typical forest environment. The Ngamba chimpanzees are not enculturated, and therefore the results of this thesis are likely to have implications for chimpanzee cognition in general.

5.3 General methodology: Chimpanzees

All chimpanzee experiments were conducted one-on-one with the chimpanzees, and their success was though to depend upon a strong bond between the subject and the experimenter, as the young chimpanzees would be separated from the rest of the group for each study. This bond was developed during a pilot visit between February and April 2000, and was strengthened with each subsequent research trip. All experiments were carried out in the holding facility. Experiment 1 was carried out in Holding Den 1, but all other experiments were conducted in the Research Room (see Fig. 5.6).

Each chimpanzee was tested individually, and therefore subjects had to be separated from the rest of the group. This was done with the help of the staff in the mornings, once the holding facility had been cleaned. Before testing, subjects waited in a holding room (Holding Den 4) adjacent to the test room (see Fig. 5.6). Subjects could choose on a daily basis whether or not they wished to participate. If they did not want to do the experiments they could refuse to enter the holding room. This occurred on a number of occasions. These individuals were allowed to remain with the rest of the group, and were often happy to co-operate the following day. In fact, the main problem was that so many individuals wished to enter the holding room and participate in the experiments, that it was difficult to isolate the correct chimpanzees each day.

Before each experiment, the apparatus for that particular study was place outside the holding facility for 24 hours, so that the chimpanzees could see, but not touch it. This was done to familiarise the subjects with the apparatus, and reduce the possibility of neophobic responses during testing.

During testing, the apparatus was secured inside the testing room, either by bolting it onto a bench (Experiment 1), or attaching it to the centre of the floor (Experiment 4). For Experiments 2 and 3, the apparatus was located outside the research room, and subjects interacted with it through the bars. In each experiment, the procedure involved a series of demonstrations to each subject followed by a series of trials by the chimpanzee.

All experiments were conducted with the help of a second person. The role of this second experimenter was played by a number of volunteers who were working for CSWCT. Experiment 1 was conducted with the help of Pauline Osbourne from Australia, Experiments 2 and 3 were conducted with the help of Ora McNaught, also from Australia. Experiment 4 was carried out with the help of Amy Clanin, from the USA, and Carla Litchfield who was working as a Research Fellow at the University of St Andrews. In addition, various members of staff stepped in to help whenever they were available.

The first experimenter was responsible for setting up the apparatus, and performing the demonstrations. The second experimenter was required to film all the demonstrations and trials on a hand-held Sony Hi8 video recorder.

5.4 Previous research histories: Chimpanzees

A number of the chimpanzees who took part in this series of studies had prior experience with social learning experiments. Sarah Marshall-Pescini conducted three studies between 1998 and 2000 with the Ngamba chimpanzees (Marshall-Pescini, 2002). The first of these was a tool-use task, designed to mimic the honey-dipping behaviour of wild chimpanzees. The aim of the study was to determine whether the chimpanzees could adopt a more complex, yet more efficient strategy by social learning once they had discovered a simpler less efficient method on their own. The second study was an experimental investigation of nut cracking, and the third study was a non tool-use task which employed a modified 'artificial fruit' to investigate whether chimpanzees could imitate the hierarchical structure of observed actions (Marshall-Pescini, 2002).

The general methodology of these studies was very similar to the experiments in this thesis. However, the tasks themselves and the hypotheses behind them were very different. Through Sarah Marshall-Pescini's work, the chimpanzees learned to tolerate being separated from the rest of the group, and being one-on-one with an experimenter in the research room. They also learned something of the general methodology of observing a demonstration and then being given the opportunity to interact with the same object in front of a camera. Their prior experience likely served to facilitate the chimpanzee's willingness to take part in the present set of studies; however, it did not teach them anything specific about the principles that were tested in this thesis.

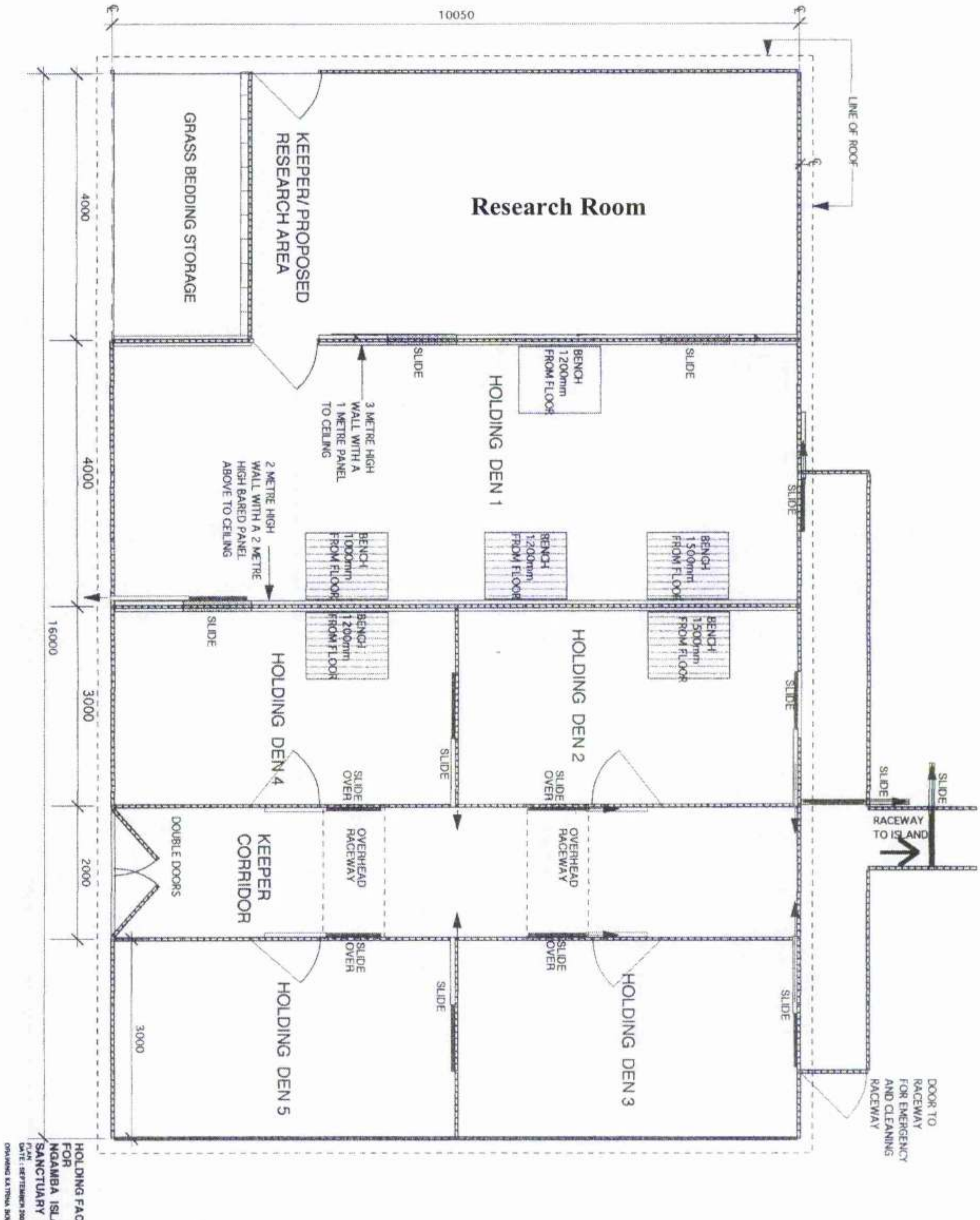


Figure 5.6 Schematic representation of the holding facility.

5.5 Study-site: Children

5.5.1 *Gaining permission to work in schools*

All the experiments with children were conducted at nursery and primary schools in Dundee, and St Andrews, UK. All experiments were conducted once the methodology had been approved by the School of Psychology Ethics Committee. Before the local education authorities could be approached to request permission to work with children, a Criminal Records Check, and a Police Background Check on the researcher had to be performed. Once the local councils had given permission to work in their schools, the head-teachers of individual schools were contacted and arrangements were made for an interview. During the interview, the researcher explained the comparative rational of working with both chimpanzees and children. The teachers were shown the experimental apparatus and photographs of chimpanzees performing the same tasks. Great care was taken to emphasise that the children were being studied as a group, and that their overall behaviour would be compared to the chimpanzees. The purpose of the experiments was not to look at individual differences, or to single out the abilities of particular children. Once the teachers were happy with the details of the study, a letter was sent out to the parents of children in the appropriate age groups, to ask if they would permit their child to participate in the investigation (see Appendix B).

5.6 Participants: Children

The participants for this series of studies were African, Asian and Caucasian children between the ages of 3- and 6-years-old. The children were recruited from schools with broad catchment areas that included many ethnic and demographic groups. For ethical reasons the names of the participants have been omitted from all experiments.

5.7 General methodology

All experiments were conducted one-on-one with individual children in a separate room within each school. The children therefore had to feel comfortable working with the researcher, and hence she spent one week at each school before the studies began in order to play and interacting with the children. Once the experiments started, each child was given the opportunity to choose whether or not they participated in the study on a daily basis. Children who did not wish to participate were not forced to do so, nor were they made to feel pressurised to take part. If a child declined to take part, they would be asked again on the following day. However, if they declined a second time, the child would not be approached again (this did not occur frequently).

Once a child had agreed to participate in a study, they followed the experimenter to a separate room where other children could not watch or hear the procedure. The apparatus for each study was always located on a table, and children were asked to sit on a chair in front of the table to watch the demonstrations. In order to keep the methodology of the chimpanzee and child experiments as comparable as possible, the children were given very little verbal information about each task. If, like the chimpanzees, the children got up and walked around the apparatus, or interacted with it during a demonstration, they were not prevented from doing so, as this was the case for the chimpanzee participants.

All demonstrations and trials were recorded on a Sony Hi8 video camera that was mounted on a tripod within the research room. The camera started recording before each child entered the room, and continued to record throughout the experiment. The children's attention was not drawn to the camera (which was usually hidden behind toys and chairs), and there was no reason to believe that the children knew their behaviour was being recorded. At the end of each experiment, every child was given a reward (usually a small toy), and praised for their performance, irrespective of their level of competence. No child was made to feel that their behaviour was different from that of the other children. The child was then taken back to their classroom where they typically showed their reward proudly to the teachers.

5.8 Data collection and statistical analysis

The experiments in this thesis have been designed to measure the frequencies of particular behaviours under different experimental conditions. For example, the number of times an individual performs behaviour A compared to behaviour B, or the number of times an individual is observed to perform behaviour C in comparison to the expected frequency. Thus, the majority of analysis has been performed using nominal or frequency data which is not normally distributed. Non-parametric statistics have therefore been used because the validity of these calculations is not bound by strict assumptions about the distribution of the data. When comparing different data populations, median values have been reported as a non-parametric measure of the central tendency. For example, the median number of correct responses by each individual in group A, compared to the median number of correct responses by each individual in group B.

When group A and group B contain different individuals (a between subjects design) a Mann-Whitney *U*-test for unmatched samples has been used to determine if the two populations are significantly different. However, if groups A and B contain the same individuals, tested under different conditions (a within subjects design), a Wilcoxon test for matched pairs has been used. These two tests are used most frequently throughout the thesis. However, in addition Chi Squared goodness of fit tests have been used to compare observed and expected behavioural frequencies, as this calculation makes very few assumptions about the normality of the data. Spearman's Rank Correlation Coefficients have been used as a non-parametric method to analyse the strength of relationships between variables. In all cases, unless stated otherwise, the Null Hypothesis has been rejected if the probability that the data have been drawn from the same population is calculated to fall below alpha level 0.05.

SUMMARY OF CHAPTER 6

The literature indicates that chimpanzees use different social learning strategies to solve different types of task (see Chapter 2). Specifically, they tend to employ imitation to solve non tool-use tasks, but use non-imitative or emulative learning to solve tasks that do involve tool-use. However, instead of assuming that the distinction lies in the difference in task domain, it could be that other factors differentiate tool-use and non tool-use tasks. One such factor is the availability of causal information. From the definitions of imitation and emulation that were given in Chapter 2, it follows that the perception of information about causal relationships should be essential for emulation, yet may be less critical for imitation. Therefore the availability of causal information may influence chimpanzees to employ either imitation or emulation to solve the same task.

In Experiment 1, chimpanzees observed a human demonstrate a tool-use task that involved both relevant and irrelevant actions. When the task was presented in a transparent condition, so that causal information about the effect of the tool was available, subjects were able to selectively exclude the irrelevant actions in favour of a more efficient technique, in accord with emulation. However, if the availability of causal information was restricted by presenting the task in an opaque condition, the chimpanzees reproduced a greater proportion of the demonstrated actions, including both relevant and irrelevant parts, in accord with imitation. This effect was not influenced by the order in which the transparent or opaque conditions were presented.

CHAPTER 6

EXPERIMENT 1: IMITATION AND EMULATION SWITCHING IN CHIMPANZEES

6.1 Introduction

The previous chapters indicate that chimpanzees use different social learning mechanisms to solve different types of problem. Specifically, they seem to use imitation to solve problems that do not involve tool-use, and non-imitative or emulative learning to solve tool-use tasks. However, the distinction in learning strategy may not be strictly related to the task domain. It could be that tool-use and non tool-use tasks differ in other central features which relate to the social leaning strategy that chimpanzees employ. One potential feature is the availability of causal information, and this will be discussed in more detail below.

The literature suggests that chimpanzee causal knowledge can best be characterised by an ability to identify observable patterns of regularity in the environment, which can be used to form associations between causes and effects. In comparison, human children appear to have a deeper understanding of causality than chimpanzees, as they actively seek explanations for observed effects, and are able to infer unobservable mediating forces such as gravity. Nevertheless, the ability of chimpanzees to extract patterns of regularity and form associative rules that can be used in different conditions is all that is required to identify many causal features of the world. The causal knowledge of chimpanzees is therefore sufficient to warrant a likely involvement in social learning, and it is therefore possible that causal information plays a part in determining whether chimpanzees use imitation or emulation to solve different types of task.

Emulation can be defined as learning about the results, object movements or affordances of a task, but not about the details of the observed behaviour (see Chapter 2). An individual would therefore be expected to learn to use a tool by observing the effect of the tool in gaining a reward, and seek to reproduce this outcome using their own efficacious actions, such as manipulating the tool with a different hand or arm movement. The critical characteristic of emulation is that the observer learns about the environment rather than the bodily actions of the model (Tomasello, 1998a).

In contrast, imitation can be defined as learning about specific aspects of the bodily actions of the model. The observer would therefore reproduce a recognisable (if not accurate) copy of the original behaviour of the model (Whiten & Ham, 1992). An individual may learn to use a tool by observing the effect of the tool in gaining a reward, and then seek to reproduce the same effect using the same hand or arm movement as the model. Imitation is distinct from emulation in that the behavioural technique of the model is attended to.

Traditionally, imitation has been viewed as the apex of social learning, producing the highest fidelity behavioural and environmental match to the actions of a model (Galef, 1992; Heyes, 1993; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993). However, this does not mean that imitation will always be the *optimal* social learning strategy. Tomasello, et al. noted that 'the most efficient strategy might be to simply observe the relation between the tool and the goal and then experiment with the specifics on one's own.' (1987, p182). Thus, emulation may be more efficient and flexible in certain situations because learning about environmental features, such as results and affordances, might enable an individual to generalise socially learned behaviours to different environmental conditions and problems (Tomasello et al., 1987; Visalberghi & Fragaszy, 1994; Want & Harris, 2001, 2002).

From the definitions above it follows that the perception of information about causal relationships will be essential for emulation, yet may be less critical for imitation (Want & Harris, 2001). During emulation an observer must piece together the causal links within a task in order to achieve the same result using a different behaviour. In contrast, imitation requires only that the observer reproduce the actions of the model with sufficient fidelity to recreate the desired outcome, without having to fully appreciate the causal relationships involved.

Emulation may therefore be the preferred strategy when critical causal relationships are apparent to an observer. In contrast, imitation may be more efficient when such causal relationships are not perceivable or are difficult to infer. Imitation may be employed in non tool-use studies such as the 'artificial fruit' because the causal features of the task may be difficult to interpret. The most appropriate way to manipulate a novel object, or remove the defences of an 'artificial fruit' may therefore be to attend to, and reproduce the actions of the demonstrator, in accord with imitation. Imitation may be used to reproduce manual and facial gestures because there is no environmental component, and therefore there are no causal relationships available to perceive.

In tool-using paradigms, such as the raking study by (Tomasello et al., 1987), the causal relationships that are involved may be more apparent to an observer. Tomasello et al,. found that after watching a conspecific use a rake to draw in out-of-reach food, chimpanzees used the tool more than a control group who observed the conspecific use the tool in a non-functional manner. However, they did not reproduce the actions of the model, only the results of their behaviour (see Chapter 2). Rather than interpret the results of this study as a deficit in imitative learning, it may be that because the chimpanzees could perceive the causal features of the task, they adopted emulation as a more appropriate strategy.

If this interpretation is correct, it would be expected that by varying the availability of causal information, chimpanzees could be influenced to switch between using imitation or emulation to solve the same task. By reducing the availability of causal information it may be possible to influence chimpanzees to selectively include parts of a demonstrated behaviour in accord with imitation. In contrast, by increasing the availability causal information, a subject could be encouraged to selectively exclude parts of a demonstration in order to develop a different or more efficient technique, in accord with emulation.

The following experiment was designed to empirically test whether chimpanzees use different social learning strategies depending on the availability of causal information. Young chimpanzees observed a human demonstrate a tool-use task that contained both relevant and irrelevant actions. It was predicted that when appropriate causal information about the task was available (by presenting the task in a transparent condition), the chimpanzees would be able to use their knowledge of causality to differentiate between the relevant and irrelevant parts of the demonstration. Chimpanzees would therefore selectively exclude the irrelevant actions so as to develop a different and more efficient technique, in accord with emulation.

However, if the task was presented in an opaque condition, so that access to causal information was restricted, it was predicted that the chimpanzees would reproduce a greater proportion of the demonstrated actions, in accord with imitation.

The methodology for this experiment has been built upon a previous, less successful pilot study that was carried out on Ngamba Island between February and April 2000. The details of that study can be found in Appendix C.

6.2 Methods

6.2.1 *Participants*

The participants for this study were 12 members of the juvenile group at Ngamba Island, who ranged in age from 2- to 6-years-old at the time of the investigation (Females: Pasa 2, Mukisa 3, Yoyo 3, Bili 4, Nkumwa 6; Males: Baluku 3, Indi 3, Asega 3, Yiki 3, Umugezi 5, Kalema 6, Umutama 6). The majority of participants arrived at the sanctuary between 1999 and 2000, and hence, despite differences in age, had been at the sanctuary for approximately the same length of time.

6.2.2 *Apparatus*

Two structurally identical $20cm^3$ polycarbonate boxes were used, one clear, the other opaque (see Fig. 6.1). On the top of each box was a square hole 3cm x 3cm, covered by a 'bolt-defence' which could be removed to expose a hole. On the front face of the box was a square hole 2cm x 2cm, connected to a sloping opaque tube housed inside the box. This hole was covered by a door-defence, described in more detail below. A food reward was placed at the bottom of the opaque tube, and could be retrieved by opening the front door, inserting an aluminium tool (22cm x 1cm) into the front hole and pulling out the reward. Actions directed to the top of the box were not necessary to retrieve the reward. Insertion of the tool in the top hole resulted only in hitting a polycarbonate barrier that prevented physical contact between the tool and the food tube. Manipulation of the box could therefore be divided into *irrelevant* actions directed at the top of the box, and *relevant* actions directed at the front.

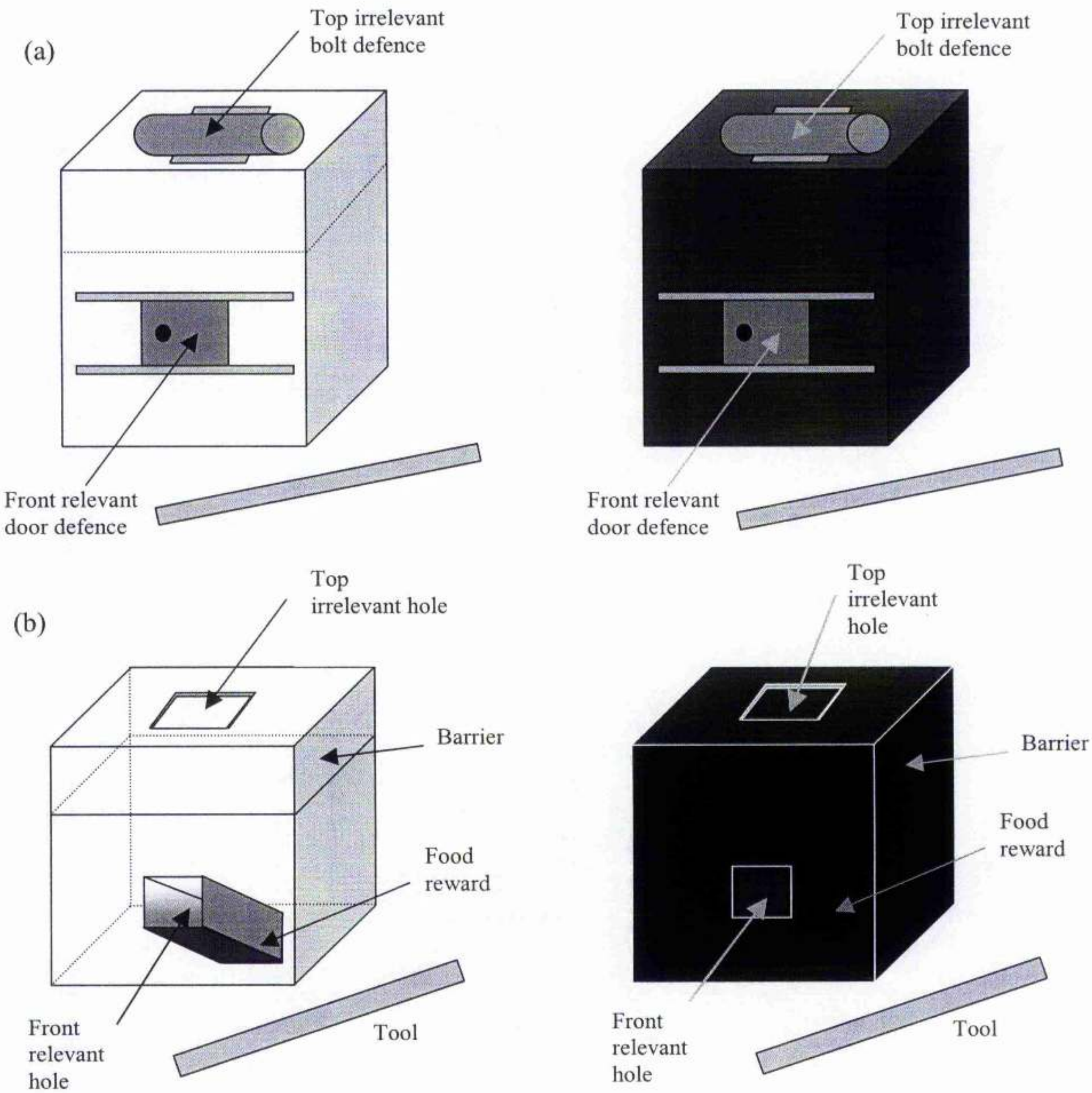


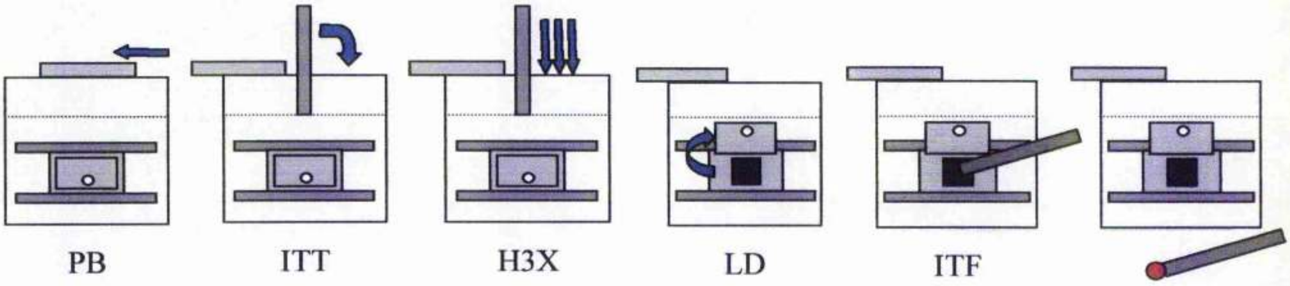
Figure 6.1 (a) External view of the clear and opaque boxes. (b) Cut-away diagram of the clear and opaque boxes. Note that in both cases the food tube housing the reward is opaque so that the location of the reward cannot be directly seen.

6.2.3 *Two-action design*

The apparatus incorporated an additional 'two-action' design to further investigate the importance of imitation (see section 2.4.1). Both the bolt and door defences could be removed in one of two ways. The bolt could either be *pushed* out from the *right*, or *dragged* out from the *left* by inserting the tool into a hole at the end of the bolt to reveal the hole beneath. The door could either be manually *lifted* or *slid* out of the way to reveal the hole beneath. Subjects were shown one of two methods of defence removal; *method 1* – push bolt, lift door, or *method 2* – drag bolt, slide door (see Fig. 6.2). If subjects performed the observed method significantly more than the alternative, this would be a strong indication of imitation (Whiten et al., 1996).

In both methods the direction of bolt movement was the same. To control for stimulus enhancement, before the bolt was removed, it was hit three times on the opposite end from that which would be pushed or dragged (see Fig. 6.3).

(a) ***Method 1*** *- Push bolts / lift door*



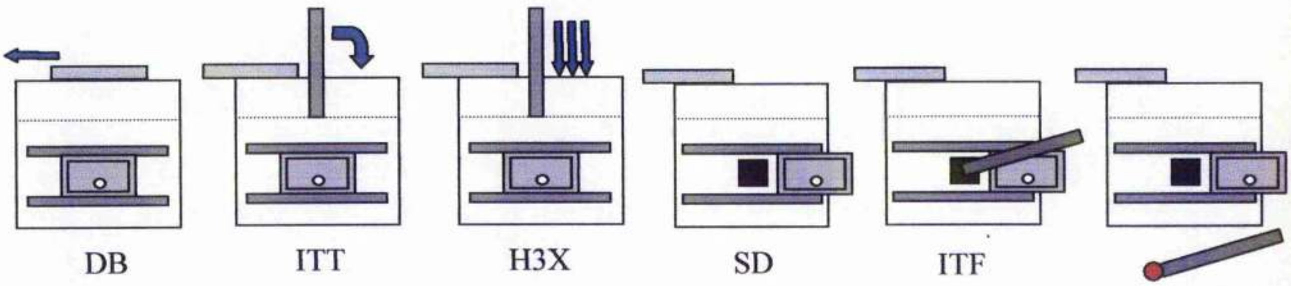
PB - push bolt with tool from right
ITT - insert tool into opened top hole
H3X - move tool up and down to hit bottom 3 times

Irrelevant actions

LD - lift open front door
ITF - insert tool in front hole
\- Retrieve reward

Relevant actions

(b) ***Method 2*** *- Pull bolts/slide door technique*



DB - drag out bolt with tool from left
IT - insert tool into opened top hole
H3X - move tool up and down to hit bottom 3 times

Irrelevant actions

SD - slide open front door
IF - insert tool in front hole
\- Retrieve reward

Relevant actions

Figure 6.2 Schematic representation of the alternative two-action methods of defence removal. (a) *Method 1* and (b) *Method 2*. The bolt can be pulled or dragged to reveal the hole beneath, and the door can be lifted or slid to reveal the food tube behind it. In both cases actions to the top of the apparatus are causally irrelevant.

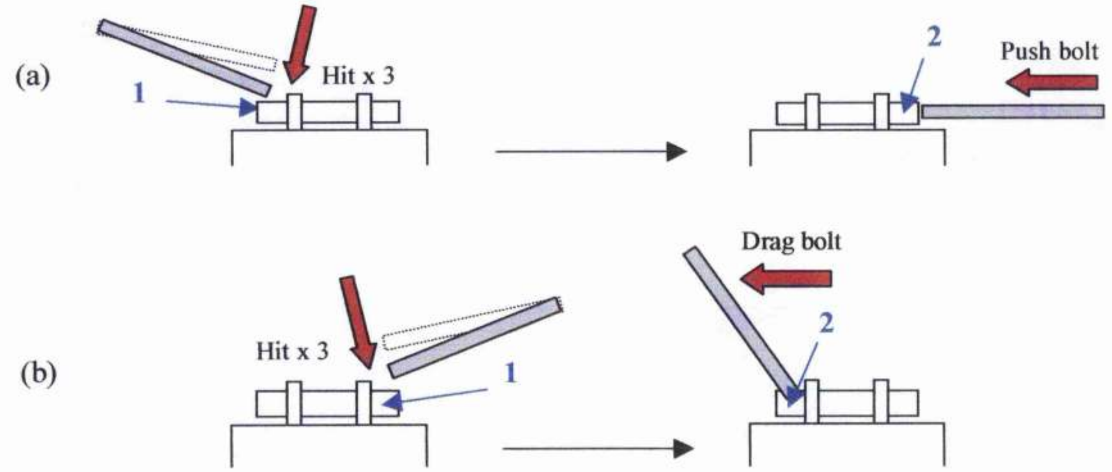


Figure 6.3 Schematic representations of two-action method of bolt removal, designed to control for stimulus enhancement. (a) *Method 1* – Hit bolt on left, push out bolt from right. (b) *Method 2* – Hit bolt on right, drag out bolt from left. The bolt can be removed in either way to reveal the irrelevant hole beneath.

6.2.4 *Procedure*

Subjects observed a human demonstrator use the tool to retrieve a food reward from one of the boxes. The demonstration involved two parts; (i) *irrelevant actions* - removing the top bolt and inserting the tool in the top hole and (ii) *relevant actions* - opening the door and inserting the tool in the front hole to retrieve the reward. As noted above, only the relevant actions to the front were required to retrieve the reward.

The apparatus was presented in two conditions, opaque and clear (see Fig 6.1). In the opaque condition, causal information was unavailable since the surfaces of the box were black so that subjects could not see the location of the food tube, or the effect of the tool within the apparatus. It was predicted that when the causal information was restricted in this way, subjects would selectively include both irrelevant and relevant actions in their own later efforts, consistent with imitation.

In the clear condition, causal information was available, as the effect of the tool inside the box could be viewed. It was therefore possible to perceive that actions in the top of the box had no causal link with the reward. It was predicted that when causal information was available in this way, subjects would be inclined to develop an alternative, more efficient strategy by selectively excluding the irrelevant top actions, consistent with emulation.

In both the opaque and clear conditions the food tube was painted black, so that subjects could not see the location of the reward within the apparatus. In addition, the reward was wrapped in black plastic so that even if a subject opened the front door and looked down the dark tube, they could not see or smell the reward at the bottom.

Subjects were tested individually in Holding Den 1 within the holding facility (see Fig. 5.6). Prior to each trial the experimenter entered the room and played with or groomed the subject for approximately five minutes. Testing began as soon as the subject was judged to be comfortable. The experimenter then moved to the apparatus, which was bolted to a bench inside the room. The chimpanzee typically sat close beside, or on the lap of the experimenter. In this respect the methodology was naturalistic in that the subject observed the demonstration from the same perspective as it was performed, and the proximity of the experimenter and subject was analogous to a mother-infant pair.

Following (Whiten, 1998b), each subject received three consecutive demonstrations before their first trial. They then received a further two demonstrations and two trials:

Demo > Demo > Demo > ***Trial 1*** *> Demo >* ***Trial 2*** *> Demo >* ***Trial 3***

Each trial lasted five minutes, or until the subject retrieved the reward, whichever occurred first. A second experimenter then re-baited the apparatus while the chimpanzee was distracted. To ensure that the subject did not observe the baiting process, they were taken to the other side of the room and engaged in a play or grooming session. After trial 3, subjects were returned to the holding room for 20-30 minutes before the testing was repeated in the alternative condition (opaque or clear; see Fig. 6.4). All demonstrations and trials were recorded by the second experimenter on a hand held Sony Hi8 video camera.

(a)

(b)

Figure 6.4 (a) Subject inserts tool into the top irrelevant hole of the opaque apparatus, (b) Subject inserts tool into front relevant hole of the clear apparatus to retrieve the food reward.

Subjects were divided into four groups (see Table 6.1). Groups A and B received three trials first with the opaque box (O1 – O3) and then three trials with the clear box (C1 – C3), to determine whether different social learning strategies were employed in each condition. However, it is possible that any change in strategy from opaque to clear condition could be due to previous experience with the opaque box. Subjects from groups C and D therefore interacted with the clear apparatus first (C1 - C3), then the opaque apparatus (O1 – O3). In order to investigate the role of imitation further, groups A and C observed *method 1* of the two-action alternatives, and groups B and D observed *method 2*. This can be seen more clearly in Table 6.1.

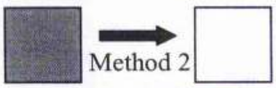
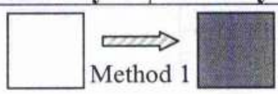
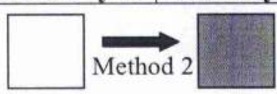
A	 Method 1			
	Mukisa **Female 3yrs**	**Baluku** **Male 3yrs**	**Kalema** **Male 6yrs**	*Mean Age* *4yrs*
B	 Method 2			
	Yoyo **Female 3yrs**	**Indi** **Male 3yrs**	**Umutama** **Male 6yrs**	*Mean Age* *4yrs*
C	 Method 1			
	Bili **Female 4yrs**	**Asega** **Male 3yrs**	**Umugezi** **Male 5yrs**	*Mean Age* *4yrs*
D	 Method 2			
	Pasa **Female 2yrs**	**Yiki** **Male 3yrs**	**Nkumwa** **Female 6yrs**	*Mean Age* *3.67yrs*

Table 6.1 Experimental design for groups A to D. Subjects were matched as far as possible for age and sex. Groups A and B worked with the opaque box first (O1 to O3) and then the clear box (C1 to C3). Groups C and D experienced the reverse order. Groups A and C observed demonstrations of *method 1*, and groups B and D observed demonstrations of *method 2*.

6.2.5 *Coding and data analysis*

The video-taped behaviour of each subject was analysed by recording each occurrence of the following categories, taken from Figure 6.2:

HBT – hit bolt with tool (left end, middle, right end)

HBH – hit bolt with hand (left end, middle, right end)

PB – push bolt from right *(method 1)*

DB – drag bolt from left *(method 2)*

ITT – insert tool in top, 'irrelevant' hole

H – hit Polycarbonate barrier (number of times recorded)

LD – lift door *(method 1)*

SD – slide door *(method 2)*

ITF – insert tool in front, 'relevant' hole

 - retrieve food reward

The proportion of irrelevant actions in each condition was determined by calculating the number of tool insertions into the top irrelevant hole (ITT), as a percentage of total tool insertions (ITT + ITF). This measure was used because tool insertions could be clearly identified and quantified. The percentage of irrelevant tool insertions (ITT) could therefore be compared for each group when tested with the opaque and clear apparatus. The data that were analysed were frequency data, and hence non-parametric statistics have been used. For each chimpanzee, the median percentage of ITT was calculated for the opaque and clear conditions. These median values were then compared both within and between groups using non-parametric statistics. When the behaviour of individuals from different groups was compared (e.g. Group A – clear condition compared to Group C – clear condition) a Mann-Whitney *U*-test for unmatched samples has been used to determine if the two populations are significantly different. However, when the behaviour of individuals from the same group was compared under different conditions (e.g. Group A – opaque condition compared to Group A – clear) a Wilcoxon test for matched pairs has been used. The remaining codes were used to determine each subject's tendency to reproduce the two-action method that they had observed.

6.3 Results

Ten random trials, representing 15 percent of the data, were re-coded by an independent observer, naïve to the hypotheses of the experiment. Inter-observer reliability was high for both the number of irrelevant tool insertions (ITT: Cronbach's Alpha = 0.96) and for the number of relevant tool insertions (ITF: Cronbach's Alpha = 0.99). With the exception of Yiki, Mukisa and Indi, all subjects were successful in retrieving the reward. These three subjects had difficulty retrieving the reward only because they mashed it into the bottom of the tube with the tool, and were not able to lever it out. They were not unsuccessful because they used a different overall technique. Success rate was not analysed, because the purpose of this study was to determine the technique that the subjects used to reach the reward following observation. Medians have been quoted as a non-parametric measure of the central tendency.

6.3.1 *Experimental groups*

There was no significant difference in the number of irrelevant actions (ITT) performed by subjects in groups A and B, who interacted with the opaque box first (median A = 21.25, median B = 35.06; Mann-Whitney *U*-test for unmatched samples, $z = -0.66$, $N_1 = 3$, $N_2 = 3$, $p = 0.7$, two-tailed). Similarly, there was no significant difference in the production of irrelevant actions (ITF) by subjects from groups C and D, who interacted firstly with the clear box (median C = 0, median D = 15.48; Mann-Whitney *U*-test for unmatched samples, $z = -0.69$, $N_1 = 3$, $N_2 = 3$, $p = 0.7$, two-tailed). Two collapsed groups, A/B (opaque > clear) and C/D (clear > opaque) have therefore been used for the following analysis.

6.3.2 *Reproduction of relevant and irrelevant actions*

Subjects from group A/B inserted the tool into the top irrelevant hole significantly more with the opaque apparatus than with the clear apparatus (median A/B opaque = 59.05, median A/B clear = 6.25; Wilcoxon test for matched pairs, $z = -2.20$, N-ties = 6, $p = 0.03$, two-tailed; see Fig. 6.5). Subjects from group C/D, who were presented with the clear box first, did not perform significantly differently from group A/B with the clear box (median A/B clear = 6.25, median C/D clear = 0; Mann-Whitney *U*-test for unmatched samples, $z = -0.36$, $N_1 = 6$, $N_2 = 6$, $p = 0.72$, two-tailed). However, there was a significant difference in the performance of group A/B with the opaque box when compared to group C/D with the clear box (median A/B opaque = 59.05, median C/D clear = 0; z = -2.61, N_1 = 6, N_2 = 6, p = 0.01, two-tailed). This suggests that the change in behaviour of group A/B from the opaque to the clear apparatus was not the result of previous experience with the opaque box. Therefore subjects from group A/B showed a tendency to ignore the irrelevant actions significantly more with the clear apparatus (see Fig. 6.5).

When subjects from group C/D then transferred from the clear box to the opaque box, although there was a slight increase in the reproduction of irrelevant actions, this was not significant (median C/D clear = 0, median C/D opaque = 8.34; Wilcoxon test for matched pairs, z = -1.60, N-ties = 3, p = 0.11, two-tailed). The data suggest that subjects generally continued to ignore the irrelevant top actions with the opaque box, indicating that they were able to generalise their previous causal knowledge about the apparatus to the new experimental condition (compare A/B and C/D in Fig. 6.5).

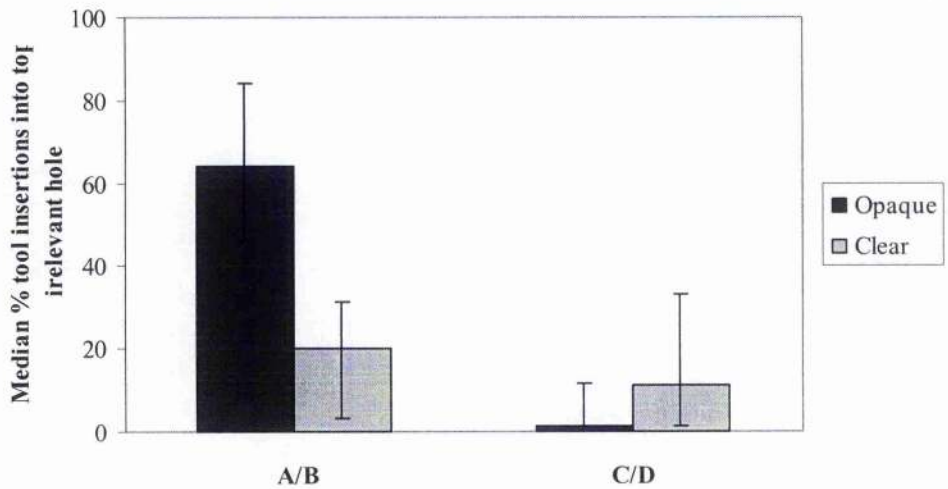


Figure 6.5 The median percentage of tool insertions into the top, irrelevant hole by subjects from groups A/B and C/D in both the opaque and clear conditions. Error bars represent the inter-quartile range.

6.3.3 *Reproduction of two-action method of door removal*

Subjects from groups A and C (A/C) who observed *method 1* to remove the door defence (lift door), employed this technique significantly more than subjects from groups B and D (B/D) who observed *method 2* – slide door (median percentage lift door A/C = 96.36, median B/D = 33.33; Mann-Whitney *U*-test for unmatched samples, $z = -2.01$, $N_1 = 6$, $N_2 = 6$, $p = 0.04$, two-tailed; see Fig. 6.6). This effect was confirmed by an independent coder who was able to correctly identify the method of door removal observed by six randomly selected subjects (6/6, two-choice binomial, $p = 0.03$). Similarly, subjects from group B/D, who observed *method 2* (slide door), employed this technique significantly more then subjects in group A/C who observed *method 1* - lift door (median percentage slide door B/D = 61.34, median A/C = 8.74; Mann-Whitney *U*-test for unmatched samples, $z = -2.01$, $N_1 = 6$, $N_2 = 6$, $p = 0.04$, two-tailed).

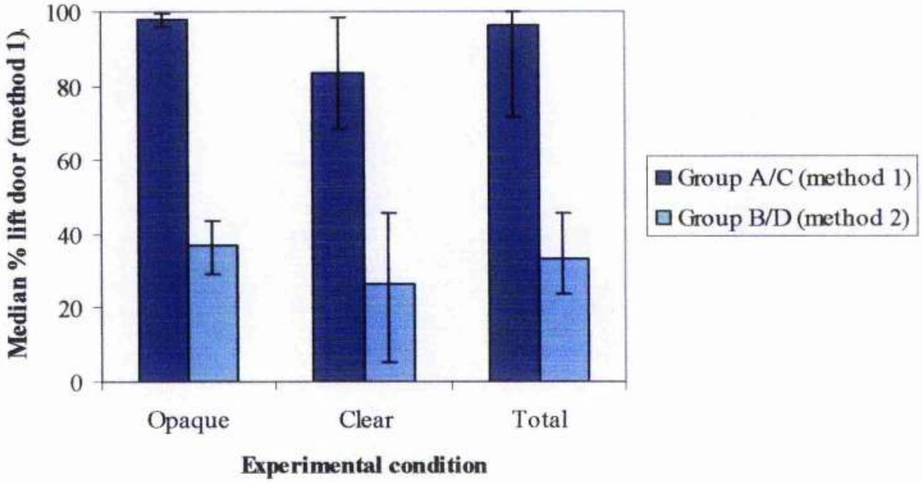


Figure 6.6 Median percentage of lift door (*method 1*) used by group A/C who saw *method 1*, and group B/D who saw *method 2*. Error bars represent the inter-quartile range.

In order to assess whether the order of presentation of the opaque and clear boxes affected subjects' tendency to reproduce the demonstrated method of door removal, a mean percentage of 'correct' door removal was calculated for each group. For group A/C 'correct' door removal was *method 1* (lift door), and for group B/D 'correct' door removal was *method 2* (slide door). It was found that the order of presentation had no significant effect on subjects' tendency to reproduce the demonstrated actions. There was no significant difference in the performance of subjects from group A/B who were presented with the opaque box first, and group C/D who used the opaque box last (median A/B = 98.05, median C/D = 83.36; Mann-Whitney *U*-test for unmatched samples, $z = -0.08$, $N_1 = 6$, $N_2 = 6$, $p = 0.94$, two-tailed). Similarly, there was no significant difference in the performance of group A/B who used the clear box last, and group C/D who used the clear box first (median A/B = 63.42, median C/D = 73.35; Mann-Whitney *U*-test for unmatched samples, $z = -0.65$, $N_1 = 6$, $N_2 = 6$, $p = 0.59$, two-tailed).

6.3.4 *Reproduction of two-action method of bolt removal*

The results for bolt removal are not so clear. All subjects performed a large number of actions to the bolt using both the tool and their hands. However, the majority of subjects discovered that the tool could be inserted into the top irrelevant hole through a small gap behind the bolt, and it was therefore not necessary to remove the bolt in order to insert the tool. Nevertheless, five subjects were observed to remove the bolt defence, four from group A/C and one from group B/D. However, they did not consistently use the observed method, and unfortunately there were insufficient data to perform statistical analysis. Although only five subjects successfully removed the bolt, it is possible that the other subjects were influenced by the demonstration, but did not, or could not completely remove the defense. However, detailed analysis revealed that subjects performed actions to the middle area of the bolt, which was not part of the demonstrated method, as often as they performed actions to either end ($x^2 = 0.63$, $df = 2$, $p = 0.73$). In addition, there was no significant difference in the order in which each part of the bolt was contacted ($x^2 = 0.09$, $df = 2$, $p = 0.96$). The large number of actions to the middle of the bolt suggests that these actions were exploratory, and subjects were not influenced by the two-action demonstration that had been observed.

6.4 Discussion of Experiment 1

6.4.1 *Reproduction of irrelevant actions*

Subjects from group A/B, who interacted first with the opaque box, performed significantly more irrelevant actions in the opaque condition than in the clear condition (see Fig. 6.5). In each condition both the structure of the apparatus and the observed demonstrations were identical. The only difference between the two conditions was whether the box was clear or opaque, and hence the availability of causal information.

Non-social learning cannot explain the results. The food tube in which the reward was located and the reward itself were opaque in both conditions, so subjects could not see the food directly, and hence food targeting cannot explain why subjects only reproduced relevant actions in the clear condition. Therefore, information about the location of the reward must have been gained by observation of the demonstrator's behaviour. Additionally, subjects' tendencies to include or exclude the irrelevant actions were present from trial 1. In each case there was no opportunity before the first trial to discover the causal features of the task by individual learning, and therefore the selective inclusion or exclusion of parts of the demonstration must be due to information that was gained by observation.

It is difficult to explain the selective inclusion of non-functional, irrelevant actions in the opaque condition by any means other than imitation. Alternative forms of social learning specify that the observer attempts to recreate the outcome or the demonstrator's actions using a lower fidelity strategy. The only outcome produced by the irrelevant actions was hitting the concealed barrier, which did not in itself result in a salient reward (i.e. the food reward). If subjects were attempting to reproduce this outcome for its own sake, they would be expected to continue to do so in the clear condition. However, the reproduction of irrelevant actions decreased significantly in the clear condition (see below). Moreover, subjects showed a significant tendency to use the observed two-action method of door removal, indicating that imitation was employed at this detailed level. The behaviour of subjects from group A/B in the opaque condition, where causal information was unavailable is therefore most consistent with imitative learning.

When the same subjects transferred to the clear box, there was a significant drop in the reproduction of irrelevant actions. This change in behaviour was not the result of prior exposure to the apparatus, as group C/D, who interacted first with the clear box, performed in a similar way (see Fig. 6.5). Again, the only difference between the two conditions was the availability of causal information. It is therefore likely that when exposed to the clear box, both groups A/B and C/D were able to utilise the available causal information to differentiate the irrelevant parts of the demonstration, and selectively exclude these actions in favour of a more efficient technique. This finding corroborates the results of Nagell, Olguin & Tomasello (1993), who found that chimpanzees used emulation to solve a tool-use task insofar as they ignored the irrelevant parts of a demonstration in favour of a more efficient technique. In their study, chimpanzees observed a human demonstrator use a rake to retrieve a desirable, but out of reach object. Chimpanzees who observed the demonstrator retrieve the reward performed significantly better than a control group who did not receive a demonstration. However, the chimpanzees did not always use the same technique as the demonstrator. They learned to flip the rake onto its flat edge rather than using the widely spaced teeth, increasing the efficiency of the tool. It seemed that "the chimpanzees were paying attention to the general functional relations in the task and to the results obtained by the demonstrator but not to the actual methods of tool use demonstrated" page 174. In the same sense, the performance of subjects in the present study from group A/B and C/D in the clear condition (where causal information was available), is most consistent with emulation, insofar as the chimpanzees ignored the actions of the demonstrator in favour of a more efficient technique.

When subjects from group C/D were then presented with the opaque box, they continued to selectively exclude the irrelevant actions, although the opportunity to monitor the causal role of the tool had been removed. This suggests that the chimpanzees may have been able to generalise the knowledge gained through previous experience to the new opaque condition.

6.4.2 *Two-action design*

The chimpanzees showed a significant tendency to use the observed two-action method of door defence removal (see Fig. 6.6). Since the method used to remove each defence was arbitrary, reproduction of the observed technique is viewed as an indicator of imitation (Whiten et al., 1996). Only five subjects successfully removed the bolt, but did not consistently use the observed two-action method. The majority of subjects discovered that it was possible to insert the tool into the top hole through a small space behind the bolt, rendering the removal of the bolt redundant. It is therefore not surprising that subjects did not consistently attend to this feature of the demonstration. Indeed, this observation provides additional evidence that subjects were sensitive to the causal relevance of the actions they observed. These conclusions are discussed in more detail in Chapter 10.

SUMMARY OF CHAPTER 7

The results of Experiment 1 suggest that chimpanzees were able to selectively ignore the irrelevant actions when the apparatus was presented in the clear condition, because they saw and understood that the tool did not make contact with the reward. However, Experiment 1 did not directly demonstrate this understanding. Experiment 2 was designed to test the chimpanzee's knowledge of the importance of contact between a tool and a reward when tested in a different context.

The same 12 chimpanzees who participated in Experiment 1 were presented with a pair of rakes that could be pulled in to potentially retrieve a food reward. However, only one of the rakes was in contact with the reward, or was in such a position so that if the rake were pulled, it would make contact with reward and drag it in. The other rake was not in contact with the reward, or was in such a position that even if the rake were pulled, it would not make contact with the reward, and therefore could not be used to retrieve it.

The chimpanzees were able to select the correct rake in each of ten pairs, significantly more often than would be expected by chance. There was no evidence of a learning effect, nor was the age of the subjects related to their performance. The chimpanzees may have performed so well because they came to the experiment with prior knowledge about contact that they had gained through previous experience with tools. Nevertheless, appreciating that a tool must make contact with a reward in order to bring about an effect, is all that is required to differentiate the causally relevant and irrelevant features of Experiment 1.

CHAPTER 7

EXPERIMENT 2: KNOWLEDGE OF TOOL-REWARD CONTACT IN CHIMPANZEES

7.1 Introduction

One hypothesis that may explain the results of Experiment 1 is that the chimpanzees ignored the irrelevant actions in the clear condition because they saw, and understood that the tool could not make physical contact with the reward. However, Experiment 1 did not directly show that such an appreciation existed. The following experiment was designed to determine whether there was evidence that subjects showed causal knowledge of the significance of tool-reward contact, tested in a different context.

7.2 Methods

7.2.1 *Subjects*

Subjects were the same 12 chimpanzees who participated in the previous experiment. This experiment was conducted one week following the completion of Experiment 1.

7.2.2 *Apparatus*

The apparatus consisted of two identical rakes with wooden handles and metal raking-heads. Both rakes were 98cm in length with a raking-head width of 25cm (see Fig. 7.1).

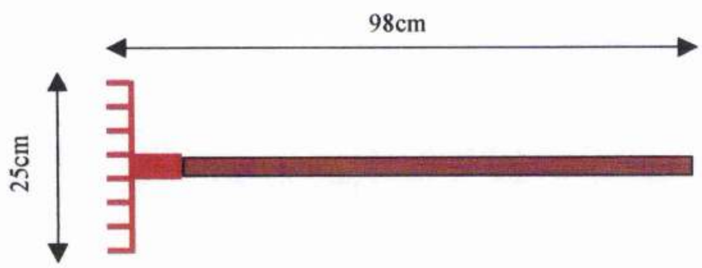


Figure 7.1 Raking apparatus used in Experiment 2. Two identical rakes were presented simultaneously to subjects.

7.2.3 *Procedure*

The rakes were placed on the ground, one metre from the holding facility for 24 hours prior to the start of the experiment. This allowed subjects to view the apparatus and reduce potential neophobic responses. During testing, the rakes were placed outside the research room (see Fig. 5.6) with the handle protruding 10cm through the bars into the room, so that subjects could pull the rakes toward them. The metal raking heads were sufficiently heavy that the rakes could not be freely manipulated or easily lifted off the ground, encouraging the chimpanzees to only pull the rakes towards them. One rake was in physical contact with a food reward, or in a configuration that would make contact with the reward if the rake were pulled. The other rake did not make contact with the reward, or was positioned so that if pulled, the raking-head would not contact the reward. Hence, in each trial there was only one correct choice of rake. The ability of subjects to select the correct rake was therefore dependent on recognition that the tool must make physical contact with the reward in order to have a salient effect. Each subject received ten trials, presented in one session, each with a different choice of rake/reward configuration (see Fig. 7.2). In every trial the position of the food reward, and side of correct choice was randomised. The food reward was always placed on the inside of the rake handle, as it would have been hidden from the subject's line of sight if placed on the outside of the rake.

7.2.4 *Data collection and statistical analysis*

Data were collected concerning the first tool choice by subjects for each trial. Subjects were allowed to select one rake and pull it towards them. If the correct rake was selected first, the subject was allowed to pull it in and retrieve the reward. If the wrong rake was selected first, the subject was allowed to pull it in and fail. In both conditions, once one rake had been pulled, both rakes were removed and the trial was terminated. During each trial an experimenter was present in the research room with the subject. Trials began once the subject was comfortable, usually after a period of approximately five minutes of grooming and playing. During each trial the experimenter sat behind the subject exactly between the two rakes (see Fig. 7.3). A second experimenter, outside the research room was responsible for setting up the apparatus for each new trial. All trials were recorded on a Sony Hi8 video camera mounted on a tripod outside the room (see Figure 7.4).

The data were analysed by comparing the number of correct tool choices that each subject made, to the number of correct choices that an individual would be expected to make by chance. A Chi Squared Goodness-of-fit test was used for this calculation because it does not make restrictive assumptions about the normality of the data.

In order to determine whether the chimpanzees showed evidence of a learning effect, a Spearman's Rank Correlation Coefficient was used to determine whether there was a significant relationship between the number of correct responses and the trial number. This non-parametric test was used because frequency data does not have a normal distribution pattern.

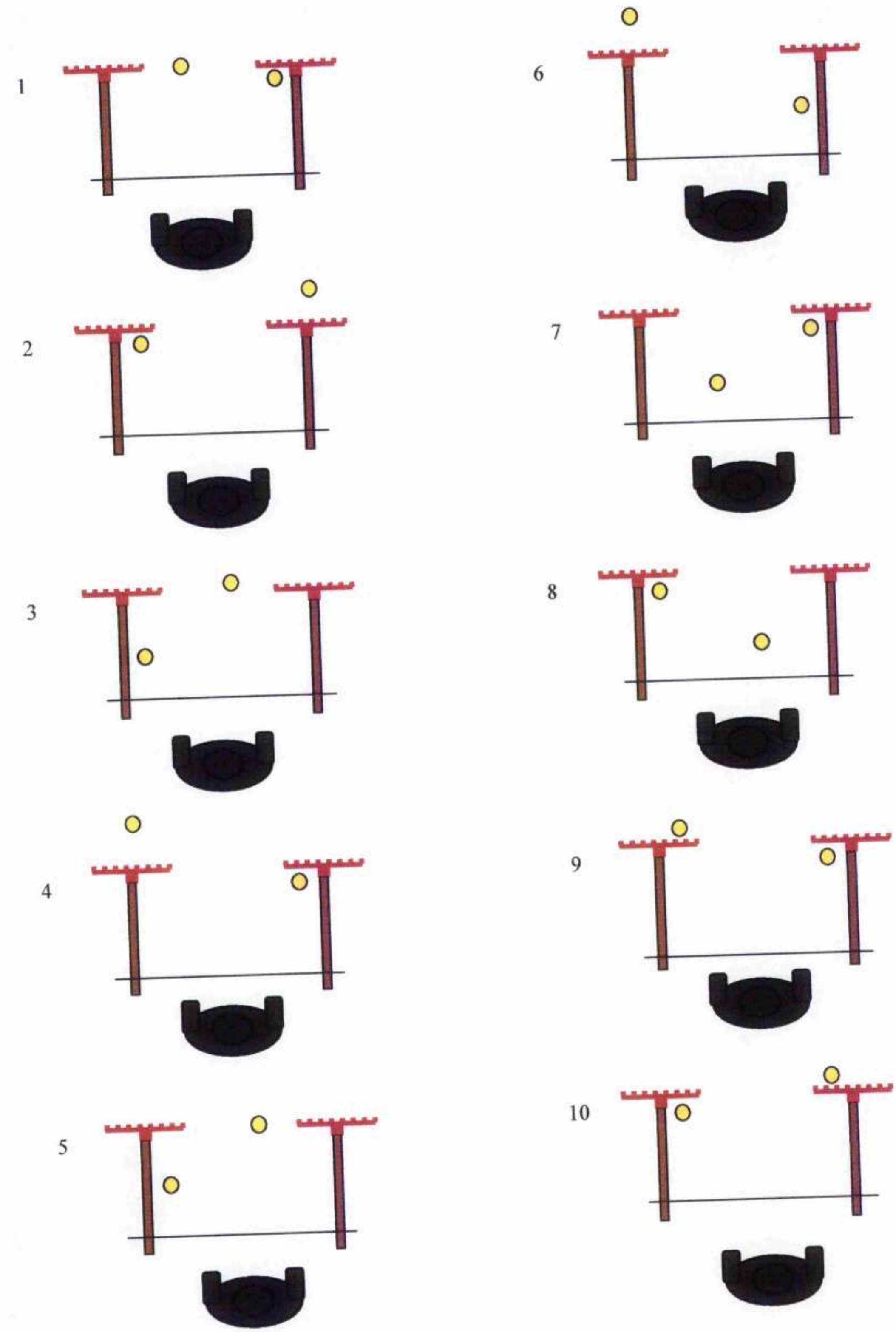


Figure 7.2 Schematic diagram of tool/reward choices presented in Experiment 2 (viewed from above). The fist experimenter sits behind the subject, exactly between the two rakes.

Figure 7.3 Subject selects the correct tool to retrieve the food reward.

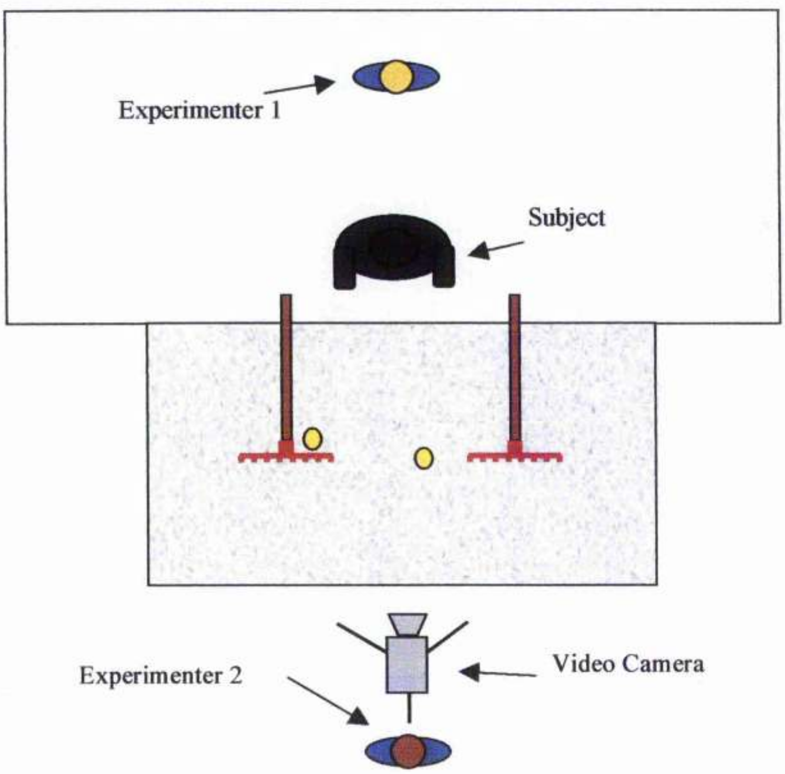


Figure 7.4 Experimental set-up for Experiment 2. The fist experimenter was present in the research room with the subject. A second experimenter outside the room was responsible for video recording, and setting up the apparatus between trails.

7.3 Results

The correct tool was chosen significantly more than would be expected by chance (median percentage correct = 80, median chance = 50; Wilcoxon test for matched pairs, z = -2.82, N-ties = 10, p = 0.01, two-tailed; see Fig. 7.5). Two subjects had a perfect score, and three subjects only made one error throughout the 10 trials.

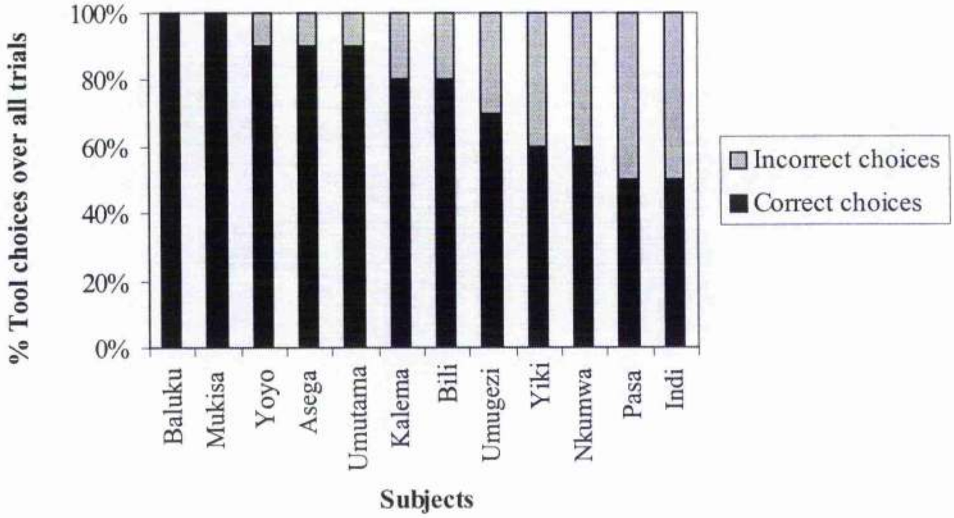


Figure 7.5 Mean percentage of correct and incorrect tool choices made by subjects for trials 1 to 10.

There was no evidence of a learning effect across the 10 trials. In fact, statistical analysis revealed that the chimpanzees found the last three trials more difficult that the rest (Spearmans *rho* = -0.78, N = 10, p = 0.008; see Fig. 7.6). There was also no discernible relationship between the age of subjects and their performance (see Fig. 7.5).

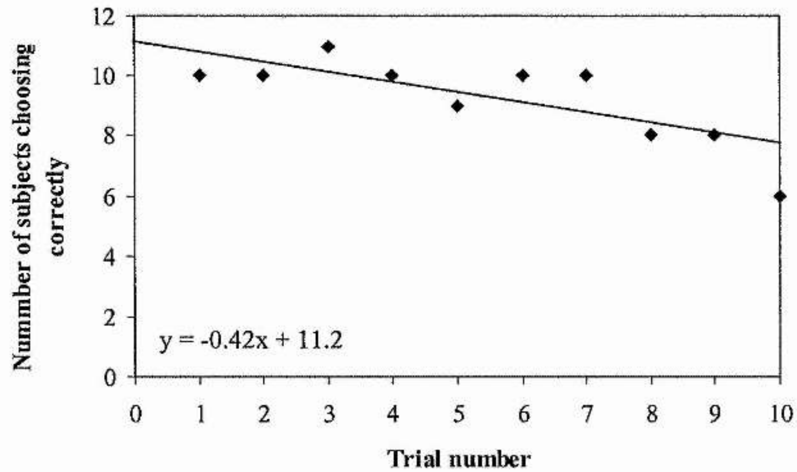


Figure 7.6 Number of chimpanzees who chose the correct rake on each of the 10 trials. The line represents the line of 'best fit'.

7.4 Discussion of Experiment 2

The primary purpose of this experiment was to determine whether chimpanzees recognised that a tool must contact an object before it can effect it. The results indicate that as a group, the chimpanzees could select the tool that was in contact, or had the potential to make contact with the reward, significantly more than the incorrect alternative. Two subjects chose correctly on every trial and three subjects made only one error. The results are consistent with Povinelli (2000) and Köhler (1927), who reported that although chimpanzees found it difficult to discriminate between physically connected objects and objects that were simply touching, they could correctly select tools that were in contact, or had the potential to make contact with a reward. The chimpanzees in the present study may have come to the experiment with prior knowledge about tool/reward contact gained from previous experience, and were able to adapt this knowledge to the new situation. Nevertheless, appreciating that a tool must make contact with a reward in a causally relevant way, is all that is required to differentiate the relevant and irrelevant features of Experiment 1. It seems likely that the ability of subjects in Experiment 1 to determine by observation that actions to the top of the clear box were irrelevant, was based on recognition that if the tool did not contact the reward, it could not bring about a salient effect. These conclusions are discussed in more detail in Chapter 10.

SUMMARY OF CHAPTER 8

In Experiment 1, actions to the top of the box were causally irrelevant because a clear plastic barrier prevented the tool from making contact with the reward. Experiment 2 indicated that the chimpanzees understood the importance of tool/reward contact, but did not show that they understood that contact was prevented by the barrier. Experiment 3 was designed to test the chimpanzees understanding of barriers in a different context.

The same chimpanzees who participated in the previous experiments were presented with a choice of eight pairs of boxes that contained a food reward. One of the boxes in each pair had a barrier across the front of the box so that access to the reward was prevented. The other box had an open front so that the reward could be retrieved with a tool.

Subjects were able to select the correct box significantly more often that the incorrect alternative. There was no evidence of a learning effect, and the age of the subjects did not influence their performance. Like Experiment 2, the chimpanzees may have had prior knowledge about the properties of barriers.

The combined results of Experiments 2 and 3 indicate that in Experiment 1, the chimpanzees were able to ignore the irrelevant actions because they recognised that the tool must make contact with the reward, and that contact was prevented by the clear barrier.

CHAPTER 8

EXPERIMENT 3: KNOWLEDGE OF BARRIERS IN CHIMPANZEES

8.1 Introduction

In Experiment 1, a clear polycarbonate barrier prevented contact between the tool and the reward. Experiment 2 indicates that subjects had knowledge about the necessity of tool-reward contact. The following experiment was designed to determine whether subjects recognised that clear barriers would prevent contact between a tool and reward.

8.2 Methods

8.2.1 *Subjects*

Subjects were the same 12 chimpanzees who participated in the previous experiments. This experiment was conducted one week after Experiment 2.

8.2.2 *Apparatus*

Two identical boxes were used to test subjects understanding of barriers. Each box was composed of a welded steel frame with transparent Perspex panels on three of the four sides. The panels were scratched slightly so that they were visible, and a rake was placed in front of each box. The rakes were the same rakes as in Experiment 2, however, the handle and metal rake-head were shortened to make the tools lighter and easier to manipulate (see Fig. 8.1).

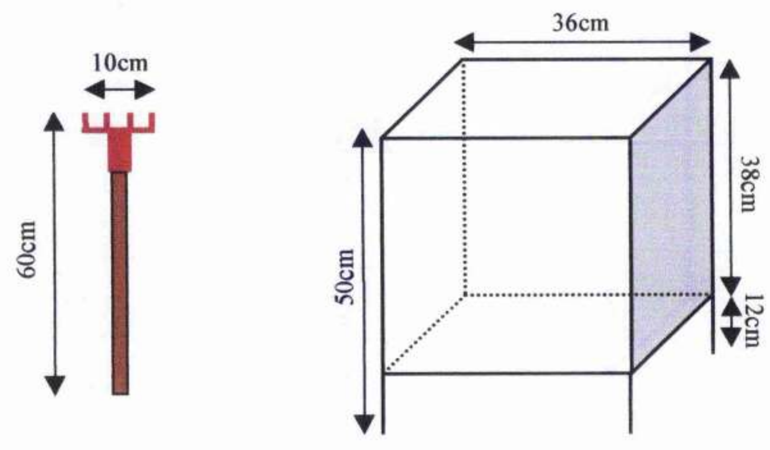


Figure 8.1 Experimental apparatus used in Experiment 3. Subjects were presented simultaneously with two identical boxes and rakes.

8.2.3 *Procedure*

The apparatus was left outside the holding facility for a period of 24 hours prior to the start of the experiment, to allow subjects to become familiar with the apparatus, and reduce the potential for neophobic responses. The procedure for this experiment was very similar to Experiment 2, in that subjects were presented with a choice of two configurations, only one of which could yield a reward. In this case, both boxes contained a visible piece of banana, but in one box access to the reward was prevented by a Perspex barrier. Subjects therefore had to select the rake in front of the correct box to retrieve the reward. Subjects were presented with 8 pairs of choices in one session. In some trials, one box was positioned with an open front and the other with a Perspex front, so that only one box could yield a reward. In other trials, both boxes had Perspex barriers, but one box had food located outside. The position of the reward relative to the box was randomised (see Fig. 8.2). Subjects were tested individually within the research room (see Fig. 5.6).

8.2.4 Data collection and statistical analysis

Data were collected concerning the first tool choice by each subject for every trial. If the correct rake was selected first, the subject was allowed to use it to retrieve the reward (see Fig. 8.3). If the wrong rake was selected first, the subject was allowed to use it to hit the barrier and fail. Both rakes were then removed and the trial was terminated.

In some cases, the younger subjects found that the smaller rakes were still too heavy to pick them up and manipulate inside the boxes. These individuals often indicated a choice by attempting but failing to use the correct rake. Subjects were not penalised for a lack of physical strength, and were rewarded for indicating the correct box, as this demonstrated an ability to discriminate whether the reward was accessible or not. An experimenter was present in the research room with each subject, and set behind the subject between the two boxes during every trial. A second experimenter was outside the room and was responsible for removing the rakes and setting up the apparatus between trials. Each trial was recorded on a Sony Hi8 video camera situated outside the room.

The data were analysed by comparing the number of correct tool choices that each subject made, to the number of correct choices that an individual would be expected to make by chance. A Chi Squared Goodness-of-fit test was used for this calculation because it does not make restrictive assumptions about the normality of the data.

In order to determine whether the chimpanzees showed evidence of a learning effect, a Spearman's Rank Correlation Coefficient was used to determine whether there was a significant relationship between the number of correct responses and the trial number. This non-parametric test was used because frequency data does not have a normal distribution pattern.

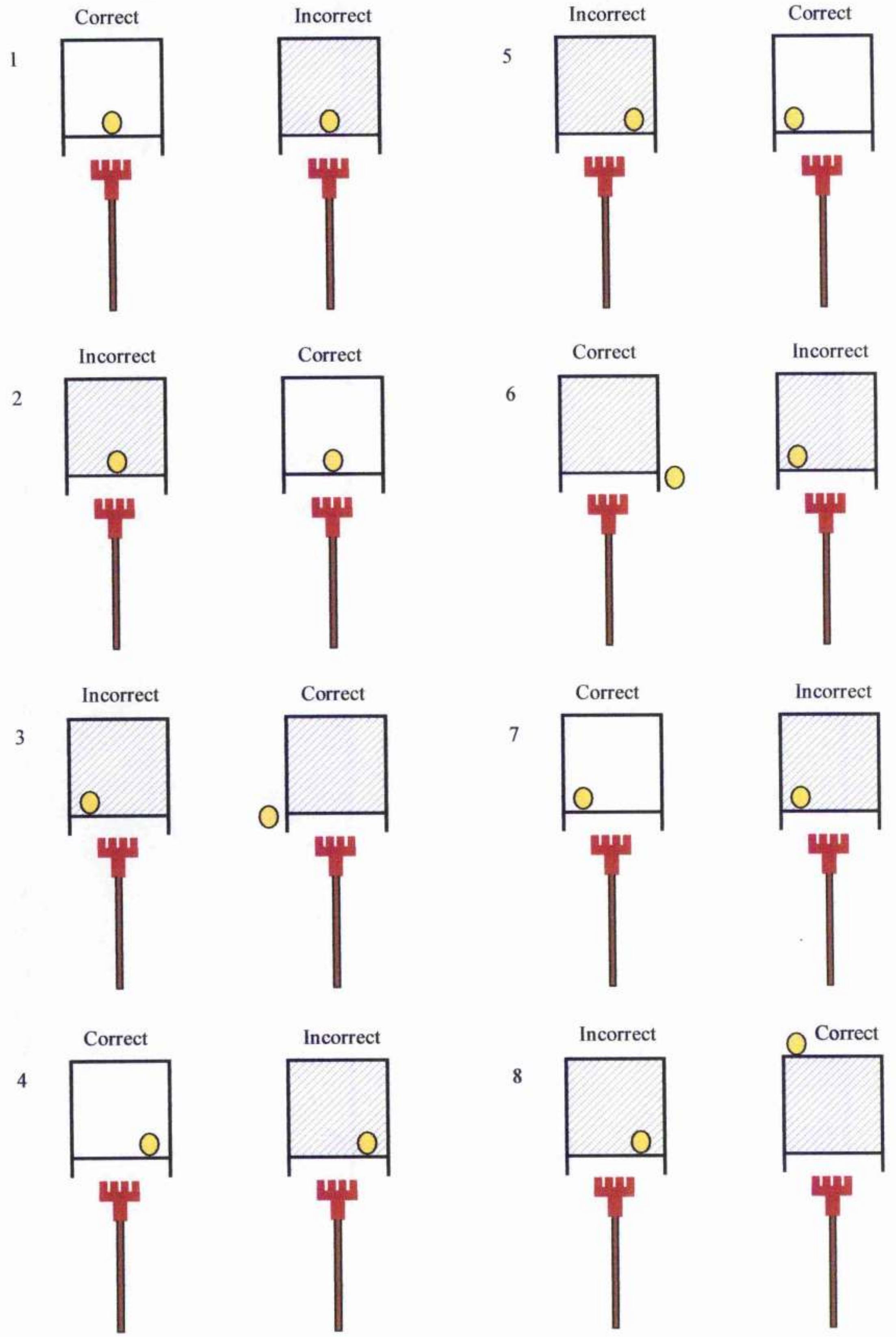


Figure 8.2 Schematic representation of tool/reward choices viewed from subjects' perspective in Experiment 3. The shaded boxes indicate conditions were a Perspex barrier prevented contact between the tool and the reward.

Figure 8.3 Subject chooses the correct rake, and retrieve food reward from one of the experimental boxes.

8.3 Results

Subjects chose the correct tool significantly more than would be expected by chance (median percentage correct = 75, median chance = 50; Wilcoxon test for matched pairs, $z = -2.97$, N-ties = 11, $p < 0.01$, two-tailed; see Fig. 8.4). Three subjects chose the correct box on every trial, with only three subjects choosing incorrectly on more than two trials.

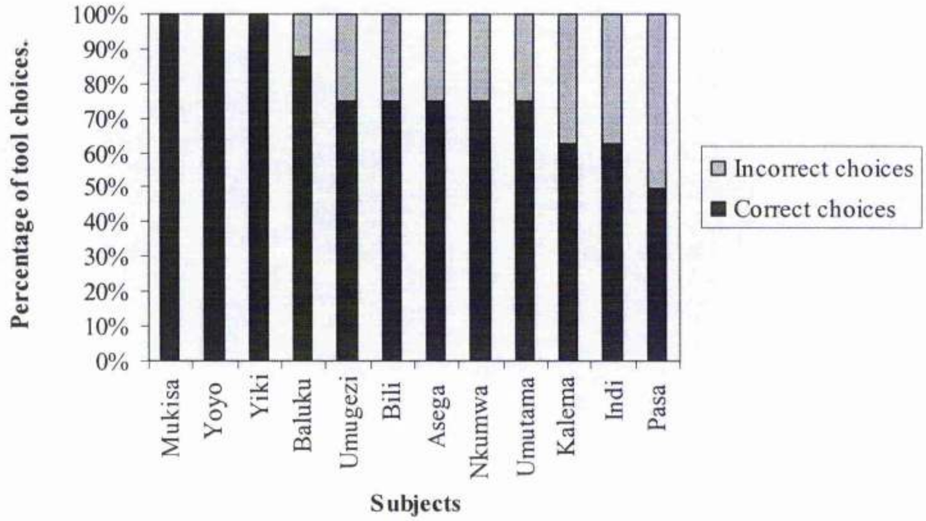


Figure 8.4 Mean percentage of correct and incorrect tool choices made by subjects for trials 1 to 8.

There was no evidence of a learning effect across the eight trials (Spearmans *rho* = 0.08, N = 8, p = 0.86; see Fig. 8.5), nor was there a relationship between the age of the chimpanzees and their success (see Fig. 8.4).

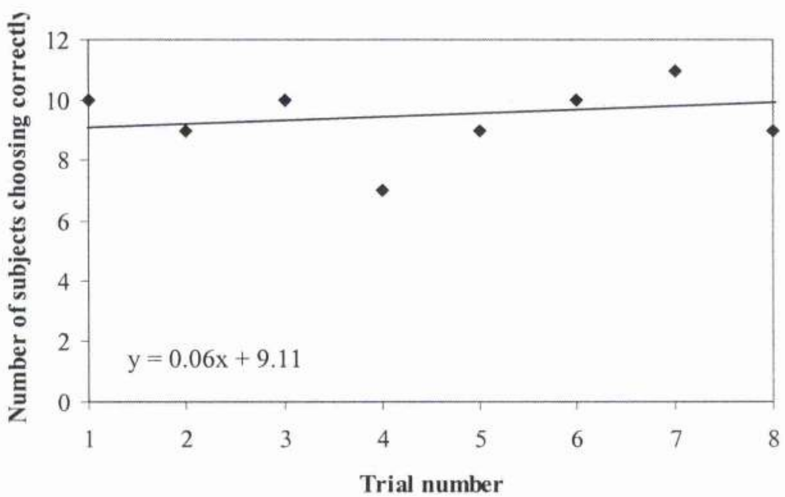


Figure 8.5 Number of chimpanzees who chose the correct rake on each of the 8 trials. The line represents that 'best fit'.

8.4 Discussion of Experiment 3

The results of this experiment indicate that chimpanzees appreciated that the Perspex barrier would prevent access to the food reward and were able to select the correct box accordingly. Three subjects chose the correct box on every trial, suggesting that subjects may have come to the experiment with previous knowledge about the properties of the tool, and barriers. As with Experiment 2, they were able to use this knowledge to form rules specific to the task that enabled the group as a whole to choose the correct box significantly more often than chance.

The combined results of Experiments 2 and 3 suggest that in Experiment 1, subjects were able to determine by observation that actions to the top of the clear box were irrelevant, because they recognised that the tool must contact the reward in order to bring about a salient result, and that contact was prevented by the physical barrier. These conclusions are discussed in more detail in Chapter 10.

SUMMARY OF CHAPTER 9

This experiment was carried out as a replication of Experiment 1, to determine whether, like chimpanzees, children could be influenced to switch between using imitation or emulation by altering the availability of causal information. However, the results indicate that 3- to 4-year-old children reproduced both the relevant and irrelevant actions, irrespective of the clear or opaque condition of the apparatus. The inclusion of functionally irrelevant actions, coupled with the high fidelity reproduction of the observed two-action method of bolt and door removal, suggest that children employed imitation to retrieve the reward in both conditions.

The condition of the apparatus, and hence the availability of causal information, did not influence the social learning strategy that children employed to solve this task. The results were not affected by either the age or the sex of the participants.

CHAPTER 9

EXPERIMENT 4: IMITATION AND EMULATION SWITCHING IN CHILDREN

9.1 Introduction

The previous experiments suggest that causal information may play an important role in chimpanzee social learning. The literature shows that children can learn socially and have a relatively sophisticated understanding of causality (see Chapter 4). However, there is little evidence that children can use this understanding to learn by emulation (Want & Harris, 2001). The following experiment was conducted as a replication of Experiment 1, to assess whether, when tested under similar conditions to the chimpanzees, children could be influenced to switch between imitation and emulation to solve the same task.

9.2 Methods

9.2.1 *Participants*

Participants were 16 children, eight female, eight male, aged between 3 years 5 months and 4 years 11 months old (mean: 4 years 1 month). The participants were African, Asian and Caucasian children recruited from St Andrews University Day Nursery, St Andrews, UK and Menzieshill Nursery School, Dundee, UK, following the completion of a letter of parental consent (see Appendix B). Children of this age were selected because previous studies have indicated that this age group can provide informative comparative data in relation to social learning (Whiten et al., 1996).

9.2.2 *Apparatus*

The boxes used in this experiment were identical to those used in Experiment 1 (see page 66). However, certain features were modified to make the task more suitable for children: (i) the reward was a Velcro-backed cartoon sticker, and (ii) the end of the tool was accordingly covered in Velcro.

9.2.3 *Procedure*

The experiment was conducted as far as possible following the same procedures as Experiment 1. The experimenter spent time at the playgroup prior to the investigation, so that the children would feel comfortable participating in the study. Children were tested individually in a separate room from the rest of the class. The apparatus was set up on a small table, and each child sat at the table on a chair beside the experimenter. Children and chimpanzees therefore observed the demonstrations from the same perspective.

During a pilot study, children told the experimenter that they believed the game to be about copying the demonstrations, and were eager to show her how well they could copy what she did. It was felt that the presence of the demonstrator was influencing the children's perception of the task, and hence two important differences in the procedure were introduced. Firstly, during each trial, the experimenter left the room while the subject interacted with the apparatus. This was thought to be the most effective way to reduce any tendency to copy the experimenter through social conforming, which may have masked any underlying appreciation of the causal features of the task.[2]

Secondly, children were told that they could do whatever they thought necessary to get the sticker, and that the experimenter would be outside the room and could not see what they did. When they had successfully retrieved the reward they were told to shout 'I've got it!' At this point the experimenter would return and give them their reward.

A video camera was set up at the back of the room behind toys and chairs so that it could not be easily seen. The camera started recording before each child entered the room, and continued to record throughout the experiment. At no point was the child's attention drawn to the camera, and there was no reason to believe that the children knew that their actions were being recorded. Indeed, after retrieving the reward, children typically replaced the bolt and door defences to their original position before calling the experimenter, thereby masking any visible evidence of their actions. The children were allocated to the same four

[2] The pilot study also indicated that children tended to imitate regardless of whether (i) the experimenter was present or absent in the room, (ii) a glove puppet was used as the model, (iii) they were given no verbal instructions at all, or (iv) they were given limited verbal instruction.

groups as the chimpanzees in Experiment 1, with four individuals in each (see Table 9.1). For ethical reasons the names of the participants have been omitted. The data was analysed using the same non-parametric statistics that were used in Experiment 1 with the chimpanzees (see section 6.2.5 for more details).

A	Method 1			
	Female 3yrs	**Male 3yrs**	**Female 4yrs**	**Male 4yrs**
B	Method 2			
	Female 3yrs	**Male 3yrs**	**Female 4yrs**	**Male 4yrs**
C	Method 1			
	Female 4yrs	**Male 3yrs**	**Female 4yrs**	**Male 4yrs**
D	Method 2			
	Female 2yrs	**Male 3yrs**	**Female 4yrs**	**Male 4yrs**

Table 9.1 Experimental groups A to D. The names of the children have been omitted for ethical reasons.

9.3 Results

9.3.1 *Experimental groups*

There was no significant difference in the reproduction of irrelevant actions between subjects from groups A and B (median A = 77.5, median B = 72.92; Mann-Whitney *U*-test for unmatched samples, $z = -2.08$, $N_1 = 4$, $N_2 = 4$, $p = 0.06$, two-tailed), or between groups C and D (median C = 78.33, median D = 77.5; Mann-Whitney *U*-test for unmatched samples, $z = -0.3$, $N_1 = 4$, $N_2 = 4$, $p = 0.87$, two-tailed). Two collapsed groups, A/B (opaque > clear) and C/D (clear > opaque) have therefore been used for the following analysis.

The reproduction of irrelevant actions was not influenced by age (median A/B 3-year-olds = 75, 4-year-olds = 74.17, Mann-Whitney *U*-test for unmatched samples, $z = -0.6$, $N_1 = 4$, $N_2 = 4$, $p = 0.69$, two-tailed; median C/D 3-year-olds = 78.33, 4-year-olds = 77.5, $z = -0.15$, $N_1 = 4$, $N_2 = 4$, $p = 0.39$, two-tailed). Nor was performance influenced by sex (median A/B female = 75, male = 76.25; Mann-Whitney *U*-test for unmatched samples, $z = -0.74$, $N_1 = 4$, $N_2 = 4$, $p = 0.49$, two-tailed; median C/D female = 80, male = 75; $z = -2.08$, $N_1 = 4$, $N_2 = 4$, $p = 0.6$, two-tailed).

9.3.2 *Reproduction of relevant and irrelevant actions*

There was no significant difference in the reproduction of irrelevant actions by children from group A/B in the opaque and clear conditions (median A/B opaque = 70.84, median A/B clear = 80; Wilcoxon test for matched pairs, $z = -1.53$, N-ties = 7, $p = 0.13$, two-tailed; see Fig. 9.1). Therefore the opaque or clear appearance of the apparatus (and hence the availability of causal information), did not effect the children's behaviour.

There was no significant difference in the reproduction of irrelevant actions by children from group C/D with the clear box, when compared to group A/B in either condition ($x^2 = 4.8$, df = 2, $p = 0.09$ two-tailed; see Fig. 9.1). Therefore, children from group A/B did not alter their behaviour between experimental conditions, and this was not influenced by previous experience with the opaque apparatus. When children from group C/D then transferred to the opaque apparatus there was no significant change in their behaviour (median C/D clear = 75, median C/D opaque = 80; Wilcoxon test for matched pairs $z = -1.83$, N-ties = 4, $p = 0.07$, two-tailed). Therefore, like group A/B, the opaque or clear appearance of the apparatus, and hence the availability of causal information, did not effect the children's behaviour.

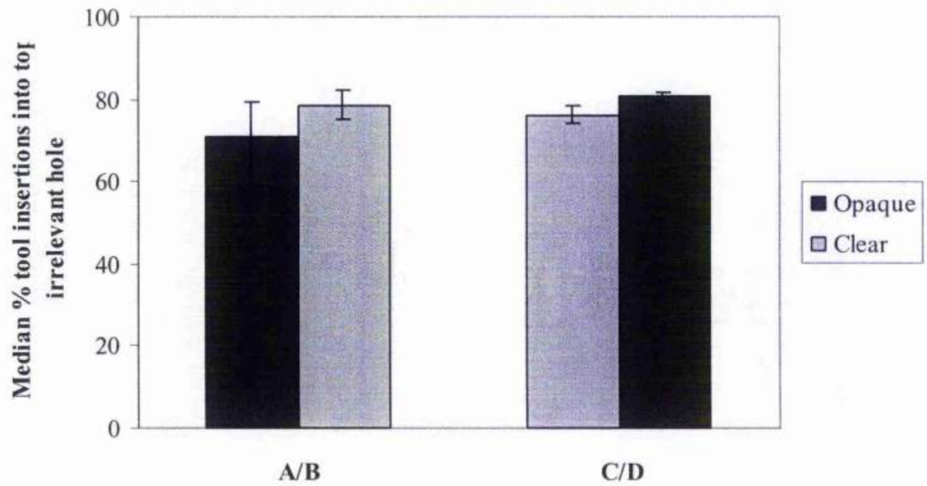


Figure 9.1 The median percentage of tool insertions into the top, irrelevant hole by subjects from groups A/B and C/D in both the opaque and clear conditions. Error bars represent the inter-quartile range.

9.3.3 *Reproduction of two-action method of bolt removal*

Children from groups A and C (A/C), who observed *method 1* (push bolt), employed this technique significantly more than children from groups B and D (B/D) who observed *method 2* (median A/C = 100, median B/D = 0, Mann-Whitney *U*-test for unmatched samples, $z = -3.57$, $N_1 = 8$, $N_2 = 8$, $p < 0.001$, two-tailed; see Fig. 9.2). Similarly, children from group B/D who observed *method 2*, employed this technique significantly more than subjects in group A/C who saw *method 1* (median B/D = 91.66, median A/C = 0; $z = -3.57$, $N_1 = 8$, $N_2 = 8$, $p < 0.001$, two-tailed).

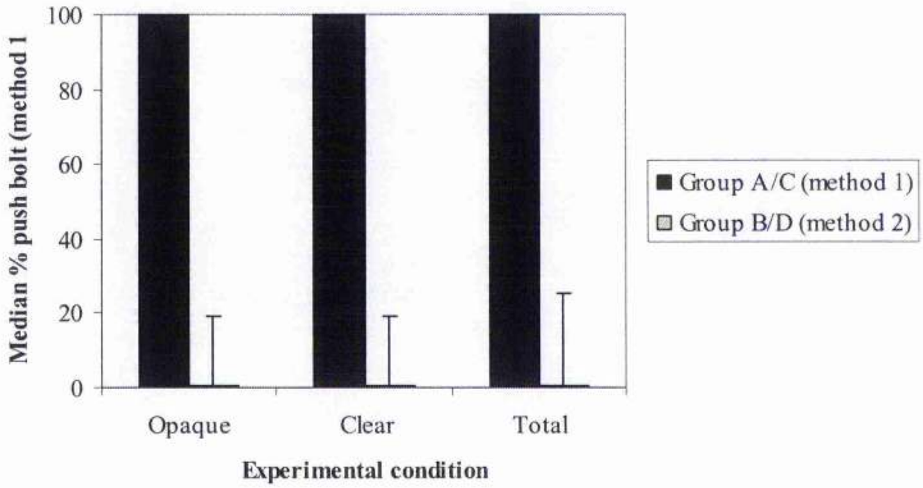


Figure 9.2 Median percentage of *method 1* (push bolt), use by subjects from groups A and C who observed *method 1*, and groups B and D who observed *method 2*.

9.3.4 *Reproduction of two-action door removal*

Children from group A/C, who observed *method 1* (lift door), employed this technique significantly more than children from group B/D who observed *method 2* (median A/C = 100, median B/D = 0; $z = -3.65$, $N_1 = 8$, $N_2 = 7$, $p < 0.001$, two-tailed). Similarly, children from group B/D who observed *method 2*, employed this technique significantly more than subjects in group A/C who saw *method 1* (median B/D = 91.66, median A/C = 0; $z = -3.65$, $N_1 = 8$, $N_2 = 8$, $p < 0.001$, two-tailed). Children therefore used the observed method of both bolt and door removal significantly more than the alternative.

9.4 Discussion of Experiment 4

The results of this experiment indicate that 3- and 4-year-old children reproduced both the irrelevant and relevant actions, irrespective of whether the apparatus was opaque or clear, or the order in which the apparatus was presented (see Fig 9.1). This suggests that the availability of causal information did not influence the social learning strategy that children employed. The inclusion of functionally irrelevant actions, coupled with the high fidelity reproduction of the observed two-action methods of both bolt and door defence removal (see Fig. 9.2), suggest that children relied strongly on imitation to retrieve the reward in both conditions. The tendency to imitate was not influenced by either the age or the sex of the children. These conclusions are discussed more fully in Chapter 10.

CHAPTER 10

GENERAL DISCUSSION OF EXPERIMENTS 1 TO 4

10.1 Causal information and chimpanzee social learning

Experiment 1 suggests that chimpanzees who interacted first with the opaque box, in which causal information was unavailable, typically used imitation to retrieve the reward. Chimpanzees performed a more complete copy of the model's behaviour by including the irrelevant parts of the demonstration. These subjects tended to switch to emulation when presented with the clear apparatus, in the sense defined by Nagell, Olguin and Tomasello (1993), insofar as "the chimpanzees were paying attention to the general functional relations in the task and to the results obtained by the demonstrator but not to the actual methods of tool use demonstrated" page 174. See section 6.4.1 for more details. Chimpanzees, who interacted with the clear apparatus first, also used emulation to retrieve the reward, and continued to do so when presented with the opaque apparatus, although the opportunity to monitor the effect of the tool inside the apparatus had been removed. This suggests that they may have been able to generalise the information gained through experience with the clear box to the new experimental condition.

The results of Experiments 2 and 3 suggest that in Experiment 1, the chimpanzees were able to determine that actions to the top of the box were irrelevant, because they recognised that the tool must make contact with the reward, and that contact was prevented by the barrier. These studies do not provide evidence about the source of this knowledge. However, even if this knowledge is the result of associative learning gained through previous experience, it does not diminish the potentially important role of causal information in chimpanzee social learning. Appreciating that the tool must make some relevant contact with a reward is all that is required to differentiate the relevant and irrelevant aspects of the observed behaviour in Experiment 1.

Therefore, the notion that commonly arises in the literature, which suggests that the predominant use of emulation by chimpanzees indicates a deficit of imitation, may be misleading. The results of these experiments suggest more generally that when chimpanzees have access to causal information, they may use this information to develop the most efficient technique, in accord with emulation. Furthermore, they may be able to generalise their existing causal knowledge to new situations. However, when causal information is restricted, and they are prevented from using alternative, more flexible forms of social learning, they can employ imitation to solve all, or part of a problem. Therefore causal information may play an important role in chimpanzee social learning by allowing individuals to identify the relevant aspects of a demonstration, which in turn determines the strategy that is employed, and ultimately the degree of behavioural fidelity which is achieved.

One of the recent criticisms of the concept of emulation in the literature is that it has been defined almost as a null hypothesis. Emulation is often claimed when apes show no evidence of imitation, but seem to learn more than would be expected through enhancement. Hence, emulation has not been empirically demonstrated in its own right (Byrne, 2002). These experiments offer the first empirical evidence for the existence of emulation as a viable social learning strategy in chimpanzees, and show that the occurrence of emulation can be determined by the use of information about causal relationships.

The ability of chimpanzees to switch from a strategy of imitation to emulation contrasts with the findings of a study by Call & Tomasello (1995). Orangutans observed both a human and conspecific demonstrator perform a number of actions to retrieve a food reward from an opaque box. As with the opaque box in the present study, the causal role of these actions on the reward could not be perceived. However, it was found that subjects failed to solve this task. Since emulation could not be used to retrieve the reward, and imitation was the only viable strategy, the failure of subjects to retrieve the reward was interpreted as a lack of imitative ability. However, the retrieval of the reward relied on the reproduction of small movements of a lever to release and retrieve the reward. It is possible that the demonstrated movements were too small or too similar to be effectively differentiated or reproduced by the apes. The actions required for the present study were perhaps clearer and therefore easier to discriminate between and execute. Although this seems to be the most likely explanation, the potential influence of species differences between the two studies cannot be ruled out.

10.2 Chimpanzees and children compared

In contrast to the chimpanzees, children tended to recreate the actions they observed without appearing to consider the causal efficiency of their behaviour. Yet the literature suggests that children of this age may have more sophisticated causal knowledge than chimpanzees (see Chapter 4). Why then did the children, unlike the chimpanzees, not utilise this knowledge to develop the most efficient technique to retrieve the reward?

A first possibility is that children's knowledge of causality is unavailable to other cognitive functions such as social learning. However, a number of studies have found that children could selectively ignore irrelevant actions in an observed sequence (Harnick, 1978; Sibulkin & Uzgiris, 1978; Want & Harris, 2001; Bauer & Kleinknecht, 2002). Similarly, Bullock et al., (1982) found that 3- to 5-year-old children could correctly predict which physical changes to a piece of apparatus were functionally relevant or irrelevant. It is therefore unlikely that the failure of children to differentiate between the irrelevant and relevant actions in the present study was the result of limitations in their causal knowledge.

A second possibility is that the children's tendency to imitate was related to the difficulty of the task. It has been shown that irrelevant actions are more likely to be ignored as the difficulty of a task decreases (Harnick, 1978; Sibulkin & Uzgiris, 1978; Bauer & Kleinknecht, 2002). However, pilot work indicated that children continued to reproduce both irrelevant and relevant actions when the defences of the box were removed, thereby making the task simpler. Hence, it is unlikely that children's homogenous behaviour was a function of task difficulty.

Thirdly, the difference in performance of chimpanzees and children may result from a differential focus of attention. Imitation may predominate in children because they attend more to the actions of others than the results of their behaviour (Bellagamba & Tomasello, 1999; Bekkering et al., 2000). Call & Carpenter (2002) have suggested that in contrast, chimpanzees attend preferentially to goals and results, and this may account for the observed tendency of chimpanzees and children to use different social learning strategies.

Finally, it is possible that the divergent results for children and chimpanzees are due to differences in inferring 'intention'. With regard to chimpanzees, although few studies have been carried out, there is conflicting evidence about whether they are able to interpret actions in the framework of intentions (Call & Tomasello, 1998; Povinelli et al., 1998). In contrast, in some situations children can differentiate between intended and accidental actions, and can use this information to complete intended but failed demonstrations (Meltzoff, 1995; Carpenter et al., 1998; Bellagamba & Tomasello, 1999; but see also Heyes & Ray, 2002; and Chapter 4). In the present study children, but not chimpanzees, may have reproduced the irrelevant actions of the demonstrator in all conditions because they viewed the actions of the demonstrator as intentional. Indeed, Gergely et al., (2002) have shown that children will imitate strange behaviours, such as using their head to work a light switch, as long as they view the actions of the demonstrator as rational.

The children's reproduction of irrelevant actions in this study contrasts with the findings of Want & Harris (2001), who found that 3-year-old children could benefit from, but selectively exclude, irrelevant actions from an observed sequence. This difference may be due to the fact that in the Want and Harris study, the accidental irrelevant actions were followed by the demonstrator saying 'Oops'. Subjects also received only one demonstration before they were given an opportunity to interact with the apparatus. Children may have reproduced the irrelevant actions in the present study because the demonstration was repeated three times before subjects could interact with the apparatus, and the demonstrator did not verbally identify the irrelevant actions as either accidental or undesirable. Children may therefore have included all the observed actions because they saw the behaviour of the demonstrator as purposeful, even if they did appreciate that some parts of the demonstration were causally irrelevant.

It may be that differences in the behaviour of chimpanzees and children can best be explained by a combination of a differential focus of attention on actions, results and goals, with the latter possibly influencing the interpretation of the actions of the demonstrator as intentional.

SUMMARY OF CHAPTER 11

The results of Experiments 1 to 3 suggest that chimpanzees are sensitive to the causal relevance of observed actions, as they are able to selectively exclude actions that are not related to task solution. An alternative way to test whether an individual understands the causal relevance of actions is to determine what is learned by observing mistakes. If chimpanzees are able to learn causal relationships by observation, they should benefit from observing errors as well as successes, as observing errors provides additional causal information about what *not* to do.

The trap-tube task was used to determine whether chimpanzees who observed errors and successes could learn to solve the task faster that those who only saw successes. Both groups were compared to a control group who saw the apparatus manipulated in the same direction and to the same extent as the experimental groups. The critical difference was that in the control demonstrations, the tool was not inserted into the tube, and therefore did not effect the reward.

Chimpanzees who observed the demonstrator use a tool to bring about an effect were more likely to use the tool themselves than subjects who observed the same movement with no effect on the reward. This result suggests that chimpanzees are able to learn the causal relevance of tool-reward contact. However, the performance of subjects in the experimental groups was not significantly influenced by the observation of errors. The two subjects who performed significantly better than chance learned to avoid the trap after approximately 50 trials. However, this strategy was dependent on an incomplete set of anticipatory rules. It seems that the demonstrations contained elements that the chimpanzees found conceptually difficult, and that acquisition of the trap tube task was not significantly aided by the observation of errors.

CHAPTER 11

EXPERIMENT 5: THE OBSERVATION OF ERRORS - CHIMPANZEES

11.1 Introduction

The results of Experiments 1 to 3 suggest that chimpanzees are sensitive to the causal relevance of observed actions, and are able to selectively include or exclude parts of a demonstration in accordance with their relevance to the task. Another way to determine whether an observer monitors the causal significance of a demonstrator's behaviour is to determine what is learned from the observation of mistakes (Want & Harris, 2001). It would be expected that if chimpanzees are able to extract causal information by observation, they might benefit more from observing both the incorrect and correct way to solve a task, than from observing only the correct solution. This is because seeing both correct and incorrect responses might enable an individual to learn what *not* to do by providing additional visual information from which causal relationships could potentially be inferred. If chimpanzees are able to learn about causal relationships by social learning, they should benefit from observing mistakes. The following study employed a trap-tube task to test this hypothesis.

Successful completion of the trap-tube task requires insertion of a tool into the correct end of a tube so as to push out a reward. An unsuccessful response pushes the reward into the trapping-hole located in the centre (see Fig. 11.1). The food reward can be placed on either side of the trapping hole, so that the correct end of tool insertion is dependent on the position of the food relative to the trap. An individual can perform at chance by either inserting the tool randomly into each end, or by consistently inserting the tool into the same end of the tube. However, performing significantly above chance levels can only be achieved by avoiding the trap.

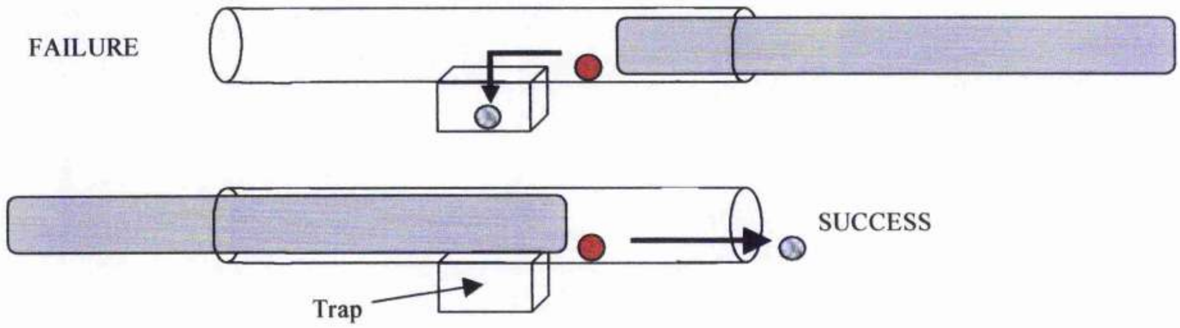


Figure 11.1 Trap-tube apparatus. In the top diagram insertion of the tool into the side nearest the reward results in the reward being pushed into the trap and lost. In the bottom diagram insertion of the tool into the side farthest from the reward results in the food being pushed away from the trap and retrieved.

This task was originally used to investigate problem solving by individual learning in monkeys and apes (see section 3.2.3). However, tube tasks have also been used in studies of social learning. Visalberghi (1993) found that capuchin monkeys who observed a conspecific demonstrator use a tool to retrieve a reward from a horizontal tube (without a trap), interacted more with the apparatus, but did not learn to insert the tool into the apparatus. However, Bard et al., (1995) found that 3- and 4-year-old chimpanzees who observed a conspecific demonstrator retrieve a reward, solved the task in fewer trials than controls. In addition, these subjects were able to generalise what they had learned to new problems in which tools had to be modified into an appropriate configuration before they could be used. Chimpanzees' mastery of the tube-tasks can therefore be aided by social learning.

Want & Harris, (2001) were one of the first to suggest that an individual may benefit from observing both errors and successes. They found that 3-year-old children who witnessed an adult demonstrator fail, then succeed, at the trap-tube task, were better able to solve the task than those who observed only the correct response. However, the methodology and apparatus used by Want & Harris may have allowed children to solve the task by individual learning.

Firstly, children observed only one demonstration followed by a block of ten trials. With only one demonstration there was a limited opportunity for social learning, making it difficult to determine whether the children's performance after trial 1 was governed more by social or individual learning. Secondly, the position of the reward was not randomised across the block of ten trials. The position of the reward, and hence the correct side of tool insertion was alternated between the left and right side on every trial, making it potentially easy to learn the pattern of correct response without understanding the causal properties of the task. This is particularly because the trap was located at one end of the tube (see Fig. 11.2), and the correct side of tool insertion was alternated by turning the tube 180° between trials.

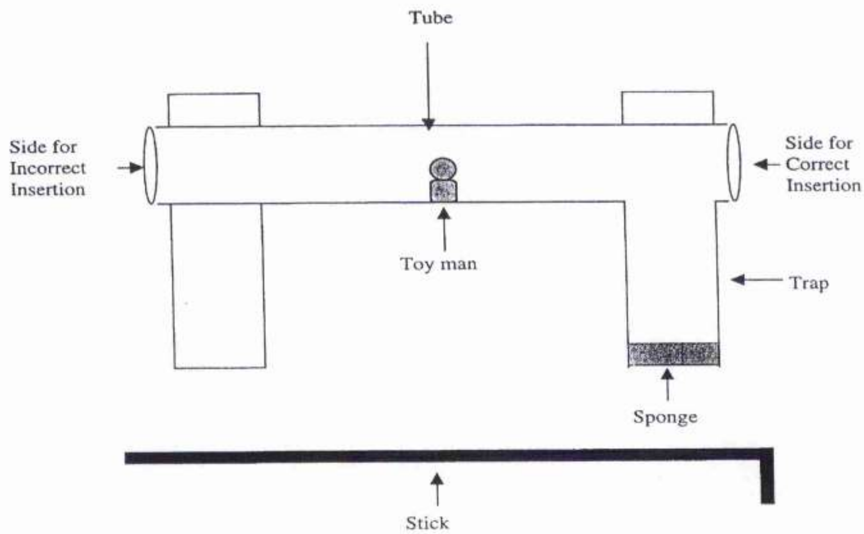


Figure 11.2 Trap-tube apparatus used by Want & Harris (2001), page 433.

The difference in position of the trap, coupled with the predictable sequence of presentation, may have made solution relatively easy by greatly elevating the potential to discover how to solve the task by associative learning. The methodology and apparatus used in the following study were designed to examine how chimpanzees would perform when tested under stricter experimental conditions. This was achieved by positioning the trap in the centre of the tube, so that the correct side of tool insertion was dependent on the position of the reward relative to the trap (see Fig. 11.1). The location of the reward was presented in a randomised order, and subjects observed multiple demonstrations throughout the experiment. These modifications will be described in more detail below.

11.2 Methods

11.2.1 *Participants*

The chimpanzees who participated in this study were 15 members of the juvenile group at Ngamba Island Chimpanzee Sanctuary, Uganda. Subjects ranged in age from 2- to 7-years-old, and were of both sexes. This experiment was conducted 5 months after the completion of Experiment 3. Although 15 chimpanzees were initially included in the study, six did not complete the task as they became frustrated after the first block of trials and refused to enter the testing room. A similar response to frustration was reported by Reaux & Povinelli (2000), who found that two chimpanzees (Mindy and Apollo) also refused to participate in a trap-tube experiment and were subsequently dropped from the study. The nine individuals whose data will be reported were three females (Ikuru, Yoyo and Pasa, aged 7, 4 and 3 years old respectively), and six males (Kalema, Asega, Baluku, Kisembo, Indi and Okech, aged 6, 4, 4, 4, 3 and 2 years old respectively). The remainder of this chapter will focus only on these individuals.

11.2.2 *Apparatus*

The trap-tube was constructed from a horizontally mounted transparent polycarbonate tube, 60 cm in length with an internal diameter of 4 cm. The tube had a rectangular trap (6 cm x 6 cm x 12 cm) in the centre (see Fig. 11.1). The trap had a small lockable door located on the side so that trapped rewards could be easily removed by the experimenter. The tube was mounted 15 cm above the ground on a wooden board that was bolted to the centre of the floor in a the research room (see Fig. 5.6). This allowed subjects to move freely around the apparatus and insert the tool into either side of the tube with equal ease.

The tool was a section of wooden broom-handle, 60 cm long and 3 cm in diameter. Both the trap-tube and the tool were placed outside the holding facility for 24 hours prior to the start of the experiment. This was done to familiarise subjects with the apparatus and reduce the potential for neophobic responses during testing. The three youngest subjects, Okech, Pasa and Indi, found the tool too heavy to manipulate. They were therefore given a lighter, hollow, aluminium tool with a slightly smaller diameter (2cm) that was easier to insert.

11.2.3 *Procedure*

A food reward, placed on either the left or right side of the central trap, could only be obtained by inserting the tool into the end of the tube furthest from the reward. Insertion of the tool into the end nearest the reward would result in pushing it into the trap where the subject could not retrieve it (see Fig. 11.1). The chimpanzees were divided into three groups, each with 3 subjects of approximately equal age. The groups observed one of the following demonstrations (see Table 11.1):

GROUP	DEMONSTRATION	OUTCOME
Correct only (C-only) *(Experimental group 1)*	Subjects observed a human demonstrator insert the tool into the correct end of the tube (farthest from the reward) and retrieve the reward.	Success only
Incorrect + correct (I + C) *(Experimental group 2)*	Subjects observed the demonstrator insert the tool into the incorrect end of the tube (nearest to the food), pushing the reward into the trap. The tube was then re-baited while the subject was distracted. The demonstrator then inserted the tool into the correct end of the tube to successfully retrieve the reward.	Failure > Success
Control (Cont.) *(Control group)*	The purpose of this group was to control for the potential effects of enhancement. The tool was moved along the top of the apparatus so that it had no effect on the reward inside the tube. During half the demonstrations the tool was moved in the same direction as the (C-only) demonstration, and on the other half it was moved in the same direction as the (I+C) demonstration.	No outcome

Table 11.1 Groups and demonstrations observed by chimpanzees in Experiment 5.

The trap-tube task can be solved using one simple procedural rule: *Always insert the tool into the end of the tube farthest from the reward.* Individuals who observe errors and successes might be able to extract this rule in fewer trials than individuals who observe only success. In addition, individuals in both experimental groups (C-only and I+C) would be expected to learn the rule in fewer trials than controls.

During demonstrations the experimenter took and ate the majority of the rewards. However, during a few demonstrations the subject monopolised the end of the apparatus and was able to scrounge the reward. Under natural foraging conditions it is not unusual for young chimpanzees to scrounge food from older conspecifics. For example Boesch (1993), found that young chimpanzees were able to scrounge up to 1000 calories per day from their mothers during bouts of nut-cracking. Scrounging was therefore kept to a minimum during demonstrations, but was not completely prevented, as limited scrounging was thought to be more naturalistic. Indeed, scrounging may be important for emphasising the relevance of the demonstrated behaviour to the observer.

The *correct only* group (C-only) and the *incorrect* + *correct* group (I+C) initially received 2 blocks of 12 trials with a demonstration before each trial. However, subjects became bored and uninterested, so the number of trials and demonstrations per block was reduced. Subjects received eight further blocks of ten trials with only four demonstrations spread over the block (see Fig. 11.3). Demonstrations occurred before trials 1, 3, 6 and 8. For two of these demonstrations (before trials 1 and 6), the correct side of tool insertion was the right, and for the other two demonstrations (before trials 3 and 8), the correct side was the left to control for stimulus enhancement. Each subject received one block of trials per day, presented as far as possible on 10 consecutive days. The control group received eight blocks of ten trials also with four demonstrations, presented as far as possible on 8 consecutive days.

The number of trials in which the food was on the left or right was counterbalanced within each block and presented in a randomised order, insofar as the reward was never placed on the same side of the trap for more than two consecutive trials to avoid learning a simple side-biased rule.

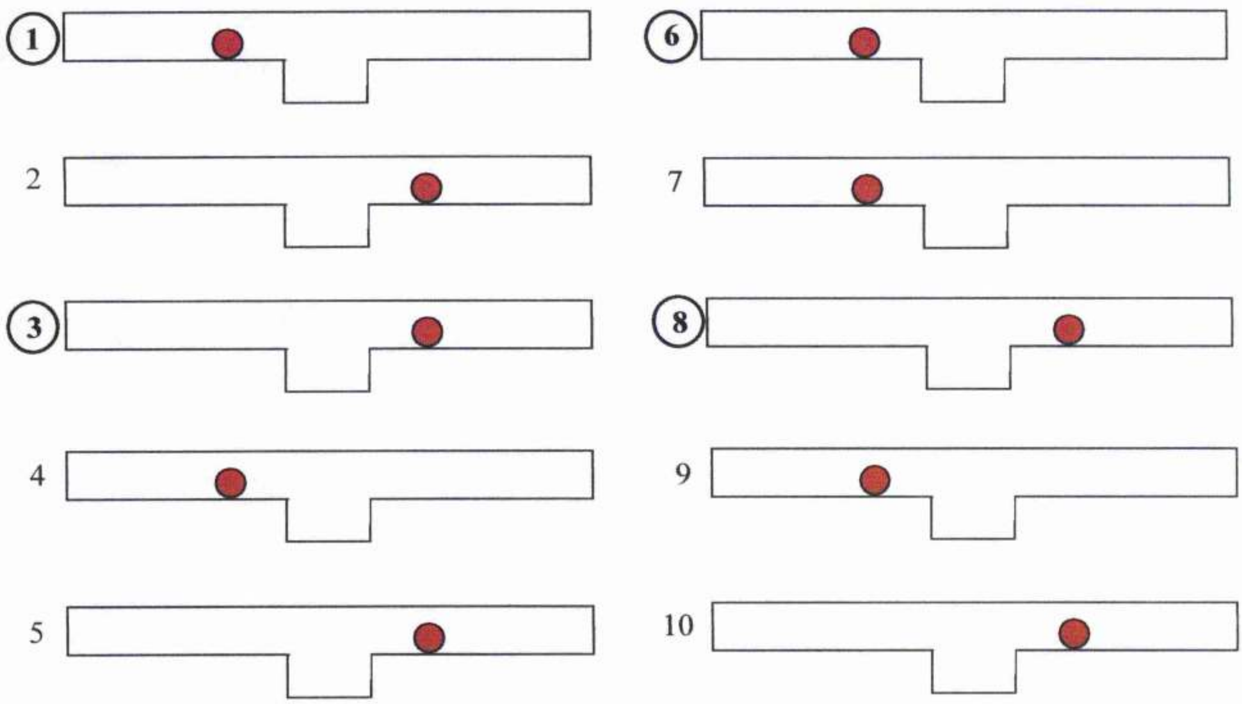


Figure 11.3 Schematic representation of the reward location during a block of ten trials. The order of presentation was randomised insofar as there was no obvious pattern, and the reward was never placed on the same side for more than two consecutive trials. Circles indicate trials that were preceded by a demonstration.

Subjects were tested individually in the research room. Before the very first demonstration, subjects were allowed a two minute familiarisation period to explore the apparatus. Subjects then observed a demonstration in accord with their group allocation (see Fig. 11.4). During demonstrations, the experimenter first pointed to the reward inside the tube and gave food grunts before using the tool to either retrieve or trap the reward.

Following an incorrect demonstration in which the food was trapped in the case of the I+C group, (or the tool was moved in the incorrect direction in the case of the control group) the experimenter said 'uhh ooh' to express disappointment. Following a successful demonstration, in the case of both experimental groups, (or in the case of the control group when the tool was moved in the correct direction) the experimenter said 'yay'. These vocalisations, with their characteristic intonations, were used to enhance the social significance of demonstrated actions, as is common in studies with human children. These particular sounds were chosen because the chimpanzees were familiar with humans making similar vocalisations in conditions of disappointment and pleasure, and it was felt that these sounds would be more appropriate than the English words ('woops' and 'there') used in human studies (Carpenter et al., 1998; Bellagamba & Tomasello, 1999; Want & Harris, 2001; discussed in Chapter 4).

The experimenter then distracted the subject while the apparatus was re-baited by a second experimenter, also present in the room. Before each trial the tool was placed on the floor near the centre of the apparatus, perpendicular to the tube. A trial lasted for four minutes, or until the reward was retrieved or trapped, whichever occurred first. All demonstrations and trials were recorded on a hand-held video recorder by the second experimenter.

11.2.4 *Video coding and data analysis*

Behavioural data was collected for each subject by coding the total number of tool-insertions, the side of tool insertion for each trial, and the number of correct tool insertions. This data was analysed using non-parametric statistics because frequency data is not normally distributed. The behaviour of subjects from each experimental group was analysed by comparing the median percentage of responses for subjects from each group using a Mann-Whitney *U*-test for unmatched samples. Evidence for learning effects were analysed using a Spearman's Rank Correlation Coefficient test. The occurrence of instructive qualitative data was also noted along with any behaviour that was not related to task solution.

Figure 11.4 Asega, a member of the *incorrect + correct* group, observes the demonstrator insert the tool into the correct end of the tube and retrieves the reward.

11.3 Results

11.3.1 *Recognition of failure*

All subjects reacted to the loss of the reward into the trap, hitting the tube with their hands or with the tool in an apparent attempt to recover the reward. By this criterion, all subjects recognised the conditions of failure. This behaviour was seen to decrease across blocks, although it was not quantified.

11.3.2 *Control group - Use of tool*

Subjects in the control group generally performed very few activities that were related to task solution. Only one subject, Ikuru, inserted the tool into the apparatus. She used the tool in only 10 out of 80 trials; on nine occasions inserting the tool into the end of the tube nearest the reward, pushing it into the trap. In each trial she reacted to the loss of the reward, biting the trap and hitting it with the tool. The remaining two subjects, Indi and Kisembo, were also highly motivated to retrieve the reward, spending the majority of the four-minute trial period unsuccessfully trying to squeeze their hand into the tube to reach the reward.

They also tried to bite the tube or hit it with the tool. However, they did not attempt to insert the tool into the tube.

11.3.3 *Experimental groups – Use of tool*

Irrespective of whether the chimpanzees chose the correct side of tool insertion, subjects in the C-only and I+C groups inserted the tool on significantly more trials than subjects in the control group (median C-only = 92.3, median controls = 0; Mann-Whitney *U*-test for unmatched samples, $z = -1.99$, $N_1 = 3$, $N_2 = 3$, $p = 0.046$, two-tailed; median I+C = 92.3; Mann-Whitney *U*-test for unmatched samples, $z = -1.99$, $N_1 = 3$, $N_2 = 3$, $p = 0.046$, two-tailed). However there was no significant difference in the number of tool insertions performed by the C-only and I+C groups (Mann-Whitney *U*-test for unmatched samples, $z = -0.44$, $N_1 = 3$, $N_2 = 3$, $p = 0.658$, two-tailed; see Table 11.2).

Subjects in the control group observed the tool being moved in the same direction and to the same extent as the C-only and I+C groups. The major difference was that during the control demonstrations the tool did not bring about an effect on the reward located inside the tube. It seems that subjects in the experimental groups, who observed the tool make contact with the reward, learned the causal relevance of tool-reward contact. They learned by observation that by inserting the tool it could be used to push the reward along the tube (regardless of retrieving or trapping the food). However, subjects in the control group, who did not observed tool-reward contact, did not learn the causal significance of this relationship.

Group	**Name**	**% of tool insertions**	
C-only	Yoyo	96	(100 / 104)
	Pasa	92	(96 / 104)
	Baluku TU	27	(28 / 104)
I+C	Asega	92	(96 / 104)
	Kalema	98	(102 / 104)
	Okech	74	(77 / 80)
Control	Ikuru	10	(10 / 80)
	Indi	0	(0 / 80)
	Kisembo	0	(0 / 80)

Table 11.2 Percentage of tool insertion performed by subjects from each group, irrespective of whether the tool was inserted into the correct or incorrect end of the tube.

11.3.4 *Alternative strategies*

One of the members of the C-only group, Baluku, developed an alternative non tool-use strategy to retrieve the reward. Baluku's left hand was badly injured during a fight with an adult male, leaving him with only an index finger and thumb. His manipulation of the tool was relatively awkward and after 24 trials he developed a strategy of vigorously shaking the apparatus to dislodge the reward. This procedure resulted in the reward being shaken towards him on approximately half the trials, increasing his success from 32% with the tool, to 56% by combining tool-use and shaking. The following statistical analysis refers only to Baluku's tool-using attempts, since the original purpose of the study was to assess chimpanzees' causal knowledge of a tool-using task.

11.3.5 *Number of correct responses*

Figure 11.5(a) suggests a trend in the predicted direction, in that subjects in the I+C group succeeded more frequently than individuals in the C-only group, and both groups succeeded more than controls. However, there was much overlap in the variance between the C-only and I+C groups (see Fig 11.5b), and the success of chimpanzees who observed both correct and incorrect responses was not significantly different from subjects who observed only the correct solution (median C-only = 10, median I+C = 26.78; Mann-Whitney *U*-test for unmatched samples, $z = -1.09$, $N_1 = 3$, $N_2 = 3$, $p = 0.275$, two-tailed).

There was no significant difference between the success of the C-only group and the controls (median C-only = 10, median controls = 0; Mann-Whitney *U*-test for unmatched samples, $z = -1.55$, $N_1 = 6$, $N_2 = 6$, $p = 0.121$, two-tailed). However, there was a significant difference in the performance of the I+C group and controls (median I+C = 26.78, median controls = 0; Mann-Whitney *U*-test for unmatched samples, $z = -2.09$, $N_1 = 6$, $N_2 = 6$, $p = 0.037$, two-tailed). Therefore, although the trend goes in the predicted direction, statistical analysis dictates that subjects were not significantly influenced by the observation of errors. However, subjects in the experimental groups did seem to learn the causal relevance of tool-reward contact by seeing the tool being inserted into the tube.

When the results for the C-only and I+C groups are taken together, the chimpanzees did not perform significantly better than would be expected by chance (Wilcoxon test for matched samples, C-only and I+C *versus* chance, $z = -1.57$, N-ties = 6, $p = 0.116$), two-tailed).

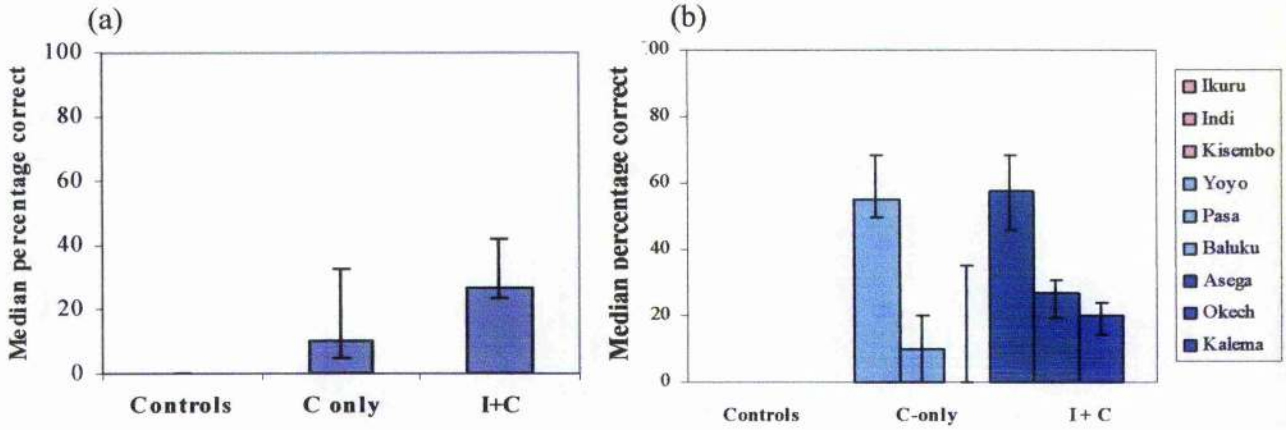


Figure 11.5 Percentage of correct responses: (a) medians for each group; (b) medians for each individual. Error bars represent the inter-quartile range.

11.3.6 *Individual performances - Unsuccessful subjects*

Only two of the chimpanzees were able to solve the task above chance levels (see Fig. 11.6 and Table 11.3). None of the remaining chimpanzees performed better than chance, and indeed, three of the unsuccessful subjects performed at levels significantly lower than chance (see Table 11.3 and Fig. 11.6). Unsuccessful subjects showed no evidence of a side bias (see Fig. 11.7). In order to perform significantly below chance levels, unsuccessful subjects must have been trapping the reward on the majority of trials. This poor performance, coupled with the lack of side bias, suggests that the unsuccessful subjects were inserting the tool into the end of the tube nearest the reward, pushing it into the trap.

SUBJECT	GROUP	PERCENTAGE CORRECT			% LEFT
		Overall	Blocks 1-5	Blocks 6-10	INSERTIONS
Yoyo	**C-only**	58	50	*67**	***91*****
Pasa		17**	21**	12**	44
Baluku (TU)		32	38	0	41
(shake + TU)		56	41	58	
Asega	**I+C**	55	43	***86*****	33**
Kalema		18**	17**	18**	52
Okech		23**	19**	31	55
Ikuru	**Control**	4**	0**	10*	61
Indi		-	-	-	-
Kisembo		-	-	-	-

Table 11.3 Percentage of correct responses by subjects from the C-only, I+C, and control groups. The '*' symbol represents a significant deviation from chance performance based on a binomial test (* $p < 0.05$, ** $p < 0.001$). For results less than 50% correct, significance indicates a performance worse than chance. '% left insertions' is a measure of side bias.

In addition, many of the unsuccessful subjects performed idiosyncratic behaviours, such as attempting to insert non-functional objects, or objects with inappropriate dimensions to fit into the tube (see Table 11.4). This indicates that the unsuccessful subjects did not clearly grasp the requirements of the trap-tube task.

SUBJECT	GROUP	BLOCK	IDIOSYNCRATIC BEHAVIOUR
Yoyo	**C-only**	-	-
Pasa		1	Insert stick too short to reach reward
		5	Insert chewed paper
Baluku		-	-
Asega	**I+C**	7	Insert stick too short to reach reward
Kalema		-	-
Okech		1	Insert chewed paper
Ikuru	**Control**	3	Attempt to insert plastic bottle
		4	Insert plastic bag
Indi		-	-
Kisembo		-	-

Table 11.4 Record of idiosyncratic behaviours performed by some chimpanzees throughout the experiment.

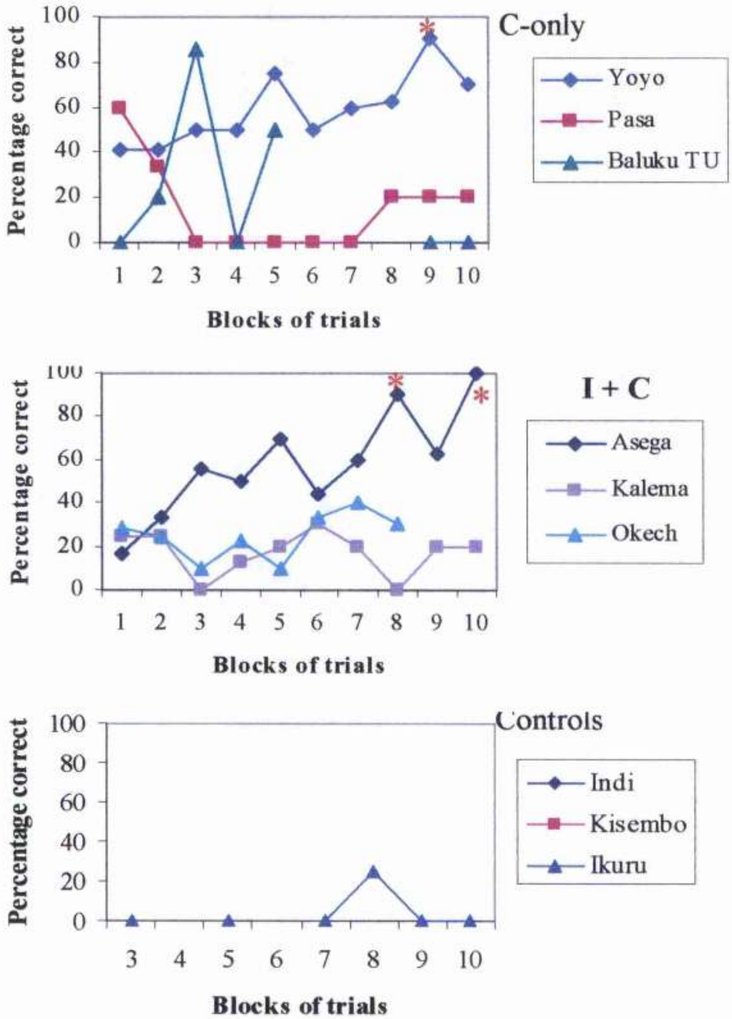


Figure 11.6 The percentage of correct responses made by subjects in each block of trials. The * symbol represents a trial where subjects performed significantly better than chance ($p<0.05$).

11.3.7 *Successful subjects*

Only two subjects, Yoyo (C-only) and Asega (I+C), performed at levels exceeding chance, and this occurred only during the second half of the experiment, during blocks 6 to 10 (see Table 11.3 and Fig. 11.6). Yoyo and Asega were also the only two subjects to have a significant side bias. Yoyo had a significant preference for the left side of the tube, and Asega for the right (see Table 11.3 and Fig. 11.7).

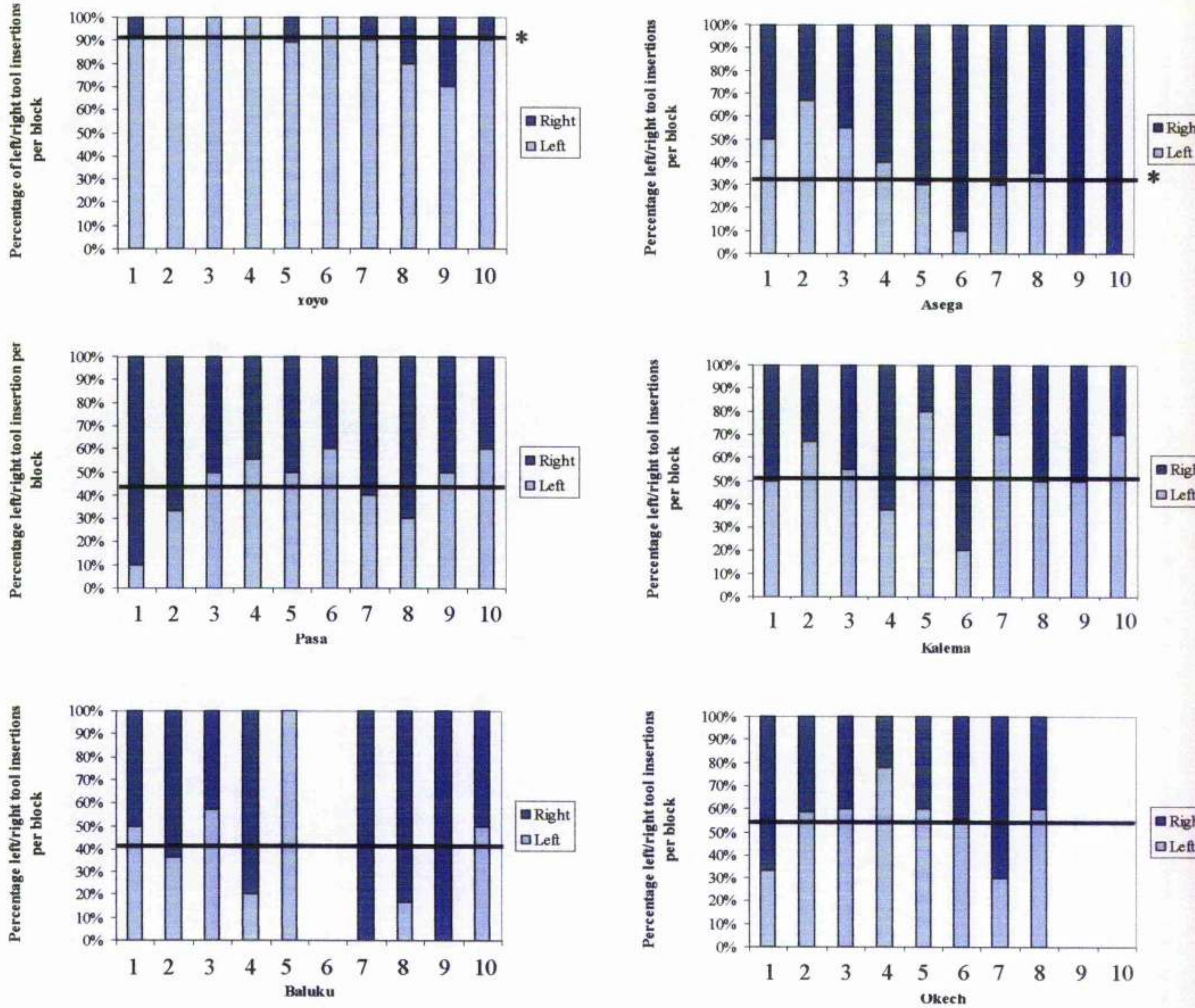


Figure 11.7 The percentage of tool insertions into each end of the apparatus by subjects from the C-only and I+C groups. The black line represents the mean percentage of insertions into the left side of the apparatus. Yoyo and Asega were the only two chimpanzees to show evidence of a significant side bias '*'.

How could Yoyo and Asega perform significantly better than chance when both chimpanzees had a side bias? The answer is that in the second half of the experiment they learned to correct their mistakes. Once the tool had been inserted into the apparatus in accord with their respective side biases, on a number of occasions both subjects withdrew the tool and reinserted it into the correct side of the tube. This rule seems to have been learned over the course of the experiment, as there was a significantly positive relationship between increasing block number and success (Spearman's *rho*: Yoyo = 0.825, p = 0.003; Asega = 0.83, p = 0.003; see Fig 11.8). However, this seemingly insightful behaviour was interspersed with errors. Having corrected a mistake on one trial, Yoyo and Asega were just as likely not to correct a mistake and trap the reward on a subsequent trial. Once they had discovered how to correct their biases they did not consistently use this information to maximise their success. Thus, this rule was incomplete.

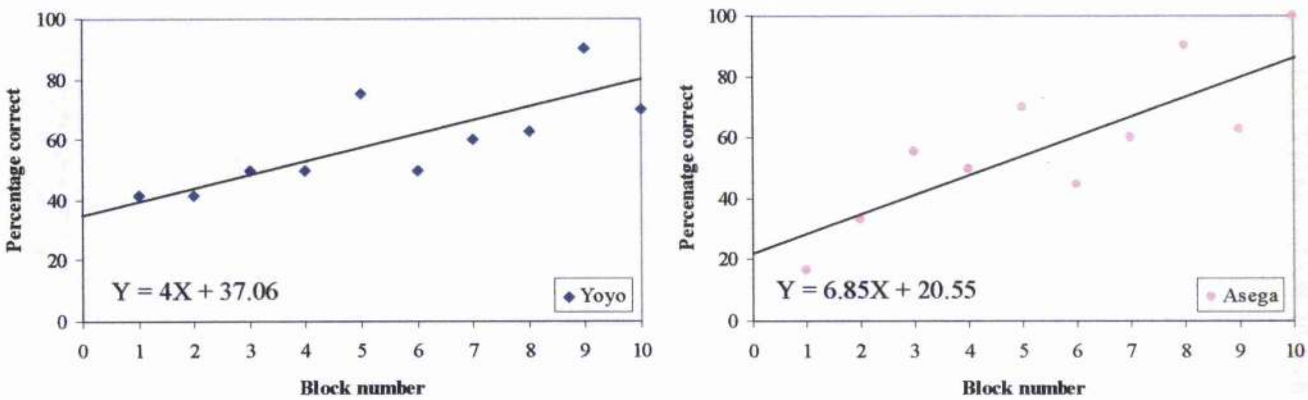


Figure 11.8 Percentage of correct trials performed by Yoyo (C-only) and Asega (I+C) for each block. The line represents the line of best-fit.

In addition, neither Yoyo nor Asega used single fluid movements to retrieve or trap the reward. They both used several small pushes of the tool on almost every trial, coupled with constant monitoring of the position of the reward. A single push was defined as contacting the reward with the tool and moving it through the tube then pausing before moving the reward again. Yoyo used a mean of 5.6 pushes per trial, and Asega used a mean of 5.8 pushes per trial. Interestingly, there was no significant difference between the number of pushes on successful trails compared to failed trials (Yoyo – median pushes on failed trials

= 2, median on successful trials = 3; Wilcoxon test for matched-pairs, N-ties = 29, $z = -1.27$, $p = 0.204$; Asega – median pushes on failed trials = 3, median on successful trials = 2; Wilcoxon test for matched pairs, N-ties = 21, $z = -1.51$, $p = 0.130$).

Yoyo and Asega were both seen to hold their hands under the food as it moved through the tube in an apparent attempt to catch it should it fall (see Figure 11.9). Even when the correct end of tool insertion had been chosen and the reward was moving away from the trap, they continued to use small tool insertions as if the reward could fall at any time.

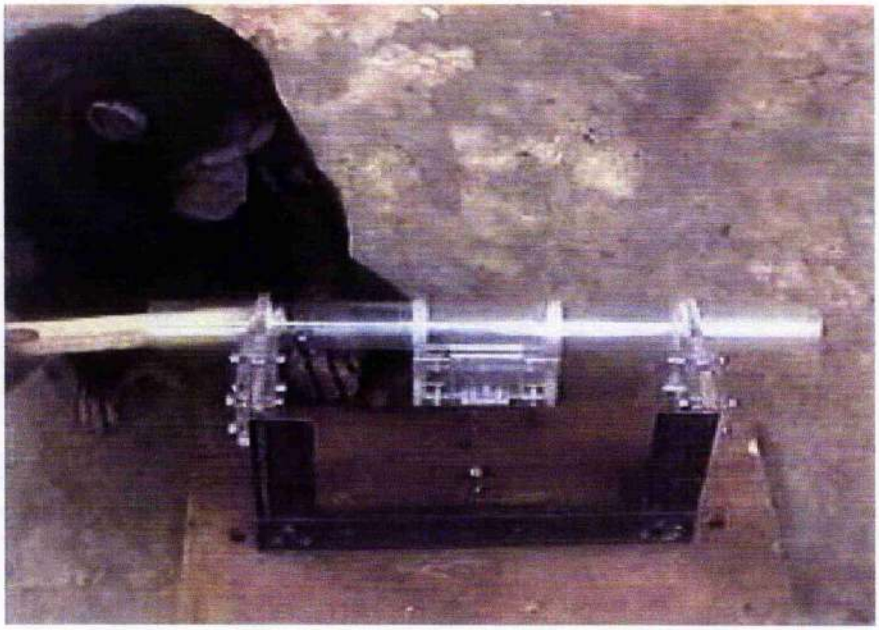


Figure 11.9 Asega moves his hand under the reward as he pushes it along the tube in an apparent attempt to catch it should it fall.

11.3.8 *Insertions on same side as previous demonstration*

One of the major concerns about using the trap-tube task in a social learning study was that success could be achieved by simply inserting the tool into the same side as the previous successful demonstration. However, the side of correct demonstration was counterbalanced within each block, therefore the side bias of Yoyo and Asega meant that they chose the same side as the demonstrator on approximately half the trials (see Table 11.5). Therefore they did not adopt a strategy of inserting the tool into the same side as the previous successful demonstration, and hence their success cannot be attributed simply to enhancement. Since the remaining subjects usually inserted the tool into the end of the tube closest to the reward, they chose to insert the tool on the opposite side from the previous demonstration significantly more than on the same side (see Table 11.5).

SUBJECT	GROUP	PERCENTAGE OF LEFT SIDE INSERTIONS	
Yoyo	**C-only**	58	(31/53)
Pasa		17 **	(9/52)
Baluku		No TU after demo	
Asega	**I+C**	52	(27/52)
Kalema		31 *	(16/52)
Okech		20 **	(8/40)
Ikuru	**Control**	0 **	(0/13)
Indi		-	
Kisembo		-	

Table 11.5 Percentage of trials in which tool insertion following a demonstration occurred on the same side as that demonstration. The '*' symbol represents a significant deviation from chance based on a binomial test (* $p < 0.05$, ** $p < 0.001$). All significant values indicate a preference for the side *opposite* from the demonstration. Baluku used his shaking strategy on all trials following a demonstration. Therefore there were no tool-using episodes to analyse.

11.4 Discussion of Experiment 5

11.4.1 *Control group* versus *experimental groups*

Subjects from both the *correct only* and the *incorrect + correct* groups inserted the tool into the apparatus (irrespective of whether the correct side had been chosen), on significantly more trials than subjects in the control group. The difference in performance between the control and experimental groups cannot be explained by differential enhancement, insofar as both groups observed the demonstrator using the tool in the same direction and to the same extent. The major difference between groups was that both experimental groups observed the tool make contact with the reward and push it along the tube. In contrast, control subjects observed the demonstrator move the tool along the top of the tube so that it did not make contact with the reward inside, and therefore did not bring about an effect. It seems that subjects in the experimental groups were able to learn the causal relevance of tool-reward contact by observation. However, control subjects did not see this regularity, and therefore did not learn this relationship. It is possible that the control subjects may have ignored the 'demonstrations' because they viewed them as irrelevant, since the tool did not bring about a significant outcome on the reward.

11.4.2 *Number of correct responses*

There was no significant difference in the performance of subjects who had observed only the correct solution and those who had additional information about the production of errors. Nevertheless, Figure 11.5 indicates that there was a trend in the predicted direction, in that subjects from the I+C group tended to retrieve the reward more frequently than subjects in the C-only group, and both groups succeeded more frequently than controls. The difference between the experimental groups and the controls was significant for the I+C, but not the C-only group, indicating that the observation of errors may have been beneficial. However, without statistical evidence, this trend is unsubstantiated, and it must be concluded that chimpanzees do not significantly benefit from observing errors in addition to successes.

The difference in performance between the control and experimental groups suggests that subjects benefited at a general level from observing the causal relationship between the tool and the reward, but not from the specific details of the demonstration. Subjects in both the C-only and I+C groups learned that the tool could be inserted into the tube in order to affect the position of the reward. However, as a group they did not appreciate that the passage of the reward into the trap was related to the side of tool insertion.

11.4.3 *Unsuccessful individuals*

Pasa (C-only), Kalema and Okech (I+C) continuously failed to avoid the trap, despite repeated opportunity to investigate an alternative strategy. On almost every trial, they inserted the tool into the end of the tube nearest the reward, pushing it into the trap. Nevertheless, all subjects seemed to recognise the conditions of failure. During both demonstrations and trials the chimpanzees were outwardly distressed by the loss of the reward, but despite recognising failure, they seemed unable to use this information to modify their behaviour in later attempts. Similar observations have been reported (Limongelli, Boysen, & Visalberghi, 1995; Reaux & Povinelli, 2000).

One explanation is that the subjects learned that once the reward dropped into the trap it could not be retrieved, but were unable to understand the conditions that led to this outcome. However, on a number of occasions subjects showed distress as the reward approached the trap. They therefore seemed to be able to anticipate the conditions of failure, but not use this information in their own later efforts. This may have been because they were able to predict and react to failure because they gained implicit knowledge about the observed sequence of events, but were unable to transfer this information into explicit knowledge that was available to higher processing systems required for planning and executing actions (Karmiloff-Smith, 1992; Povinelli, 2000).

Baluku's innovative strategy deserves special attention. Due to his injured left hand, he found it exceedingly difficult to manipulate the tool, and therefore developed an alternative non-tool-using strategy of shaking the reward out of the tube. There have been a number of studies of the effects of hand injury on food acquisition in wild chimpanzees with snare injuries. The results suggest that in the context of manual food processing, feeding efficiency may not be significantly effected (Stokes & Byrne, 2001). Injured individuals seem to compensate for disability by finding novel ways to achieve specific details of the 'normal' technique of conspecifics, but maintain the same overall method used by able-bodied peers (Stokes & Byrne, 2001; Byrne & Stokes, 2002). From this data, it might be expected that Baluku would adopt the same technique as the demonstrator, by inserting the tool with either his feet, or his mouth. However, he developed a totally novel non tool-use technique. This may have been because the size of the tool made it difficult to manipulate with another body part, leaving him no option but to develop a shaking strategy. Alternatively, he may have developed an individual technique because he was not strongly influenced by social learning. However, without comparative data about tool-use for wild populations with injuries it is not possible to offer more informed explanations.

11.4.4 *Successful individuals*

Yoyo and Asega were the only two chimpanzees who learned to successfully avoid the trap. Yoyo was a member of the *correct only* group, and Asega was a member of the *incorrect + correct* group. However despite observing different demonstrations their performances did not differ greatly. During the first half of the experiment, both subjects performed at chance levels because they each had a side bias. However, they were able to perform significantly better than chance during the second half of the study because they learned to correct their initial mistakes. After inserting the tool in accordance with their respective side biases, on a number of trials they withdrew the tool and reinserted it into the correct side of the apparatus. It is possible that because both chimpanzees had a side bias, the constancy of their behaviour (in that only the position of the reward altered between trials) allowed then to identify the conditions of success and failure where the other subjects could not.

The ability to correct mistakes appears at first to rely on a sophisticated understanding of the task and of the conditions of success and failure. However, for both subjects this seemingly insightful behaviour was interspersed with errors. Having corrected a mistake on one trial, it was possible that they would trap the reward on the following trial. In addition, both subjects did not seem to appreciate that once the correct side of tool insertion had been chosen, the tool could be pushed through the tube in one movement without endangering the reward. Both chimpanzees used several small pushes per trial to move the reward. There was no significant difference in the number of pushes that were used for successful or failed trials. This indicates that they regarded the whole tube area as a 'danger zone', and did not appreciate that if the reward was moving away from the trap it was safe.

On a number of occasions they both moved their hand underneath the reward as it moved through the tube, in what appeared to be an attempt to catch it should it fall, and gave distress vocalisations as they pushed the reward into the trap. Once the reward had dropped into the trap, they continued to push the tool back and forth in the tube in a vain attempt to retrieve the food. Visalberghi & Limongelli (1994) distinguished between *representational* task solution and *anticipatory* task solution. A representational strategy predicts that an individual has a mental representation of the requirements of the task, enabling them to succeed in any given trial by deciding *a priori* which is the correct response without trial and error. In contrast, an anticipatory strategy predicts that an individual constantly monitors the outcome of their actions and uses this information to determine the next manoeuvre. Yoyo and Asega's multiple push strategy, coupled with the idiosyncratic tendency to move their hand under the reward, indicated that they were constantly monitoring the outcome of each action before performing the next movement. Hence, their behaviour conforms most closely to an *anticipatory* rule-based strategy.

Before the experiment started, it was predicted that successful subjects would solve the task using the procedural rule *'always insert the tool into the end of the tube furthers from the reward'*. Instead both the successful subjects seemed to rely on an incomplete set of rules that were deployed in some, but not all appropriate conditions. For example, both Yoyo and Asega appear to have used the rule *'always insert the tool into the same side of the tube, but if it gets too close to the trap try the other end'*. However, on a number of trials where this rule would have been appropriate, they trapped the reward. This behaviour suggests that there were elements of the task that they found conceptually difficult. Both chimpanzees seemed to learn about the relevance of tool-reward contact by observation. However, they were unable to learn about the other causal relationships involved in the task. The direction in which the reward moved was dependent on the *force* applied by the tool, and passage of the reward into the trap was mediated by *gravity*. A number of authors have suggested that chimpanzees cannot learn about causal principles that are unobservable (Köhler, 1927; Tomasello & Call, 1997; Povinelli, 2000). The chimpanzees may therefore have been unable to form a comprehensive set of rules because they were unable to learn about the unobservable principles of force and gravity. However, this will be discussed in more detain in Chapter 14.

It is likely that the side biases of both Yoyo and Asega imposed a level of constancy to their behaviour that led them to uncover these rules where other subjects did not. By always inserting the tool into the same side, so that their behaviour was constant, and only the location of the reward altered, they may have been better able to learn that if the reward moved towards the trap, it would be lost.

Nevertheless, both Yoyo and Asega did develop a strategy, however incomplete, that allowed them to avoid the trap on significantly more trials than chance. Control subjects, who observed the stimulus enhancement demonstration, saw the tool moved in the same direction and to the same extent, and were given the same opportunity to interact with the apparatus, but did not learn such rules. The only difference between the demonstrations that were observed by Yoyo and Asega and the controls was that in the stimulus enhancement demonstration the tool did not contact the reward. It seems likely that the causal information that was available in the experimental group's demonstrations helped Yoyo and Asega to form their strategy. It therefore remains a possibility that chimpanzees benefit from observing causal relationships. However, the causal relationships that are involved in successful completion of the trap-tube task may be too cognitively demanding to clearly demonstrate this.

SUMMARY OF CHAPTER 12

The trap-tube task was used to determine whether 3- to 4-year-old children, unlike chimpanzees, could benefit from the observation of errors. This experiment was therefore conducted as a replication of Experiment 5. Children in the control group observed the tool being manipulated in the same direction, and to the same extent as children in the experimental groups. However, the tool was moved across the top of the apparatus, and therefore had no effect on the reward. Children in the experimental groups who observed the tool make contact with the reward were significantly more likely to insert the tool into the apparatus than the control group. However, like the chimpanzees, 3- to 4-year-old children were not significantly influenced by the observation of errors.

CHAPTER 12

EXPERIMENT 6: THE OBSERVATION OF ERRORS - 3- TO 4-YEAR-OLD CHILDREN

12.1 Introduction

Experiment 5 indicated that in the context of the trap-tube task, chimpanzees did not seem to benefit from observing errors. However, they were able to extract causal information about the causal relevance of tool reward contact by observation. Previous studies have shown that 3-year-old children who observed an adult perform errors and successes in a similar, but not identical study, performed significantly better than children who observed only successes (Want & Harris, 2001). However, for the reasons discussed in the previous chapter, the methodology and apparatus of that experiment may have made the children's task relatively easy. The following study was designed to examine how children would perform when tested on the same task as the chimpanzees.

12.2 Methodology

12.2.1 *Participants*

The participants for this study were 12 children aged 3-years-old (mean = 3:5, range = 3:0 – 3:11) and 18 children aged 4-years-old (mean = 4:3, range = 4:0 – 4:6) of both sexes (16 male; 14 female). The children were recruited from St Andrews Nursery School, UK following the completion of a letter of parental consent (see Appendix B).

12.2.2 *Apparatus*

The experimental apparatus was the same trap-tube that was used to test chimpanzees in Experiment 5. However, there were a number of minor alterations that made the apparatus more appropriate for children. Firstly, the tube was mounted on legs so that it could stand on a table 10 cm from the surface. Secondly, the tool was a smooth plastic tube 3.5 cm in diameter and 60 cm in length instead of a piece of wood, as it was felt that this would be more hygienic. Finally, the rewards were 10 brightly coloured plastic dinosaur eggs instead of food rewards, as a number of the children were known to have food allergies.

12.2.3 *Procedure*

The children were split into the same three groups as the chimpanzees, with an approximately equal number of males and females of each age and sex (see Table 12.1). Each group observed the same demonstrations as the chimpanzees in Experiment 5. However, the children were only presented with one block of ten trials. The position of the reward relative to the trap, and hence the correct side of tool insertion was randomised throughout the block, in that there was no discernible pattern, and the reward was never placed in the same location for more than two consecutive trials. There were four demonstrations spread throughout the block that were counter-balanced for the correct side of tool insertion, as in Experiment 5 with chimpanzees.

A pilot investigation revealed that children were reluctant to interact with the apparatus during the two-minute familiarisation period received by the chimpanzees. Therefore in order to ensure that both species had equivalent information about the apparatus before the first experiment began, the experimenter drew the children's' attention to specific feature of the apparatus that would be discovered by physical exploration. Each participant was told:

> *'This is the dinosaur game. This a long plastic tube, it has a hole at this end (demonstrate by inserting finger), and a hole at that end (demonstrate by inserting finger), and in the middle is the trap. The idea is to get the dinosaur egg out of the tube without it going into the trap.'*

The children were then told that there were 10 'goes' and they were to retrieve as many eggs as possible from the tube in order to win a plastic toy dinosaur. At the end of the session, each participant was praised for their participation and given a toy irrespective of their performance. During demonstrations the experimenter used the same vocalisations following successful and unsuccessful trials as the chimpanzee study.

Each child was tested individually in a separate room within the nursery. The apparatus was placed on a small table and the child was asked to sit on a chair in front of the apparatus for the initial explanation and the first demonstration. Following the first trial, the majority of subjects chose to stand up and were allowed to move freely around the apparatus, as was the case for chimpanzee participants. In addition, the children were not prevented from interacting with the apparatus or walking around during demonstrations. The chimpanzees were free to observe the demonstration from any angle, as well as participating in co-action in some cases, and it was felt that the best comparative data would be collected under testing conditions that were as similar as possible. The video coding and data analysis were the same as in experiment 5 (see section 11.2.4).

12.3 Results

12.3.1 *Control group*

The majority of subjects in the control group performed very few actions that were related to task solution. Only four subjects inserted the tool into the apparatus (see Table 12.1). None were able to succeed better than would be expected by chance (see Table 12.2). Of the remaining six children, one, (JL) did not interact with the apparatus at all during either demonstrations or trials. Another, (CB) inserted his fingers into the end of the tube nearest the reward in a vain attempt to reach the reward, on every trial. The remaining four children picked up the tool and moved it back and forth along the top of the apparatus in a similar manner to the control 'demonstrations'. Indeed, one subject (JW) repeated the sounds that the experimenter had made ('uuh ooh' and 'yay').

12.3.2 *Experimental groups*

Subjects in the C-only and I+C groups inserted the tool into the tube (irrespective of whether the correct side of insertion had been chosen) on significantly more trials than subjects in the control group (median C-only = 10, median controls = 0; Mann-Whitney *U*-test for unmatched samples, $z = -3.28$, $N_1 = 10$, $N_2 = 10$, $p = 0.001$, two-tailed; median I+C = 10; Mann-Whitney *U*-test for unmatched samples, $z = -3.12$, $N_1 = 10$, $N_2 = 10$, $p = 0.002$, two-tailed). However there was no significant difference in the number of tool insertions performed by either the C-only or I+C groups (median C-only = 10, median I+C = 10; Mann-Whitney *U*-test for unmatched samples, $z = -0.61$, $N_1 = 10$, $N_2 = 10$, $p = 0.542$, two-tailed; see Table 12.1).

Subjects in the control group observed the tool being moved in the same direction and to the same extent as the C-only and I+C groups. The major difference was that during the control demonstrations the tool did not bring about an effect on the reward located inside the tube. It seems that subjects in the experimental groups, who observed the tool make contact with the reward, like the chimpanzees, learned the causal significance of tool-reward contact. However, control subjects did not.

In contrast, the majority of children in the control group seem to have learned to reproduce the irrelevant actions (and in some cases sounds) that they observed during the first demonstration. Control subjects who did insert the tool were not able to perform significantly better than would be expected by chance (see Table 12.2).

CONTROLS			**C-ONLY**			**I + C**		
Subject	Age/Sex	**Trials**	Subject	Age/Sex	**Trials**	Subject	Age/Sex	**Trails**
KL	3M	**8**	BB	3M	**10**	DC	3M	**10**
JW	3M	**0**	CG	3M	**10**	MH	3M	**10**
RR	3F	**0**	KE	3F	**10**	JJ	3M	**10**
EC	3F	**8**	RG	3F	**10**	AB	3F	**10**
JP	4M	**10**	JT	4M	**10**	MO	4M	**9**
CB	4M	**0**	CM	4M	**10**	RC	4M	**10**
JL	4M	**0**	BL	4M	**10**	L	4M	**10**
JT	4F	**10**	SA	4F	**10**	HP	4F	**10**
CG	4F	**0**	SD	4F	**9**	CA	4F	**9**
C	4F	**0**	ER	4F	**10**	ML	4F	**10**
	Median	0		*Median*	10		*Median*	10

Table 12.1 Number of trials in which subjects inserted the tool into the apparatus, irrespective of whether the correct side of tool insertion was chosen.

12.3.3 *Number of correct responses*

There was no significant difference between the number of correct response performed by children in the C-only versus the I+C groups (median C-only = 50, median I+C = 55; Mann-Whitney *U*-test for unmatched samples, $z = -0.27$, $N_1 = 10$, $N_2 = 10$, $p = 0.798$, two-tailed). Neither of these groups retrieved the reward significantly more often that would be expected by chance (Wilcoxon test for matched samples, C-only v. chance, $z = -0.51$, N-ties = 7, $p = 0.611$, two-tailed; I+C v. chance, $z = -1.55$, N-ties = 8, $p = 0.121$, two-tailed). However, both experimental groups performed significantly better than controls (median control = 0, median C-only = 50; Mann-Whitney *U*-test for unmatched samples, $z = -2.36$, $N_1 = 10$, $N_2 = 10$, $p = 0.018$, two-tailed; median control = 0, median I+C = 55; Mann-Whitney *U*-test for unmatched samples, $z = -2.84$, $N_1 = 10$, $N_2 = 10$, $p = 0.005$, two-tailed; see Fig. 12.1 and Table 12.2). This result was not effected by the age of the participants (controls - median 3yr = 68.75, median 4yr = 40; Mann-Whitney *U*-test for unmatched samples, $z = -1.55$, $N_1 = 4$, $N_2 = 6$, $p = 0.121$, two-tailed: C-only – median 3yr = 50, median 4yr = 48.33; $N_1 = 4$, $N_2 = 6$, $p = 0.515$; two-tailed: I+C – median 3yrs = 55, median 4yrs = 47.22; $N_1 = 4$, $N_2 = 6$, $p = 0.747$). The results therefore suggest that 3- and 4-year-old children, like the chimpanzees, did not significantly benefit from the observation of errors.

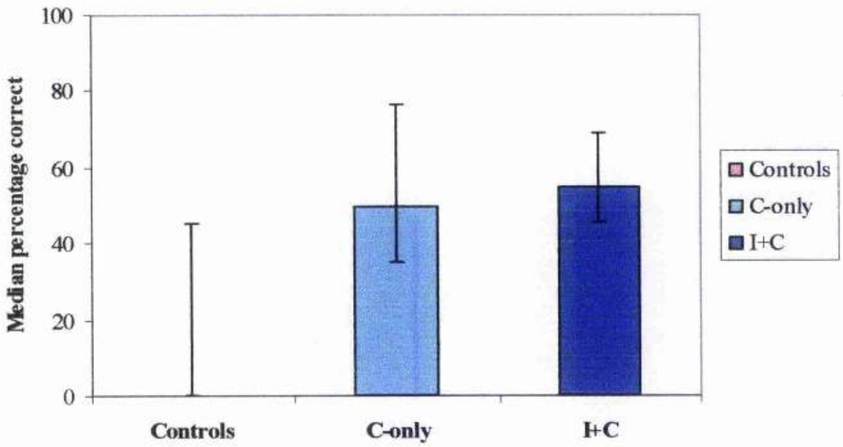


Figure 12.1 Median percentage of correct responses by subjects from each experimental group. Error bars represent the inter-quartile range.

CONTROLS			C-ONLY			I + C		
Subject	Age/Sex	**Success**	Subject	Age/Sex	**Success**	Subject	Age/Sex	**Success**
KL	3M	**62.5**	BB	3M	**100***	DC	3M	**40**
JW	3M	-	CG	3M	**50**	MH	3M	**50**
RR	3F	-	KE	3F	**50**	JJ	3M	**60**
EC	3F	**75**	RG	3F	**50**	AB	3F	**70**
JP	4M	**30**	JT	4M	**80**	MO	4M	**44.44**
CB	4M	-	CM	4M	**30**	RC	4M	**90***
JL	4M	-	BL	4M	**80**	L	4M	**40**
JT	4F	**50**	SA	4F	**30**	HP	4F	**50**
CG	4F	-	SD	4F	**66.67**	CA	4F	**66.67**
C	4F	-	ER	4F	**10***	ML	4F	**70**
	Median	0		*Median*	50		*Median*	55

Table 12.2 Percentage of successful trials. The '*' symbol represents a significant result based on a binomial test (* $p < 0.05$). For results less than 50% correct, significance indicates a performance significantly below chance.

12.3.4 *Patterns of success*

There was a positive correlation between increasing trial number and group performance. However, this relationship was not significant for any of the experimental groups, and hence the children did not show a progressive learning effect (Spearman's *rho*: controls = 0.39, p = 0.253; C-only = 0.44, p = 0.199; I+C = 0.451, p = 0.191; See Fig. 12.2).

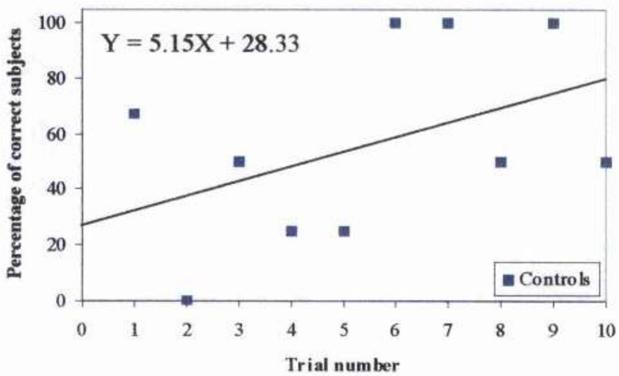
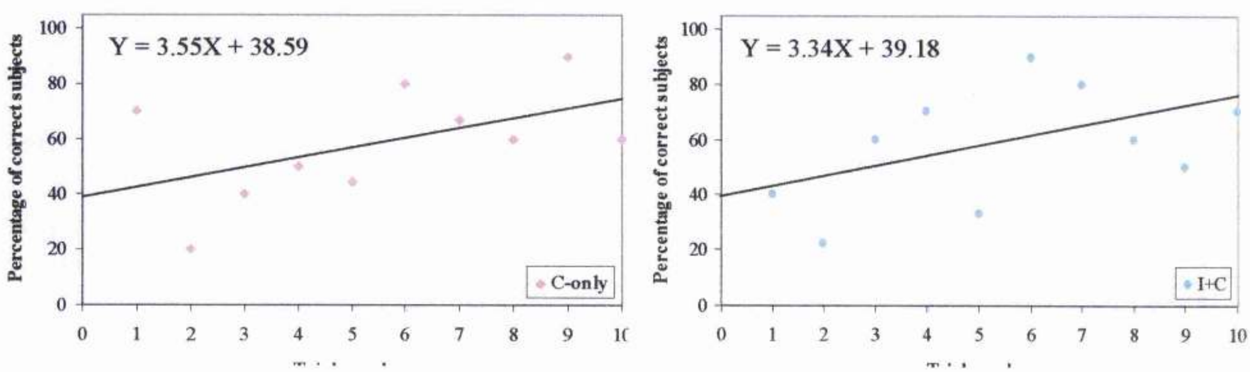


Figure 12.2 Percentage of children from each group who chose the correct side of too insertion on each trial. The line represents the linear best-fit, and suggests that there is a positive relationship between trial number and group performance. However this relationship is not significant for any of the groups.



12.3.5 *Side biases*

A greater number of subjects in the C-only group showed a significant tendency to insert the tool into the same side of the apparatus. However, when analysed as a group there was no significant difference in the side bias of children from the C-only and I+C groups (median C-only = 50, median I+C = 52.22; Mann-Whitney *U*-test for unmatched samples, z = -0.53, N_1 = 10, N_2 = 10, p = 0.593, two-tailed; see Table 12.3). Interestingly, each child who showed evidence of a side bias had a preference for the left side of the tube, which was the correct side of tool insertion for the first demonstration and trial. In addition, the majority of the remaining subjects tended to insert the tool more frequently into the left side of the tube. This suggests that children tended to reproduce the same behaviour that they observed during the first successful trial, rather than taking account of the causal properties of the task that determined the correct side of insertion on subsequent trials.

CONTROLS			**C-ONLY**			**I + C**		
Subject	Age/Sex	**% Left**	Subject	Age/Sex	**% Left**	Subject	Age/Sex	**% Left**
KL	3M	**37.5**	BB	3M	**50**	DC	3M	**40**
JW	3M	-	CG	3M	**50**	MH	3M	**100***
RR	3F	-	KE	3F	**100***	JJ	3M	**90**
EC	3F	**50**	RG	3F	**100***	AB	3F	**20**
JP	4M	**80**	JT	4M	**50**	MO	4M	**44.44**
CB	4M	-	CM	4M	**100***	RC	4M	**60**
JL	4M	-	BL	4M	**50**	L	4M	**70**
JT	4F	**100***	SA	4F	**60**	HP	4F	**80**
CG	4F	-	SD	4F	**30**	CA	4F	**44.44**
C	4F	-	ER	4F	**40**	ML	4F	**40**
				Median	50		*Median*	52.22

Table 12.3 The percentage of trials in which the tool was inserted into the left-hand side of the tube. Percentage of left insertions is used as a measure of side bias.

12.4 Discussion of Experiment 6

The results suggest that like chimpanzees, 3- and 4-year-old children did not significantly benefit from the observation of errors in the context of this study. Subjects who observed both success and failure were unable to utilise this additional information to extract the causal relationships involved in task solution, and perform significantly better than children who observed only solutions. However, children in the experimental groups who observed the tool being inserted into the apparatus seemed to learn the causal relevance of tool-reward contact. Children in the control group saw the tool being manipulated in the same direction and to the same extent as the other groups. The major difference was that in the control demonstration the tool was moved along the top of the apparatus and therefore had no significant effect on the reward located inside the tube. Observing that the tool could potentially be used to effect the position of the reward helped children to learn about contact. However they did not learn that the correct side of tool insertion was related to the position of the reward relative to the trap.

Children from each group showed a tendency to insert the tool more frequently into the left-hand side of the tube. Indeed, a number of children showed a significant left side bias (see Table 12.3). The left side was the correct side of insertion for each group during the first demonstration and trial. It therefore seems that children were more influenced to reproduce the behaviour that they observed during the first successful trial, than take account of the causal properties of the task that determined the correct side on subsequent trials. In addition, a number of the children in the control group were seen to reproduce the irrelevant actions and in some cases vocalisations of the demonstrator.

The results of this study contrast with the findings of Want & Harris (2001), who found that 3- year-old children were able to benefit from observing mistakes. However, there are a number of important ways in which the current study differs from theirs. Firstly, subjects received four demonstrations throughout the block of ten trials that were counter-balanced for the correct side of tool insertion. The increased number of demonstrations meant that subjects had a greater opportunity to learn by social, rather than individual learning. Secondly, the position of the reward was presented in a randomised sequence throughout the block of ten trials. It was therefore not possible to solve the task by learning to reverse responses on alternate trials. Finally, the trap was located in the middle of the tube so that the apparatus did not have to be rotated between trials.

The methodology of the present experiment was designed to test children under the same level of control that would be expected for work with any non-human species. When the same strict controls were applied, the results were not radically different from the chimpanzee subjects in the previous chapter. Both chimpanzees and children were able to learn the causal relevance of contact. However, control subjects who could not learn this rule behaved differently in each case. Chimpanzee control subjects responded by ignoring the demonstrations, and trying to reach the reward with their fingers. However, children in the control group responded by reproducing the irrelevant actions and vocalisations of the demonstrator. This finding is in accord with several studies that have demonstrated that young children have a tendency to reproduce observed actions at the expense of efficiency (Nagell et al., 1993; Whiten et al., 2003; Whiten et al., In press; see Chapter 4).

However, it is possible that the differences in experimental design meant that although the task was conceptually difficult for children of this age, it may be solved by older children. The following chapter will discuss whether the ability to solve the trap-tube task is related to the age of the participants.

SUMMARY OF CHAPTER 13

Experiment 7 was designed to determine whether children's ability to benefit from the observation of errors is related to age. The previous experiment showed that like chimpanzees, 3- to 4-year-old children do not benefit from the observation of errors in the context of the trap-tube task. This experiment was therefore conducted with 5- to 6-year-old children, to investigate whether older children would perform differently.

The results show that there was no difference in the performance of children from any of the three experimental groups, and that all groups performed significantly better than would be expected by chance. It seems that by the age of 5- to 6-years-old, children understand the causal principles involved in the trap-tube task, and hence do not benefit from observing errors.

CHAPTER 13

EXPERIMENT 7: THE OBSERVATION OF ERRORS - 5- TO 6-YEAR-OLD CHILDREN

13.1 Introduction

The results of the previous chapter indicate that 3- and 4-year-old children, like chimpanzees, were unable to significantly benefit from the observation of errors. The design of the current methodology may have made the task conceptually more difficult than previous studies which have tested children of this age (Want & Harris, 2001). It is possible that the ability to solve the trap-tube task is related to the age of the participants. The following study was designed to investigate the potential effect of age on task solution.

13.2 Methods

13.2.1 *Participants*

The participants for this study were 9 children aged between 5- and 6-years-old (mean = 5:6, range = 5:0 – 6:3) of both sexes (4 males and 5 females). The children were recruited from Kilrymont Primary School, UK, following completion of a letter of parental consent (see Appendix B).

13.2.2 *Apparatus*

This study used the same apparatus and rewards that were used in Experiment 6 (see Chapter 12).

13.2.3 *Procedure*

The children were divided into the same experimental groups as Experiment 6, with approximately equal numbers of males and females of each age (see Table 13.1). The children were tested in a separate room within the school, following the same procedure as Experiment 6. The video coding and data analysis was similar to that used in experiment 5 (see section 11.2.4).

13.3 Results

13.3.1 *Experimental groups*

There was no significant difference in the performance of children from the control group and either of the experimental groups. This was true for the number of tool insertions (see Table 13.1), the number of successful trials (median controls = 90, median C-only = 90; Mann-Whitney U-test for unmatched samples, $z = -0.47$, $N_1 = 3$, $N_2 = 3$, $p = 0.637$, two-tailed; median I+C = 90; Mann-Whitney U-test for unmatched samples, $z = -0.471$, $N_1 = 3$, $N_2 = 3$, $p = 0.637$, two-tailed; see Fig. 1), and the tendency to develop a side bias (median controls = 50, median C-only = 50; Mann-Whitney U-test for unmatched samples, $z = -0.69$, $N_1 = 3$, $N_2 = 3$, $p = 0.487$, two-tailed; median I+C = 40; Mann-Whitney U-test for unmatched samples, $z = -0.94$, $N_1 = 3$, $N_2 = 3$, $p = 0.346$, two-tailed). Therefore children from all three experimental groups performed in a similar way.

Subject	Age/Sex	Group	No. Tool Insertions	% Correct Trials	% Left Side Insertions
JW	6M	**Control**	10	90*	40
DS	6F	**Control**	10	90*	60
EG	5F	**Control**	10	100*	50
SC	6M	C-only	10	100*	50
SR	5M	C-only	10	90*	50
AW	5F	C-only	10	80	30
G	6F	I+C	10	100*	50
DN	5M	I+C	10	90*	40
LM	5F	I+C	10	70	40

Table 13.1 The number of tool insertions, percentage of correct tool insertions and percentage of left-hand side insertions performed by subjects from each group. The '*' symbol represents children who were able to solve the task significantly better than would be expected by chance (binomial test $p < 0.05$).

Since there were only three children in each group, it was not possible to determine whether each group performed above chance levels. However, when the performances of all the children were analysed together, they solved the task significantly more often than would be expected by chance (Wilcoxon test for matched samples, $z = -2.67$, N-ties = 9, $p = 0.007$, two-tailed).

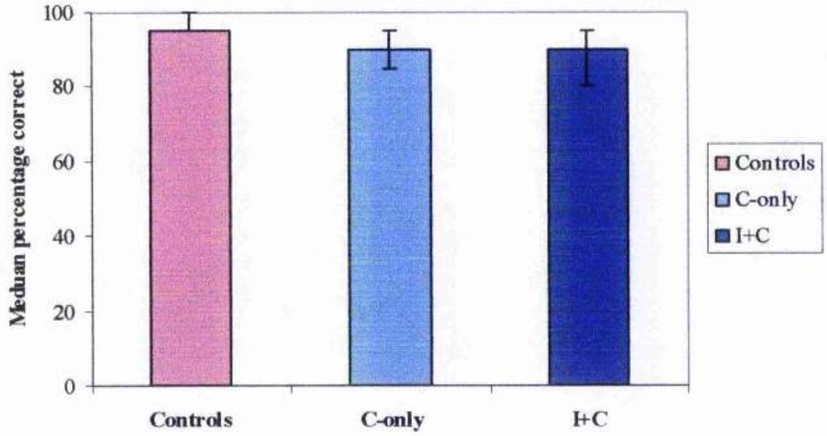


Figure 13.1 Median percentage of successful trials performed by children for each experimental group. The error bars represent the inter-quartile range.

13.3.2 *The success of the control group*

The control group observed demonstrations that were designed to eliminate the potential effects of stimulus enhancement. It is unlikely that their success was the result of emulation, since the actions of the demonstrator provided no information about the causal relationship between the tool and the reward. Similarly, the performance of this group cannot be explained by imitation, as the children inserted the tool into the apparatus on every trial despite never having been shown how to do this. If imitation were involved, the children would be expected to reproduce the irrelevant actions of the demonstrator, as was the case for the younger children in the previous chapter.

The performance of the control group did not improve across the block of trials, and hence was not influenced by a learning effect (Spearman's *rho*: controls = 0, p = 1; see Fig. 13.2). It seems most likely that children in the control group were able to perform above chance because they came to the experiment with a prior understanding of the causal principles that were involved in the trap-tube task.

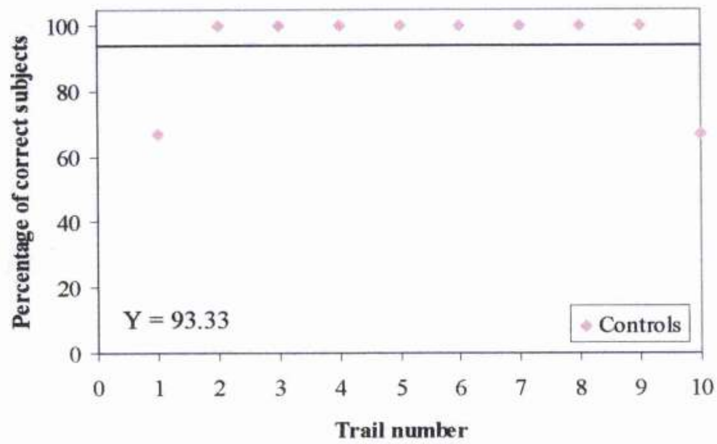


Figure 13.2 Percentage of children from the control group who chose the correct side of tool insertion on each trial. The line represents the line of best-fit.

13.3.3 *The success of the experimental groups*

The performance of children in both the control group and the experimental groups, suggests that 5- and 6-year-old children had prior knowledge about the causal principles that were required to solve the trap-tube task. It is therefore unsurprising that there was no significant difference in the performance of subjects from the C-only and the I+C groups. This was true for the number of tool insertions (see Table 13.1), the number of successful trials (median C-only = 90, median I+C = 90; Mann-Whitney *U*-test for unmatched samples, $z = -0.25$, $N_1 = 3$, $N_2 = 3$, $p = 0.822$, two-tailed), and the tendency to develop a side bias (median C-only = 50, median I+C = 40; Mann-Whitney *U*-test for unmatched samples, $z = -0.24$, $N_1 = 3$, $N_2 = 3$, $p = 0.814$, two-tailed). It seems likely that the children did not benefit from the observation of errors because they already knew how to solve the task.

The only difference in the performance of children in the C-only and I+C groups was in the pattern of success. Children in the C-only group showed no evidence of a learning effect across the block of ten trials (Spearman's *rho*: C-only = -0.114, p = 0.754; see Fig 13.3). However, in contrast, subjects in the I+C group did show a significant improvement in performance across trials (Spearman's *rho*: I+C = 0.742, p = 0.014; see Fig. 13.3). This effect was brought about because the majority of children in this group chose the incorrect side of tool insertion on the first trial (but chose correctly on subsequent trials).

The failure of the I+C group on the first trial is unlikely to have resulted from a lack of understanding of the task, since children in the control group were able to perform above chance on trial 1. Instead, it seems more plausible that the children's tendency to reproduce the actions of the demonstrator (incorrect side first), on the first trial over-shadowed their ability to take account of the causal properties of the task. In other words, they went for the same side as had the demonstrator, but this was now incorrect. However, once they had experienced failure themselves, their own understanding of the task took over.

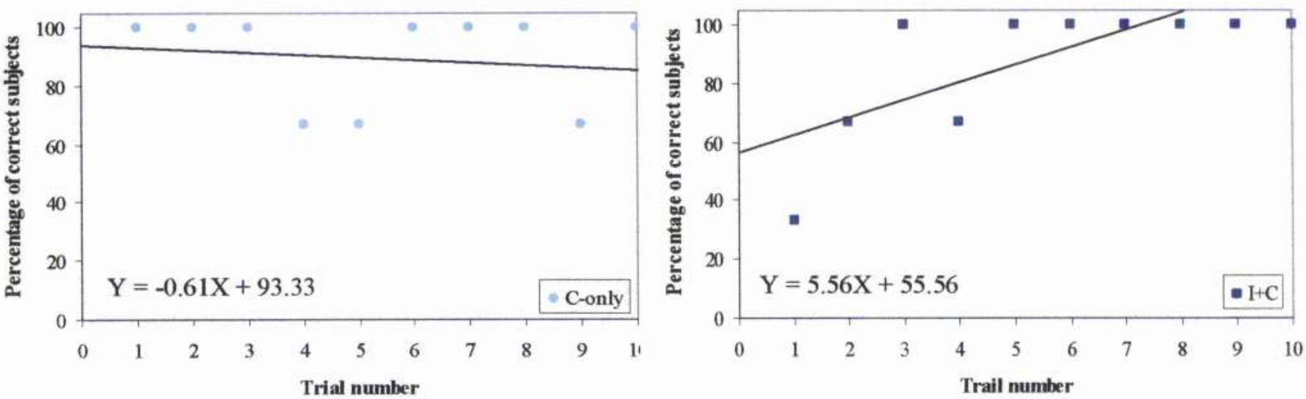


Figure 13.3 Percentage of subjects from the C-only and I+C groups who chose the correct side of tool insertion on each trial. The line represents the line of best-fit.

13.4 Discussion of Experiment 7

The successful performance of children in the control group indicates that 5- and 6-year-old children understood the causal principles that were involved in the trap-tube task, and were able to use this knowledge to perform significantly better than chance. Since children of this age already knew how to solve the task before the first trial, or were able to use the demonstrations to infer how to solve the task, there was no significant difference in the behaviour of children irrespective of which demonstration they observed. The slight difference in the performance of the I+C group on the first trial provides further evidence that the behaviour of children can be influenced by their tendency to reproduce observed actions at the expense of efficiency (Nagell et al., 1993; Whiten et al., 1996; see Chapter 4).

CHAPTER 14

GENERAL DISCUSSION OF EXPERIMENTS 5 TO 7

The results of Experiments 1 to 3 suggested that chimpanzees are sensitive to the causal relevance of observed actions, as they can differentiate and selectively exclude the irrelevant parts of a demonstration. If chimpanzees are able to learn causal information by observation, it follows that they could benefit more from observing errors and success, than just success, since errors provide additional information about what *not* to do. The trap-tube task was employed to test this hypothesis with chimpanzees and children aged 3- to 6-years-old.

14.1 The trap-tube task: Summary

The trap-tube is a clear, plastic, horizontal tube with a trapping hole located in the centre. When a food reward is placed in the tube it can only be retrieved by dislodging the reward with a thick tool. However, because of the trap, the end in which the tool is inserted determines whether the food is pushed into the trap, or out of the opposite end of the tube. The reward can only be successfully retrieved by always inserting the tool into the end of the tube farthest from the reward, thereby passing over the trap and pushing the food out of the opposite side. In Experiments 5 to 7, the food reward was placed on different sides of the trap during each trial in a randomised sequence.

Subjects were divided into three groups. The *correct only* group (C-only) observed a human experimenter always succeed in retrieving the food reward from the trap-tube. The *incorrect + correct group* (I+C) observed the demonstrator first fail by trapping the food, then succeed and retrieve the reward. Both these experimental groups were compared to a control group, who observed the demonstrator move the tool in the same direction, and to the same extent as the experimental group. The major difference was that the tool was moved across the top of the apparatus, and did not make contact with the food reward located inside.

14.2 Chimpanzees

14.2.1 *Experimental results*

Chimpanzees who observed either success alone (C-only), or successes and failure (I+C) performed better than the control subjects. It seems that by observing the tool make contact with the reward, chimpanzees in the experimental groups learned the causal relevance of tool-reward contact. However, there was no significant difference in the performance of the C-only or I+C groups, and therefore the chimpanzees did not seem to benefit specifically from the observation of errors.

Two subjects learned to avoid the trap. However, this strategy only emerged during the second half of the study, and was based on an incomplete set of rules that revealed many of their misconceptions. For example, their tendency to use multiple tool insertions, and place their hands under the reward as it moved along the tube, revealed that they did not fully understand the properties of the trap, or the relationship between the direction in which the reward moved and whether it would be trapped or retrieved. It seems that the chimpanzees understood the relevance of contact, as subjects in the experimental groups learned by observation to insert the tool into the apparatus. However, they did not fully understand the other causal principles involved in the task.

14.2.2 *Multiple causal relationships*

Visalberghi & Tomasello (1998) and Povinelli (2000) have argued that the trap-tube task may be conceptually difficult, as it involves a number of specific causal principles, which together may overwhelm chimpanzees. For example, it involves *contact* between the tool and reward, *force* exerted by the tool in order to move the reward, and *gravity* which mediates the passage of the reward into the trap. The literature indicates that chimpanzees have little knowledge of unobservable causal principles such as force and gravity. They may be able to form rules about the regularities imposed by these principles, but do not interpret this in a framework of abstract concepts. Povinelli (2000) has argued that chimpanzees may be able to learn rules of action in order to cope with unobservable principles, and may therefore perform better if these principles are tested individually. However, in the current study, the combination of causal relationships involved in the trap-tube task may have been too great for them to integrate.

Other studies have shown that chimpanzees are able to successfully solve the trap-tube task. For example, Visalberghi et al., (1995) and Reaux & Povinelli (2000) found that chimpanzees could form rules that allowed them to avoid the trap, even when the difficulty of the task was increased by altering the position of the trap (see Chapter 3). However, the current task may have made it more difficult for the chimpanzees to extract patterns of regularity because it involved social learning. Bard et al., (1995) found that chimpanzees could benefit from observing a model solve a tube task. However, the tube did not contain a trap, and therefore only one causal relationship was involved in solution; contact between the tool and the reward. The findings of the present study support the finding of Bard et al., (1995) that chimpanzees can learn the relevance of contact by observation. However, the additional causal relationships involved in the trap-tube task may have made the demonstrations confusing for the chimpanzees, and hindered their ability to extract patterns of regularity that involved multiple causal relationships.

In the wild, chimpanzees are able to learn tool-use tasks such as nut-cracking that involve multiple causal relationships. However, it takes many years for a young chimpanzee to become proficient. Longitudinal studies have shown that youngsters learn to nut-crack in stages, first combining nuts and anvils, then hammers and anvils, only later combining all three relationships to successfully crack nuts (Inoue-Nakamura & Matsuzawa, 1997). This observation supports the hypothesis that chimpanzees learn single causal relationships first, and then with experience learn to combine these relationships to solve tasks involving multiple principles.

14.2.3 *Presenting simultaneous choices*

Povinelli (2000) has argued that when multiple causal relationships are involved, chimpanzees may perform better if alternative solutions to a problem are presented simultaneously and the chimpanzees are required to choose between then. For example, he found that chimpanzees were able to solve the 'trap-table task' more frequently than the 'trap-tube task'. In the trap-table task, chimpanzees are presented with two tables; on each table is a food reward and a tool, that can be used to rake the reward towards the subject. However, one of the tables contains a trap in front of the reward, so that if the reward is pulled over the trap, it will fall and be lost. On the other table, in the same position as the trap, is a painted square, mimicking the trap (see Fig. 14.1). Povinelli argued that chimpanzees perform better at this task, although it taps the same knowledge as the trap-tube task, because each alternative can be seen. The chimpanzees therefore do not have to imagine and hold in mind both outcomes at the same time. He argued that the trap-tube task is difficult because subjects must imagine two outcomes (inserting tool into the left or the right side of the tube), in order to determine which action will lead to success. Thus, if the trap-tube task does overwhelm chimpanzees in this way, it may be too demanding a paradigm to investigate chimpanzee's ability to benefit from observing errors.

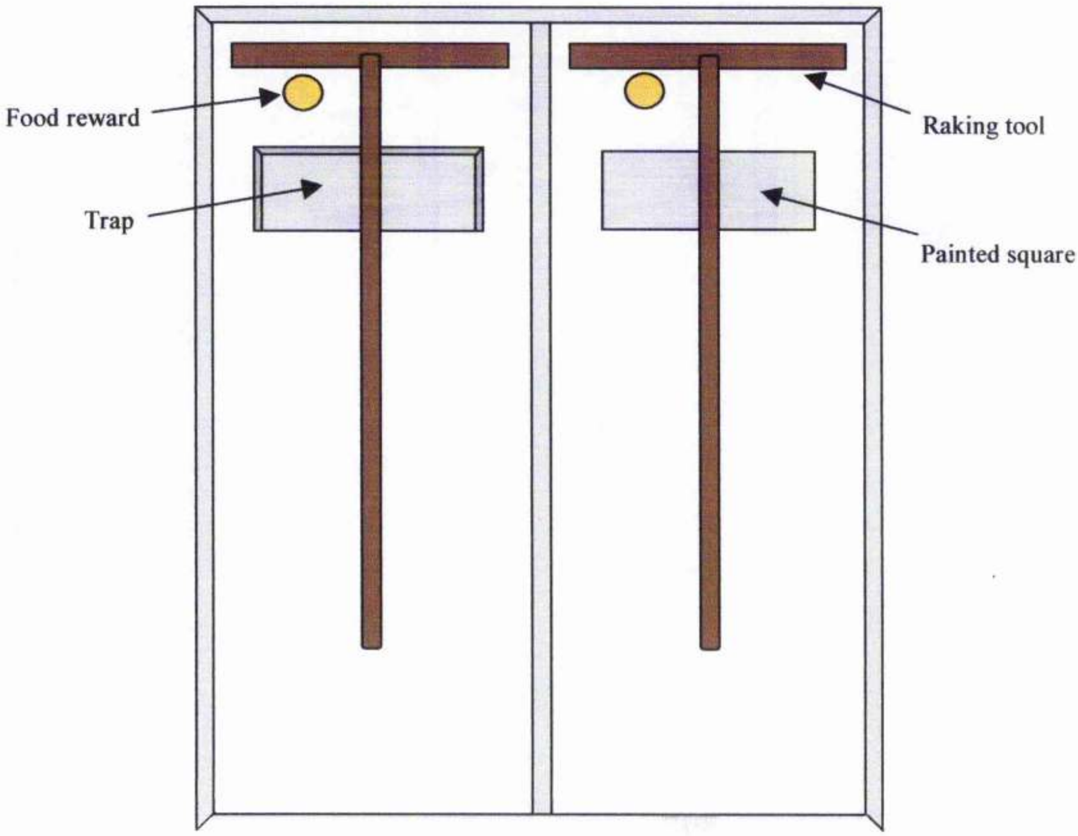


Figure 14.1 Trap-table apparatus used by Povinelli et al (2000), page 133.

14.3 3- to 4-year-old children

14.3.1 *Experimental results*

When the same experiment was conducted with 3- to 4-year-old children, they also did not benefit from the observation of errors. However, their mistakes revealed a different set of misconceptions. Children from the control group, like the chimpanzees, rarely inserted the tool into the apparatus. However, instead of trying in vain to insert their hands into the tube (as the chimpanzee controls had done), they tended to reproduce the irrelevant actions of the demonstrator. Many of the children from the control group recreated the irrelevant movements of the tool across the top of the tube, and in some cases repeated the irrelevant vocalisations of the demonstrator. It seems that when the children did not understand the principles of the task, they did not ignore the demonstration like the chimpanzees, but opted to include a greater proportion of what they saw.

Children from the experimental groups also showed a tendency to recreate the actions of the demonstrator, as they each showed a bias throughout the experiment for inserting the tool into the same side of the tube as the demonstrator had done on the first trial. However, they inserted the tool significantly more frequently than the control group. Therefore, like the chimpanzees, they seemed to benefit from observing the tool make contact with the reward, but did not significantly benefit from the observation of errors.

14.3.2 *Comparisons with published studies*

The literature suggests that by the age of 3-years-old, children have knowledge of the causal principles that are involved in successful completion of the trap-tube task, such as contact, force and gravity (see Chapter 4). However, in the majority of these studies, knowledge of each of these principles is tested individually, and it could be that children do not learn to combine this knowledge until later. Bullock et al., (1982) showed that 3-year-old children were able to combine their knowledge of these principles to correctly predict the outcome of an observed sequence of events (see section 4.3.2). However, the children were required to determine the only possible outcome, and did not have to choose between alternative solutions. It is therefore possible that the children could solve that task at age 3-

years because there was only one alternative. The trap-tube task may present a more difficult problem, as there are two potential outcomes; success and failure.

14.4 5- to 6-year-old children

14.4.1 *Experimental results*

In contrast, 5- to 6-year old children performed better than the younger children and the chimpanzees. Subjects from all three groups, including the control group, were able to perform significantly better than chance. The successful performance of children in the control group indicates that 5- to 6-year-old children understood the causal principles involved in the trap-tube task. They may have understood how to solve the task before the experiment began, or were able to use their causal knowledge to deduce how to solve the task once their attention had been drawn to the movements of the tool. Therefore it is not surprising that they did not benefit from observing errors.

The results suggest that although younger children (and possibly chimpanzees), may have knowledge about the principles involved in the trap-tube task, they are not able to combine this knowledge until the age of 5- to 6-years-old.

14.5 Developmental sequence

The findings of this set of studies contrast with the results of Want & Harris (2001), who found that 3-year-old children benefited from observing errors in a similar, yet not identical task. However, the methodology used by Want and Harris may have made the task easier than the present design by increasing the potential for children to solve the task by association (see Chapter 12).

In the present set of experiments, the observation of errors did not significantly benefit children from either age group. Want & Harris (2002) have suggested that children go through a developmental progression, from mimicry at birth, through imitation and finally to emulation by the age of 3 years. The results of this study agree with the order of the developmental sequence, but cast doubts over the age at which children are able to emulate. All studies to date (Brown, 1990; Bauer, 1992; Chen, Sanches, & Campbell, 1997; Bauer &

Kleinknecht, 2002) have failed to provide convincing evidence for emulation in children. For example, many of these studies involve children observing the solution to one task and then being asked to transfer the causal relationships inherent in the solution of the first task to a second task. However, the children are given the opportunity to interact with the first set of apparatus before transferring the causal relationships to the second task. Therefore individual learning, rather than social learning may underlie children's appreciation of the causal relationships (Want & Harris, 2002).

14.6 Comparative conclusions

The performance of the children and chimpanzees in the control groups reveals interesting species differences. It seems that when chimpanzees have an incomplete understanding of a task, they respond by ignoring the demonstration and trying their own alternative strategy, such as trying to retrieve the reward with their fingers. In the context of the trap-tube task, this was manifested in an incomplete set of associations, combined with learning the general relevance of inserting the tool into the apparatus. In contrast, when human children have an incomplete understanding of the causal relationships in an observed sequence, they tend to copy a large proportion of the actions that they see, irrespective of their causal relevance. In the context of the trap-tube task this was seen in the 3- to 4-year-old children's tendency to develop a side bias that was probably influenced by copying the first successful action of the demonstrator. In addition, children in the control group were seen to reproduce the irrelevant actions and vocalisations of the demonstrator. However, by the age of 5- to 6-years-old, children were able to combine their knowledge of contact, force and gravity to succeed at the trap-tube task. Nevertheless, they did not benefit from the observation of errors, and the current study does not provide any additional evidence that children of this age are able to emulate. This finding fits with other studies that have found children to imitate in situations where a task could be solved more efficiently by emulation (Nagell et al., 1993; Whiten et al., 1996).

CHAPTER 15

OVERALL DISCUSSION

The results of each experiment have been discussed in some detail in Chapters 10 and 14. The purpose of this final chapter is to give a summary of the conclusions that were drawn from the literature review, and the key findings of each empirical chapter. The results of each experiment will be discussed in terms of their general implications for chimpanzee and child cognition.

15.1 Review of the literature: Chimpanzees

15.1.1 *Causal knowledge*

The literature suggests that chimpanzee causal knowledge can best be characterised by an ability to rapidly detect patterns of regularity in the events that they observe, and use these patterns to form associations that link causes to effects (Köhler, 1927; Tomasello & Call, 1997; Visalberghi & Tomasello, 1998; Povinelli, 2000). It seems that chimpanzees can form rules about many regularities that they can see, such as event A is always followed by event B. However, there is little evidence that chimpanzees learn about unobservable causal principles that bind a cause and effect, such as force and gravity. While chimpanzees may be able to rapidly form rules about these principles, such as dropping an object causes it to fall, or that pushing an object causes it to move, they do not interpret these regularities in a framework of abstract concepts.

It seems that chimpanzees can form rules about many different events, however they may be cognitively overwhelmed when presented with tasks that involve more than one causal relationship (for example in an experimental setting). Many of the natural behaviours of chimpanzees do involve multiple causal relationships, such as nut-cracking. However, it takes chimpanzees many years to become proficient nut-crackers. Observational studies suggest that young chimpanzees first learn individual rules about the relationship between the hammer and anvil, hammer and nut, and anvil and nut, which are then combined together over many years to accomplish the final behaviour (Inoue-Nakamura & Matsuzawa, 1997).

Thus, complex tool-use behaviours that involve many causal interactions may be conceptually difficult for chimpanzees.

Nevertheless, the ability of chimpanzees to extract patterns of regularity is impressive in comparison to other non-human primates, and sufficient for their way of life. Their rule-based causal knowledge allows them to use tools, and interact with a diverse variety of objects (see Chapter 3). Indeed, Povinelli (2000) has suggested that rule formation is such a successful adaptive strategy in chimpanzees, that they are able to extract rules with impressive speed. It has been argued that chimpanzees may outperform monkeys in causal tasks, not because they have a deeper understanding of the tasks, but because they are so good at forming rapid associations (Visalberghi & Tomasello, 1998; Povinelli, 2000).

As long as chimpanzees can observe the regularities inherent in the solution to a particular problem (causal information), they are able to extract adaptive rules which can then be used to solve the task in their own later efforts. Hence, chimpanzees do have causal knowledge, and it is possible that they can identify relevant regularities by observation. The causal knowledge of chimpanzees is therefore sufficient to potentially be involved in social learning.

15.1.2 *Social learning*

The social learning literature indicates that chimpanzees employ different social learning strategies under different experimental conditions. Specifically, it seems that chimpanzees employ imitation more readily in non tool-use tasks, such as those involving the reproduction of gestures or single object manipulations. In contrast, they seem to employ emulation more readily to solve tasks that involve tool-use. However, rather than assuming that it is the task domain which dictates the social learning strategy which chimpanzees employ, Chapter 2 suggests more generally that chimpanzees might be influenced by the availability of causal information.

Studies that have found evidence for emulation have typically involved tool-use, and thus have involved causal relationships between objects, such as a tool and a reward. In these situations, chimpanzees may employ emulation because they have access to information about the causal relationships of the objects involved. They are able to use this information to detect the relevant parts of a behaviour, and form associative rules about cause and effect. Chimpanzees may preferentially employ emulation because it is a highly flexible strategy. Learning rules of action allows socially learned information to be generalised to different situations (Tomasello et al., 1987; Visalberghi & Fragaszy, 1994; Want & Harris, 2001, 2002).

In contrast, studies that have found evidence for imitation, such as the 'Do-as-I-do!' paradigm used by Hayes & Hayes (1952) and Custance et al., (1995), do not involve environmental components, and thus no causal information is available to the subjects. Similarly, in studies that have involved object manipulation, such as the 'artificial fruit' (Whiten et al., 1996; Whiten, 1999; Marshall-Pescini, 2002), the tasks involved the manipulation of a single object with the hands, and did not involve causal relationships between objects. Causal information was therefore either relatively restricted or difficult to infer, and the chimpanzees may have employed imitation to solve each task because emulation could not be so readily implemented. Thus, the trend for imitation in non tool-use tasks, and emulation in tool-use tasks may be related to the availability of causal information, and not the task domain *per se*.

15.2 Experimental predictions

(i) If this interpretation of the literature is correct, it follows that chimpanzees could be influenced to switch between imitation and emulation to solve the same task by altering the availability of causal information. It was predicted that if chimpanzees had access to relevant information about the causal relationships involved in a task, they could use this information to solve the task by emulation. However, if access to causal information is restricted, it was predicted that chimpanzees would be able to switch to imitation to solve the same problem.

(ii) Similarly, if chimpanzees are able to learn causal relationships by observation, they should benefit more from watching errors and successes and successes alone. This is because observing errors provides additional causal information about what *not* to do.

15.3 Experimental results

15.3.1 *(i) Imitation and emulation switching in chimpanzees*

Young chimpanzees observed a human demonstrate a tool-use task that involved both relevant and irrelevant actions. When the apparatus was presented in an opaque condition, in which access to information about the causal relationship between the tool and the reward was restricted, the chimpanzees reproduced a more complete copy of the model's behaviour. They reproduced both the relevant and irrelevant parts of the demonstration, in accordance with imitation. However, when the same task was presented in a transparent condition, so that the causal relationship between the tool and the reward was visible, the chimpanzees switched to emulation, insofar as they reproduced only the results of the model's actions, while ignoring the irrelevant parts of the observed behaviour. This ability to switch between imitation and emulation was not the result of increasing experience with the apparatus, as subjects who interacted with the transparent box first also excluded the irrelevant actions, in accord with emulation. When these individuals were then given access to the opaque apparatus, they continued to exclude the irrelevant action, although the opportunity to monitor the causal relationships between the tool and reward had been removed. This suggests that the chimpanzees were able to transfer some of what they had learned about the causal relevance of their actions from the transparent apparatus to the new experimental condition.

Thus, the notion that commonly arises in the literature that the prevalence of evidence for emulation in social learning indicates a deficit of imitative capacity in chimpanzees may be misleading. The results of Experiment 1 suggest more generally that when causal information is available, chimpanzees tend to use emulation. This may be because emulation is a highly flexible strategy, which allows socially learned information to be generalised to different situations. It seems that chimpanzees are able to imitate, but do so mainly in situations were emulation is not possible. Thus, the availability of causal information plays an important role in chimpanzee social learning, by determining which learning strategy is employed, and ultimately the degree of behavioural fidelity that is achieved.

15.3.2 *(ii) Observation of errors*

The trap-tube task was included in this study to determine whether chimpanzees could learn about causal relationships by observing errors. However, with the benefit of hindsight, it appears that the trap-tube task may have presented the chimpanzees with too complex a problem to tap their ability to learn from mistakes. In order to successfully solve the task, rules must be formed about the regularities of the task. However, some of these regularities are mediated by unobservable phenomena, such as force and gravity. Hence the multiple causal relationships involved in the task may have overwhelmed the chimpanzees. However, the trap-tube task did provide some interesting data about the types of causal information that can be learned by observation.

15.3.3 *Types of causal information that can be learned by observation*

In the trap-tube task, chimpanzees from both experimental groups who observed tool-reward contact, inserted the tool into the tube significantly more than the control group who did not see tool-reward contact. Thus, as in Experiment 1, the chimpanzees seemed to learn a rule about the causal relevance of tool-reward contact by observation. Contact is an observable regularity that is basic to many, if not all, tool-use activities. The causal relevance of contact between a tool and a reward can be easily recognised, and it is therefore unsurprising that the chimpanzees were able to learn this rule by observation.

The results of Experiments 2 and 3 confirmed that chimpanzees were able to learn about contact, as it seems they were able to determine that actions to the top of the box in Experiment 1 were causally irrelevant, because the tool did not contact the reward.

The central feature of chimpanzee knowledge is that it is based on rules that are not embedded in a framework of concepts. Therefore, although the chimpanzees were able to generalise the rules of contact learned in Experiment 1 from the transparent box to the opaque box, and later to solve Experiments 2 and 3, they did not understand the conditions of contact at a deeper level. Therefore, when presented with the trap-tube task (a completely different task), the chimpanzees had to learn new rules. Hence, only subjects who observed tool-reward contact in the context of the trap-tube task, were able to form useful rules.

Subjects from the control group, who did not see tool-reward contact, behaved as if they had no knowledge of the requirements of the task, although the same subjects had successfully learned contact rules that were specific to the previous experiments.

The ability to form rules about the relevance of contact accounts for only one of the causal principles involved in the trap-tube task. Successful completion of the trap-tube task involves *contact* between the tool and the reward, as well as *force* which must be exerted to move the reward along the tube, and *gravity* which mediates the passage of the reward into the trap. Hence, rules must be formed about each of these principles in order to perform significantly better than chance.

Two subjects from the experimental groups learned to avoid the trap. However, the rules that they formed to retrieve the reward were incomplete. Both chimpanzees used multiple pushes of the tool to move the reward along the tube, constantly pausing to monitor its passage. In addition, they both held their hand under the reward as it moved, indicating that they expected it to drop at any time, even when it was moving away from the trap. These observations suggest that, although the chimpanzees had knowledge about contact, they did not fully recognise certain other causal relationships involved in the task, i.e. force and gravity. Their incomplete knowledge of these unobservable principles seems to have hindered their performance.

The results of this set of experiments support the theory that chimpanzees are able to learn about certain causal features of the world by observation. They are able to rapidly detect patterns of regularity in the events that they observe, and differentiate between relevant and irrelevant actions. They use this information to form rules that link a cause to an effect. However, these rules can only be formed about events that can be directly observed. Chimpanzees show little, if any, knowledge of unobservable phenomena such as gravity. Chimpanzee's ability to emulate seems to be based on their ability to rapidly form such rules, and be able to generalise previous rules to similar problems. In some situations these rules can be generalised, as in Experiments 1 to 3. However, in other situations they can not, as in

Experiment 5. This is because chimpanzees do not interpret the knowledge that they have in a framework of abstract principles.

If a subject were able to represent causal relationships in a framework of abstract principles, it would be expected that they could generalise knowledge gained through experience with one problem to a completely novel situation that involved the same causal principle. In the scenario above, it would be expected that if the chimpanzee had an abstract concept of contact, they would be able to solve all contact problems, including the trap-tube task, and perhaps determine the solution to such problems *a priori*. An additional way to test this hypothesis would be to present specific generalisation tests. For example, a subject could observe a demonstrator use a rake to retrieve an out of reach reward. Before the observer was allowed to interact with the apparatus, they would then be presented with a different task in which the reward itself, the location of the reward and the configuration of the tool was different. The ability to generalise knowledge gained through observation to this novel situation would indicate that the subject had knowledge of the general principle of contact. If the subject was able to generalise in this way when presented with a variety of problems that tested different causal principles (such as contact, force and gravity tasks), it would suggest that they were able to represent causal relationships in framework of abstract principles.

15.3.4 *Causal information and emulation*

The ability to emulate suggests that chimpanzees are able to remember rules that have proved useful in the past, since they are able to find efficient solutions to novel problems. Studies have shown that chimpanzees are able to remember a diverse range of information. For example, they are able to remember the spatial location of nut-cracking sites (Boesch & Boesch, 1984) and termite mounds (Goodall, 1986). They are also able to recall social information about previous acts of support from individual group members, which can be used to determine coalition formation, and differential levels of reconciliation (de Waal, 1990, 1991, 1992). It is therefore possible that chimpanzees can also remember specific causal rules.

Chimpanzee causal knowledge may therefore not be based on a transient ability to form dyadic links between events. Rather, it may be based on a 'store' of rules formed from previous experience with their environment. Therefore, when faced with a task, such as the raking experiment of Tomasello et al., (1987), they are able to either quickly identify regularities and form new task-specific rules, or draw on rules from memory in order to solve the same task in a different, more efficient way. However, when causal information is not available, such rules are ineffective, and chimpanzees therefore switch to a strategy of imitation if an appropriate model has been observed.

15.4 Conclusions from the literature: Children

15.4.1 *Causal knowledge*

The developmental literature indicates that children develop a more sophisticated understanding of the world than do chimpanzees. Unlike chimpanzees, they do seem to have knowledge of unobservable causal principles, which they can use to form abstract concepts. A number of authors have suggested that children may be sensitive to phenomena such as force and gravity from birth (Spelke et al., 1995; In-Kyeong & Spelke, 1999). By the age of 3-years-old children are able to combine different forms of causal knowledge to solve tasks that involve prediction and action, and thus rely on more than simple association (Bullock et al., 1982; Shultz et al., 1982; Krist et al., 1993; Hood, 1995; von Hofsten et al., 1998). This would suggests that children would also be inclined to employ emulation in similar situations to chimpanzees.

15.4.1 *Social learning*

Comparative studies, which have tested chimpanzees and children under similar experimental conditions, have found that children tend to employ imitation in the same situations in which chimpanzees tend to emulate (Nagell et al., 1993; Whiten et al., 1996). Imitation is known to play an important role in early language acquisition (Meltzoff, 1988) and object knowledge (Abravanel & Gingold, 1985; Barr et al., 1996), and some authors have argued that the capacity for imitation may be present from birth (Meltzoff & Moore, 1977, 1983, 1989, 1994). Indeed, it has been suggested that it is because imitation is such an adaptive learning strategy in child development, that it is routinely employed in situations where alternative learning strategies would be more efficient (Whiten et al., 1996). Children may employ imitation more readily because, unlike the chimpanzees, they preferentially focus on the actions, rather than results and goals of a demonstrator. They may also reproduce a high fidelity copy of a demonstrator's behaviour because they have a greater tendency to infer intentions, and are more influenced by social conformity.

15.5 Experimental predictions

(i) From the review of the literature on causal knowledge, it would be expected that, like the chimpanzees, children would be able to learn about causal relationships by observation. However, the social learning literature provides no conclusive evidence that children use emulation to solve experimental tasks (Want & Harris, 2002). Therefore the appropriate predictions for this set of experiments was unclear. The comparative studies in this thesis were therefore conducted from a neutral perspective, in order to determine whether children would perform differently in a tool-use task that was conducted with the same level of control as a study with a non-human primate.

15.6 Experimental results

15.6.1 *Imitation and emulation switching in children*

In contrast to the chimpanzees, children tended to recreate the actions that they observed without appearing to consider the causal efficiency of their behaviour. The inclusion of functionally irrelevant actions, coupled with the high fidelity reproduction of the observed two-action methods of defence removal, strongly suggest that children relied on imitation to retrieve the reward in both conditions. The tendency to imitate was not influenced by either the age or the sex of the children.

Yet the literature (see Chapter 4) suggests that children of this age may have more sophisticated causal knowledge than chimpanzees. Why then did the children not utilise this knowledge to develop the most efficient technique to retrieve the reward? It seems most likely that, although the children may have appreciated that some of their actions were not necessary to solve the task, they reproduced them because the demonstrator did not indicate that they were either accidental or undesirable. Therefore differences in the behaviour of chimpanzees and children can perhaps best be explained by a differential focus of attention on actions, results and goals, with the latter possibly influencing the interpretation of the actions of the demonstrator as intentional.

The results of this experiment are therefore consistent with other studies that have found children to imitate in situations were emulation would lead to a more efficient solution.

15.6.2 *Observation of errors: 3- to 4-year-old children*

Like chimpanzees, the young children did not seem to benefit from observing errors. However, the performance of children in the control group revealed interesting species differences. The 3- to 4-year-old children from the control group performed much like the chimpanzees, in that they rarely inserted the tool into the tube. However, unlike the chimpanzees (who typically hit the apparatus with the tool or tried in vain to reach the reward with their fingers), the children tended to recreate the actions of the demonstrator. For example, they moved the tool across the top of the apparatus, and in some cases reproduced the vocalisations that the demonstrator had used. Again, as in Experiment 4, the children were reproducing the causally irrelevant behaviour that they had observed.

The 3- to 4-year-old children from the experimental groups, like the chimpanzees, learned the causal relevance of tool-reward contact, since they inserted the tool into the tube significantly more often that the control group. However, they did not significantly benefit from observing errors. Instead, they showed a tendency to reproduce the first successful action of the demonstrator. Thus, in the majority of trials the children showed a bias for the left side of the tube, which was the side used by the experimenter during the first demonstration. Again, it seems that they were more influenced by the actions of the demonstrator, rather than the causal relevance of their behaviour.

15.6.3 *Observation of errors: 5- to 6-year-old children*

Children approximately one year older behaved differently from both the younger children and the chimpanzees. Children from all three experimental groups (including the control group) were able to solve the task significantly more frequently than would be expected by chance. The children did not seem to benefit from the observation of errors, but they did seem to take account of the causal relevance of their behaviour. The fact that the control subjects were also able to solve the task suggests that by the age of 5-years-old, children have knowledge of the causal relationships involved in the trap-tube task. In addition, this knowledge does not seem to take the form of associative rules, as the children could solve the task in the majority of trials, and used neither the multiple push strategy, nor the hand moving strategy used by the chimpanzees. Therefore the children seemed to have some understanding of the unobservable causal relationships inherent in solution; force and gravity.

The literature indicates that 3- to 4-year-old children may also have knowledge of these principles. However, for the same reasons as with the chimpanzees, the multiple causal relationships that were presented in the trap-tube task may have overwhelmed them. Therefore, although they may be able to solve a trap-tube task at this age when it is not presented as a social learning paradigm (Limongelli, 1995; cited in Visalberghi & Tomasello, 1998), they found the demonstrations in the present study confusing.

Indeed, this study highlights the importance of age as a variable in child cognition. At the age of 3- to 4-years-old the children appeared to be overwhelmed by the multiple causal relationships presented in the trap-tube task, and relied strongly on imitation to retrieve the reward. However, 5- to 6-year-old children did not seem to imitate the actions of the demonstrator. It appears that as the children's individual understanding of the causal relationships they observed increased, their reliance on imitation decreased. In the context of the present study, it seems that a critical level of understanding was reached by the children between the ages of 5- and 6-years-old when their reliance on individual learning outweighed their reliance on social learning.

15.7 Species differences

When the chimpanzees were overwhelmed by the trap-tube task, they responded by ignoring the demonstrations, and trying their own method of reaching the reward, consistent with emulation. In contrast, when the younger children were overwhelmed by the demonstrations, they opted for a strategy of including a greater proportion of the demonstrator's actions and vocalisations. Thus, although the experiments with the opaque/clear box and the trap-tube were designed to investigate different hypotheses, the results of both experiments support comparative studies which have found children to employ imitation in situations where alternative social learning strategies may be more efficient (Nagell et al., 1993; Whiten et al., 1996).

The predominance of imitation in children, and the important role that it plays in the acquisition of language and motor skills, has lead some authors to suggest that imitation may be such an adaptive human strategy, that it is often employed at the expense of efficiency (Whiten et al., 1996). Likewise, it may also be true that emulation is such an adaptive strategy in chimpanzees that it is often employed at the expense of copying fidelity.

15.8 The question of culture

Chapter 2 uncovered some of the disagreements in the literature about the claim for chimpanzee culture. Some authors have argued that only particular social learning mechanisms, such as imitation, can guarantee that a behaviour is transmitted accurately enough for a cultural variant to be maintained (Galef, 1992; Heyes, 1993; Tomasello, Kruger et al., 1993; Tomasello, Savage-Rumbaugh et al., 1993). They argue that other forms of social learning are too inaccurate for variants to remain distinct over time. The results of this study indicate that different social learning processes may predominate in acquiring different types of behaviour. For example, tasks such as nut-cracking, which involve observable causal relationships between objects may rely more heavily on emulation than tasks such as termite fishing. In termite fishing, the causal relationship between the tool and the reward cannot be viewed inside the opaque termite mound, and thus chimpanzees may rely more heavily on imitation. However, in both situations, other learning strategies such as enhancement are likely to be incorporated into the chimpanzee's experience. It is therefore more realistic to acknowledge that cultural behaviours are probably acquired through a mixture of different social learning processes (McGrew, 1992; Whiten & Ham, 1992; Boesch, 1993; McGrew, 1993; Boesch, 1996b; Boesch, 1998; McGrew, 1998). The results of this set of studies suggest that chimpanzees are able to learn by both imitation and emulation, depending on the type of task. The key feature of emulation is that an observer recreates the results of a model's behaviour. Thus, as long as chimpanzees are able to reproduce the final product of an observed behaviour, either by emulation or imitation, a cultural variant may be maintained. Thus, the results presented in this thesis support the notion of chimpanzee culture.

REFERECES

Abravanel, E., & Gingold, H. (1985). Learning via observation during the second year of life. *Developmental Psychology, 21*, 614-623.

Aisner, R., & Terkel, J. (1992). Cultural transmission of pine-cone-opening behaviour in the black rat *(Rattus rattus). Animal Behaviour, 44*, 327-336.

Baillargeon, R., & Graber, M. (1988). Evidence of location memory in 8-month-old infants in a non-search AB task. *Developmental Psychology, 24*(4), 502-511.

Baillargeon, R., Kotovsy, L., & Needham, A. (1995). The acquisition of physical knowledge in infancy. In D. Sperber, D. Premack & A. J. Premack (Eds.), *Causal cognition: A multidisciplinary debate* (pp. 79-116). New York: Oxford University Press.

Baillargeon, R., Needham, A., & DeVos, J. (1992). The development of young infants' intuitions about support. *Early Development and Parenting, 1*, 69-78.

Bard, K. (1998). Imitation and mirror self-recognition may be developmental precursors to theory of mind in human and nonhuman primates. *Behavioural and Brain Sciences, 21*(1), 115-115.

Bard, K., & Russell, C. L. (1999). Evolutionary foundations of imitation: Social, cognitive, and developmental aspects of imitative processes in non-human primates. In J. Nadel & G. Butterworth (Eds.), *Imitation in infancy* (pp. 89-123). Cambridge: Cambridge University Press.

Bard, K. A., Fragaszy, D., & Visalberghi, E. (1995). Acquisition and comprehension of a tool-using behaviour by young chimpanzees *(Pan troglodytes):* Effects of age and modelling. *International Journal of Comparative Psychology, 8*, 47-68.

Barr, R., Dowden, A., & Hayne, H. (1996). Developmental changes in deferred imitation by 6- to 24-month-old infants. *Infant behaviour and development, 19*, 159-170.

Bates, E., Carlson-Lunden, V., & Bretherton, I. (1980). Perceptual aspects of tool using in infancy. *Infant Behaviour and Development, 3*, 127-140.

Bauer, P. J. (1992). Holding it all together: How enabling relations facilitate young children's event recall. *Cognitive Development, 7*, 1-28.

Bauer, P. J., & Kleinknecht, E. E. (2002). To 'ape' or to emulate? Young children's use of both strategies in a single study. *Developmental Science, 5*(1), 18-20.

Beck, B. B. (1980). *Animal Tool Behaviour: The Use and Manufacture of Tools by Animals*. New York: Garland STPM Press.

Bekkering, H., Wohlschlager, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology, 53A*, 153-164.

Bellagamba, F., & Tomasello, M. (1999). Re-enacting intended acts: Comparing 12- and 18-month-olds. *Infant Behaviour and Development, 22*(2).

Bering, J. M., Bjorklund, D. F., & Regan, P. (2000). Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Developmental Psycobiology, 36*, 218-232.

Bjorklund, D. F., Bering, J. M., & Regan, P. (2000). A two-year longitudinal study of deffered imitation of object manipulation in a juvenile chimpanzee *(Pan troglodytes)* and orangutan *(Pongo pygmaeus)*. *Developmental Psycobiology, 37*, 229-237.

Bjorklund, D. F., Yunger, J. L., Bering, J. M., & Regan, P. (2002). The generalisation of deferred imitation in enculturated chimpanzees *(Pan troglodytes)*. *Animal Cognition, 5*, 49-58.

Boesch, C. (1991). Teaching in wild chimpanzees. *Animal Behaviour, 41*, 530-532.

Boesch, C. (1993). Transmission of tool-use in wild chimpanzees. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language and Cognition in Human Evolution* (pp. 171-183). New York: Cambridge University Press.

Boesch, C. (1996a). Aspects of transmission of tool-use in wild chimpanzees. In W. C. Runciman, J. Maynard-Smith & R. I. M. Dunbar (Eds.), *Evolution of social behaviour patterns in primates and man* (pp. 244-265). Oxford: Oxford University Press.

Boesch, C. (1996b). The emergence of cultures among wild chimpanzee. In W. G. Runciman, J. Maynard-Smith & R. I. M. Dunbar (Eds.), *Evolution of Social Behaviour Patterns in Primates and Man* (pp. 244-265). Oxford: Oxford University Press.

Boesch, C. (1998). Three approaches for assessing chimpanzee culture. In A. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought : The minds of the great apes* (pp. 404-429). Cambridge: Cambridge University Press.

Boesch, C. (2003). Is culture the Golden Barrier between human and chimpanzee? *Evolutionary Anthropology, 12*, 82-91.

Boesch, C., & Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of hammer transport for nut cracking. *Primates, 25*(2), 160-170.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica, 54*, 86-99.

Boesch, C., & Boesch-Acherman, H. (2000). *The chimpanzees of the Tai forest.* Oxford: Oxford University Press.

Boesch, C., & Tomasello, M. (1998). Chimpanzee and human cultures. *Current Anthropology, 39*(5), 591-614.

Bonner, J. T. (1980). *The evolution of culture in animals.* Princeton: Princeton University Press.

Brewer, S. M., & McGrew, W. C. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica, 54*, 100-104.

Brown, A. L. (1990). Domain-specific principle affect learning and transfer in children. *Cognitive Science, 14*, 107-133.

Bshary, R., Wickler, W., & Fricke, H. (2002). Fish cognition: A primate's eye view. *Animal Cognition, 5*, 1-13.

Bullock, M., & Gelman, R. (1979). Preschool children's assumptions about cause and effect: Temporal ordering. *Child Development, 50*, 89-96.

Bullock, M., Gelman, R., & Baillargeon, R. (1982). The development of causal reasoning. In W. J. Friedman (Ed.), *The developmental psychology of time* (pp. 209-254). New York: Academic Press.

Byrne, R. W. (1996). *The Thinking Ape.* Oxford: Oxford University Press.

Byrne, R. W. (1998). Commentary on Boesch, C. and Tomasello, M. Chimpanzee and human culture. *Current Anthropology, 39*, 604-605.

Byrne, R. W. (2002). Emulation in apes: Verdict 'not proven'. *Developmental Science, 5*(1), 20-22.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences, 21*, 667-721.

Byrne, R. W., & Stokes, E. J. (2002). Effects of manual disability on feeding skills in gorillas and chimpanzees. *International Journal of Primatology, 23*(3), 539-554.

Caldwell, C. A., Whiten, A., & Morris, K. D. (1999). *Observational learning in the marmoset monkey (Callithrix jacchus).* Paper presented at the AISB Convention.

Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In K. Dautenham & C. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 211-228). Cambridge, MA: MIT Press.

Call, J., & Tomasello, M. (1995). Use of social information in the problem solving of Orangutans *(Pongo pygmaeus)*and Human children *(Homo sapiens). Journal of Comparative Psychology, 109*, 308-320.

Call, J., & Tomasello, M. (1998). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371-403). Cambridge: Cambridge University Press.

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans *(Pongo pygmaeus)*, chimpanzees *(Pan troglodytes)* and human children *(Homo sapiens). Journal of Comparative Psychology, 112*(2), 192-206.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology, 67*(2), 151-174.

Carpenter, M., Akhtar, N., & Tomasello, M. (1998). Fourteen-through 18-month-old infants differentially imitate intentional and accidental actions. *Infant behaviour and development, 21*(2), 315-330.

Carpenter, M., & Call, J. (2002). The chemistry of social learning. *Developmental Science, 5*(1), 22-24.

Catchpole, C. K., & Slater, P. J. B. (1995). *Bird songs: Themes and variations*. Cambridge: Cambridge University Press.

Celli, M. L., & Tomonaga, M. (2001). Learning processes in the acquisition of a tool using task by captive chimpanzees. *Psychologia, 44*, 70-81.

Charman, T., & Huang, C. (2002). Delineating the role of stimulus enhancement and emulation learning in the behavioural re-enactment paradigm. *Developmental Science, 5*(1), 25-27.

Chen, Z., Sanches, R. P., & Campbell, T. (1997). From beyond to within their grasp: The rudiments of analogical problem solving in 10- and 13-month-olds. *Developmental Psychology, 33*, 790-801.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour, 50*, 1441-1453.

Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit task in Capuchin monkeys *(Cebus apella)*. *Journal of Comparative Psychology, 113*(1), 13-23.

Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees *(Pan troglodytes)* imitate arbitrary actions? Heyes and Heyes (1952) revisited. *Behaviour, 132*, 837-838.

Dautenhahn, K., & Nehaniv, C. L. (Eds.). (2002). *Imitation in animals and artifacts*: MIT Press.

Dawson, B. V., & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour, 13*, 470-474.

de Waal, F. B. M. (1990). *Chimpanzee politics: Power and sex among apes*. London: Johns Hopkins University Press.

de Waal, F. B. M. (1991). *Peacemaking among primates*. London: Penguin Books.

de Waal, F. B. M. (1992). Coalitions as a part of reciprocal relations in the Arnhen chimpanzee colony. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 233-255). Oxford: Oxford University Press.

de Waal, F. B. M. (1998). No imitation without identification. *Behavioural and Brain Sciences, 21*(5), 689.

Dorrance, B., & Zentall, T. (2001). Imitative learning in Japanese quail *(Coturnix japonica)* depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology, 115*(1), 62-67.

Fragaszy, D. (2003). Making space for traditions. *Evolutionary Anthropology, 12*, 61-70.

Galef, B. (1988). Imitation in animals. In B. Galef & T. Zentall (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale: Lawrence Earlbaum.

Galef, B. (1992). The question of animal culture. *Human Nature, 3*(2), 157-178.

Galef, B. (In press). Breathing new life into the study of animal imitation: What and when do chimpanzees imitate. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science*. Cambridge, MA: MIT Press.

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

Gattis, M. (2002). Imitation is mediated by many goals, not just one. *Developmental Science, 5*(1), 27-29.

Gergely, G., Bekkering, H., & Kiraly, I. (2002). Rational imitation in preverbal infants. *Science, 415*, 755.

Gibson, K. R. (1993). Animal minds, human minds. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language and cognition in human evolution* (pp. 3-19). Cambridge: Cambridge University Press.

Goodall, J. (1973). Cultural elements in a chimpanzee community. In E. W. Menzel (Ed.), *Precultural primate behaviour* (Vol. 1): Karger.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behaviour*. Cambridge, Massachusetts: Harvard University Press.

Goswami, U. (1998). *Cognition in children*. Hove: Psychology Press.

Green, S. (1975). Dialects in Japanese monkeys. *Z. Tierpsychologie*(38), 305-314.

Hannah, A. C., & McGrew, W. C. (1987). Chimpanzees using stones to crack open oil palm nuts in Liberia. *Primates, 28*, 31-46.

Harnick, F. S. (1978). The relationship between ability level and task difficulty in producing imitation in infants. *Child Development, 49*, 209-212.

Hayes, K., & Hayes, C. (1952). Imitation in a home-raised chimpanzee. *Journal of comparative and physiological psychology, 45*, 450-459.

Helfman, G. S., & Schultz, E. T. (1984). Social transmission of behavioral traditions in coral reef fish. *Animal Behaviour, 32*, 379-384.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46*, 99-1010.

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Review of the Cambridge Philosophical Society, 6*, 207-231.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioural and Brain Sciences, 21*, 101-154.

Heyes, C. M., & Ray, E. D. (2000). What is the significance of imitation in animals? *Advances in the Study of Behaviour, 29*, 215-245.

Heyes, C. M., & Ray, E. D. (2002). Distinguishing intention-sensitive from outcome-sensitive imitation. *Developmental Science, 5*(1), 34-36.

Hirata, S., & Morimura, N. (2000). Naive chimpanzees' *(Pan troglodytes)* observation of experiences conspecifics in a tool-using task. *Journal of Comparative Psychology, 114*(3), 291-296.

Hirata, S., Watanabe, K., & Kawai, M. (2001). "Sweet-potato washing" revisited. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 487-508). Heidelberg: Springer-Verlag.

Hood, B. M. (1995). Gravity rules for 2- to 4-year-olds? *Cognitive Development, 10*, 577-598.

Huang, C., Heyes, C., & Charman, T. (2001). Infants' behavioural re-enactment of 'failed attempts': Exploring the role of emulation learning, stimulus enhancement and understanding of intentions. *in press*.

Huber, L. (1998). Movement imitation as faithful copying in the absence of insight. *Behavioural and Brain Sciences, 21*, 694.

Hurley, S., & Chater, N. (Eds.). (In press). *Perspectives on imitation: From cognitive neuroscience to social science*: MIT Press.

Imanishi, K. (1952). The evolution of human nature. In K. Imanishi (Ed.), *Man* (pp. 36-94). Tokyo: Mainichi-shinbunsha.

In-Kyeong, K., & Spelke, E. S. (1999). Perception and understanding of effects of gravity and inertia on object motion. *Developmental Science, 2*(3), 339-362.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees *(Pan troglodytes). Journal of Comparative Psychology, 111*, 159-173.

Itani, J., & Nishimura, A. (1973). *The study of infrahuman culture in Japan.* Paper presented at the Precultural primate behavior, Basel.

Jones, S. S. (2003). Why don't apes ape more? In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science*. Cambridge, MA: MIT Press.

Karmiloff-Smith, A. (1992). *Beyond modularity: A developmental perspective on cognitive science.* Cambridge, Massachusetts: MIT Press.

Kawai, M. (1965). Newly acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima Islet. *Primates, 6*, 1-30.

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

Kearton, C. (1925). *My friend Toto Adven*. London.

Kohler, W. (1927). *The mentality of apes* (2nd ed.). New York: Vintage Books.

Krings, M. (1997). Neanderthal DNA sequences and the origins of modern humans. *Cell, 90*, 19-30.

Krist, H., Fieberg, E. L., & Wilkening, F. (1993). Intuitive physics in action and judgement: The development of knowledge about projectile motion. *Journal of Experimental Psychology: Learning, Memory and Cognition, 19*, 952-966.

Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology, 12*, 150-159.

LeVine, R. A. (1984). Properties of culture: An ethnographic view. In R. A. Schweder & R. A. LeVine (Eds.), *Cultural theory: Essays on mind, self and emotion* (pp. 67-87). Cambridge: Cambridge University Press.

Limongelli, L. (1995). *Comprehensione delle relazioni di causa-effetto nei primati: Uno studio sperimentale.*Unpublished manuscript.

Limongelli, L., Boysen, S. T., & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-using task by chimpanzees *(Pan troglodytes)*. *Journal of Comparative Psychology, 109*, 18-26.

Marler, P., & Tamura, M. (1964). Song "dialects" in three populations of white-crowned sparrows. *Science, 146*, 1483-1486.

Marshall-Pescini, S. (2002). *Observational learning in chimpanzees (Pan troglodytes) using naturalistic experimental tasks*. Unpublished manuscript.

Matheson, M. D., & Fragaszy, D. M. (1998). Imitation is not the 'holy grail' of comparative cognition. *Behavioural and Brain Sciences, 21*, 697-698.

Mathieu, M., & Bergeron, G. (1981). Piagetian assessment on cognitive development in chimpanzee *(Pan troglodytes)*. In A. B. Chiarelli & R. S. Corruccini (Eds.), *Primate behaviour and sociobiology* (pp. 142-147). Berlin: Springer-Verlag.

Mathieu, M., Daudelin, N., Dagenais, Y., & Decarie, T. G. (1980). Piagetian causality in two house-reared chimpanzees *(Pan troglodytes). Canadian Journal of Psychology, 34*, 179-186.

Matsuzawa, T., & Yamakoshi, G. (1996). Comparison of chimpanzees material culture between Bossou and Nimba, West Africa. In A. Russon, K. Bard & S. T. Parker (Eds.), *Reaching into thought* (pp. 211-232). Cambridge: Cambridge University Press.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution.* Cambridge: Cambridge University Press.

McGrew, W. C. (1993). The intelligent use of tools: Twenty propositions. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language and cognition in human evolution* (pp. 151-170). Cambridge: Cambridge University Press.

McGrew, W. C. (1994). Tools compared: The material of culture. In R. M. Wrangham, W. C. McGrew, F. B. M. de Wall & P. G. Helter (Eds.), *Chimpanzee Cultures* (pp. 25-39). Cambridge, Massachusetts: Harvard University Press.

McGrew, W. C. (1998). Culture in nonhuman primates? *Annual Reviews in Anthropology, 27*, 301-328.

McGrew, W. C., Ham, R. M., White, L. T. J., Tutin, C. E. G., & Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology, 18*, 353-374.

Meltzoff, A. (1988a). Infant imitation after a one-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental Psychology, 24*, 470-476.

Meltzoff, A. (1988b). Infant imitation and memory: Nine-month-olds in immediate and deferred tests. *Child Development, 59*, 217-225.

Meltzoff, A., & Moore, K. (1989). Imitation in new-born infants: Exploring the range of gestures imitated and the underlying mechanisms. *Developmental Psychology, 25*, 954-962.

Meltzoff, A. N. (1988). Imitation, objects, tools and the rudiments of language in human ontogeny. *Human Evolution, 3*, 45-64.

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology, 31*, 1-16.

Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science, 198*, 75-78.

Meltzoff, A. N., & Moore, M. K. (1983). Newborn infants imitate adult facial gestures. *Child Development*(54), 702-709.

Meltzoff, A. N., & Moore, M. K. (1994). Imitation, memory and the representation of persons. *Infant Behaviour Development, 17*, 83-99.

Meltzoff, A. N., & Prinz, W. (Eds.). (2002). *The imitative mind: Development, evolution and brain bases*. Cambridge: Cambridge University Press.

Mercader, J., Pagner, M., & Boesch, C. (2002). Excavation of a chimpanzees stone tool site in the African rainforest. *Science, 296*, 1452-1455.

Miklosi, A. (1998). In the search for the functional homology of human imitation: Take play seriously! *Behavioural and Brain Sciences, 21*, 699-700.

Miklosi, A. (1999). From grasping to speech: imitation might provide the missing link. *Trends in Neurosciences, 22*, 151-152.

Morin, P. A., Moore, J. J., Chakrabrty, R., Jin, L., Goodall, J., & Woodruff, D. S. (1994). Kin selection, social structure, gene flow and the evolution of chimpanzees. *Science, 265*, 1193-1201.

Myowa, M. (1996). Imitation of facial gestures by an infant chimpanzee. *Primates, 37*, 207-213.

Myowa, M., & Matsuzawa, T. (2000). Imitation of intentional manipulatory actions in chimpanzees *(Pan troglodytes)*. *Journal of Comparative Psychology, 114*(4), 381-391.

Nagell, K., Olgin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees *(Pan troglodytes)*and human children *(Homo sapiens)*. *Journal of Comparative Psychology, 107*(2), 174-186.

Needham, A., & Baillargeon, R. (1993a). Intuitions about support in 4.5-month-old infants. *Cognition, 47*, 121-148.

Needham, A., & Baillargeon, R. (1993b). Reasoning about support in 3-month-old infants. *In press*.

Nishida, T. (1987). Local traditions and cultural transmission. In S. S. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Strusaker (Eds.), *Primate Societies* (pp. 462-474). Chicago: University of Chicago Press.

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M. N., & Jenner, K. C. S. (2000). Cultural revolution in whale songs. *Nature, 408*(6812), 537-537.

Panger, M., Perry, S., Rose, L. M., Gros-Luis, J., Vogel, E., MacKinnon, K. C., et al. (2002). Cross-site differences in the foraging behavior of white-faced capuchins *(Cebus capuchinus). American Journal of Physical Anthropology, 119*, 52-66.

Paquette, D. (1992). Discovering and learning tool-use for fishing honey by captive chimpanzees. *Human Evolution, 7*(3), 17-30.

Perry, S., Baker, M., Fedigan, L., Gros-Luis, J., Jack, K., MacKinnon, K. C., et al. (In press). Social conventions in wild white-aced capuchin monkeys: Evidence for tratitions in a neotropical primate. *Current Anthropology*.

Perry, S., & Manson, J. H. (2003). Traditions in monkeys. *Evolutionary Anthropology, 12*, 71-81.

Piaget, J. (1952). *The origins of intelligence in children*. New York: Norton.

Piaget, J. (2000). Piaget's theory. In K. Lee (Ed.), *Childhood cognitive development: The essential readings* (pp. 33-47). Oxford: Blackwell.

Poti, P., & Spinozzi, G. (1994). Early sensori-motor development in chimpanzees *(Pan troglodytes). Journal of Comparative Psychology, 108*, 93-103.

Povinelli, D. J. (2000). *Folk physics for apes: A chimpanzee's theory of how the world works*. Oxford, N.Y.: Oxford University Press.

Povinelli, D. J., & Dunphy-Lelii, S. (2001). Do chimpanzees seek causal explanations? Preliminary comparative investigations. *Canadian Journal of Experimental Psychology, 55*(2), 185-193.

Povinelli, D. J., Perilloux, H. K., Reaux, J. E., & Bierschwale, D. T. (1998). Young and juvenile chimpanzees' *(Pan troglodytes)* reaction to intentional versus accidental and inadvertent actions. *Behavioural Processes, 42*, 205-218.

Povinelli, D. J., & Reaux, J. E. (2000). The trap-tube problem. In D. J. Povinelli (Ed.), *Folk physics for apes: A chimpanzee's theory of how the world works* (pp. 132-148). Oxford, NY: Oxford University Press.

Premack, D. (1976). *Intelligence in ape and man.* Hillshale, NJ: Lawrence Earlbaum.

Premack, D. (1983). The codes of man and beasts. *Behavioural and Brain Sciences, 6*, 125-167.

Premack, D., & Premack, A. J. (1994). Levels of causal understanding in chimpanzees and children. *Cognition, 50*, 347-362.

Premack, D., & Premack, A. J. (1999). Why animals have neither culture nor history. In T. Ingold (Ed.), *Companion Encyclopaedia of Anthropology.* London: Routledge.

Reaux, R. E., & Povinelli, D. J. (2000). The trap-tube problem. In D. J. Povinelli (Ed.), *Folk physics for apes: A chimpanzee's theory of how the world works* (pp. 108-131). Oxford, NY: Oxford University Press.

Rendell, L., & Whitehead, H. (2001). Cultures in whales and dolphins. *Behavioural and Brain Sciences, 24*, 309-382.

Ridley, M. (1996). *Evolution* (2nd ed.). Cambridge: Blackwell Science.

Rogoff, B., Chavajay, P., & Matusov, E. (1993). Questioning assumptions about culture and individuals. *Behavioural and Brain Sciences, 16*(3), 533-534.

Russon, A. E. (1998). Imitation in everyday use: Matching and rehearsal in the spontaneous imitation or rehabilitant orangutans. In A. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 152-176). Cambridge: Cambridge University Press.

Russon, A. E., & Galdikas, B. M. F. (1995). Constraints on great apes' imitation: Model and action selectivity in rehabilitant orangutans *(Pongo pygmaeus)*imitation. *Journal of Comparative Psychology, 109*, 5-17.

Sakura, O., & Matsuzawa, T. (1991). Flexibility of wild chimpanzee nut-cracking behaviour using stone hammers and anvils: An experimental analysis. *Ethology, 87*, 237-248.

Sheak. (1917). *Proceedings of the Indian Academy of Science*, 301.

Shettleworth, S. J. (1998). *Cognition, evolution and behavior.* Oxford: Oxford University Press.

Shultz, T. R., Pardo, S., & Altmann, E. (1982). Young children's use of transitive inference in causal chains. *British Journal of Psychology, 73*, 235-241.

Sibulkin, A. E., & Uzgiris, I. C. (1978). Imitation by preschoolers in a problem-solving situation. *Journal of Genetic Psychology, 132*, 267-275.

Slater, P. J. B. (1986). The cultural transmission of bird song. *Trends in Ecology and Evolution, 1*, 94-97.

Somerville, S. C., & Capuani-Shumaker, A. (1984). Logical searches of young children in hiding and finding tasks. *British Journal of Developmental Psychology, 2*, 315-328.

Spelke, E. S., Katz, G., Purcell, S. E., Ehrlich, S. M., & Breinlinger, K. (1994). Early knowledge of object motion: Continuity and inertia. *Cognition, 51*, 131-176.

Spelke, E. S., Phillips, A., & Woodward, A. L. (1995). Infants knowledge of object motion and human action. In D. Sperber, D. Premack & A. J. Premack (Eds.), *Causal cognition: A multidisciplinary debate* (pp. 44-78). New York: Oxford University Press.

Stokes, E. J., & Byrne, R. W. (2001). Cognitive capacities for behavioural flexibility in wild chimpanzees *(Pan troglodytes)*: the effect of snare injury on complex manual food processing. *Animal Cognition, 4*, 11-28.

Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great apes and other animals. *Psychological Bulletin, 127*(5), 629-650.

Sugiyama, Y. (1981). Observations on the population dynamics and behaviour of wild chimpanzees at Bossou, Guinea, 1979-1980. *Primates, 22*, 435-444.

Sugiyama, Y. (1985). The brush-stick of chimpanzees found in Southwest Cameroon and their cultural characteristics. *Primates, 26*(4), 361-374.

Sugiyama, Y., & Koman, J. (1979). Tool using and tool making behaviour in wild chimpanzees at Bossou, Guinea. *Primates, 20*(4), 513-524.

Sumita, K., Kitahara-Frisch, J., & Norikoshi, K. (1985). The acquisition of stone-tool use in captive chimpanzees. *Primates, 26*, 168-181.

Suzuki, A. (1965). An ecological study of wild Japanese monkeys in snowy areas - focused on their food habits. *Primates, 6*, 31-72.

Suzuki, S., Kuroda, S., & Nishihara, T. (1995). Tool-set for termite fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour, 132*(3-4), 219-235.

Terkel, J. (1996). Cultural transmission of feeding behaviour in the black rat *(Rattus rattus)*. In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture*. London: Academic Press.

Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S. T. Parker & K. R. Gibson (Eds.), *Language and Intelligence in Monkeys and Apes* (pp. 247-273). Cambridge: Cambridge University Press.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture* (pp. 319-346). London: Academic Press.

Tomasello, M. (1998a). Emulation learning and cultural learning. *Behavioural and Brain Sciences, 21*, 703-704.

Tomasello, M. (1998b). Uniquely primate, uniquely human. *Developmental Science, 1*(1), 1-30.

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

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool use by young chimpanzees and enculturated chimpanzees. *Human Evolution, 2*, 175-183.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioural and Brain Sciences, 16*, 495-552.

Tomasello, M., Savage-Rumbaugh, E. S., & Kruger, A. (1993). Imitative learning of actions on objects by children, chimpanzees and enculturated chimpanzees. *Child Development, 64*, 1688-1705.

Tonooka, R., Tomonga, M., & Matsuzawa, T. (1997). Acquisition and transmission of tool making and use for drinking juice in a group of captive chimpanzees. *Japanese Psychological Research, 39*, 2593-2265.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., et al. (2003). Orangutan cultures and the evolution of material culture. *Science, 299*, 102-105.

Vauclair, J., & Bard, K. (1983). Development of manipulations with objects in ape and human infants. *Journal of Human Evolution, 12*, 631-645.

Visalberghi, E. (1993). Capuchin monkeys: A window into tool use in apes and humans. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language and Cognition in Human Evolution* (pp. 138-150). Cambridge: Cambridge University Press.

Visalberghi, E., & Fragaszy, D. (1994). Do monkeys ape? In S. T. Parker & K. Gibson, R. (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 247-273). Cambridge: Cambridge University Press.

Visalberghi, E., Fragaszy, D. M., & Savage-Rumbaugh, S. (1995). Performance in a tool-using task by common chimpanzees *(Pan troglodytes)*, bonobos *(Pan paniscus)*, an orangutan *(Pongo pygmaeus)*, and capuchin monkeys *(Cebus apella). Journal of Comparative Psychology, 109*(1), 52-60.

Visalberghi, E., & Limongelli, L. (1994). Lack of Comprehension of cause-effect relations in tool-using capuchin monkeys *(Cebus apella). Journal of Comparative Psychology, 108*(1), 15-22.

Visalberghi, E., & Limongelli, L. (1998). Acting and understanding: Tool use revisited through the minds of capuchin monkeys. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 57-79). Cambridge: Cambridge University Press.

Visalberghi, E., & Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behavioural Processes, 42*, 189-203.

Visalberghi, E., & Trinca, L. (1989). Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates, 30*(4), 511-521.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour, 60*(2), 195-202.

von Hofsten, C., Vishton, P., Spelke, E. S., Feng, Q., & Rosander, K. (1998). Predictive action in infancy: Tracking and reaching for moving objects. *Cognition, 67*, 255-285.

Want, S. C., & Harris, P. L. (1998). Indices of program-level comprehension. *Behavioural and Brain Sciences, 21*(5), 706-707.

Want, S. C., & Harris, P. L. (2001). Learning from other peoples' mistakes: Causal understanding in learning to use a tool. *Child Development, 72*(2), 431-443.

Want, S. C., & Harris, P. L. (2002). How do children ape? Applying concepts from the study of non-human primates to the developmental study of 'imitation' in children. *Developmental Science, 5*(1), 1-41.

Warner, R. R. (1988). Traditionality of mating-site preferences in coral reef fish. *Nature, 335*, 719-721.

Wellman, H. M., Somerville, S. C., & Haake, R. J. (1979). Development of search procedures in real-life spatial environments. *Developmental Psychology, 15*, 530-542.

Whiten, A. (1998a). How imitators represent the imitated: The vital experiments. *Behavioural and Brain Sciences, 21*(5), 707-708.

Whiten, A. (1998b). Imitation of the sequential structure of actions by chimpanzees *(Pan troglodytes)*. *Journal of Comparative Psychology, 112*(3), 270-281.

Whiten, A. (1999). *Imitation of sequential and hierarchical structure in action: Experimental studies with children and chimpanzees.* Paper presented at the AISB Convention, Edinburgh.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science, 24*(3), 477-508.

Whiten, A. (2002a). Imitation of sequential and hierarchical structure in action: Experimental studies with children and chimpanzees. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 191-209): MIT Press.

Whiten, A. (2002b). The imitator's representation of the imitated: Ape and child. In A. Meltzoff & W. Prinz (Eds.), *The imitative mind: Development, evolution and brain bases*. Cambridge: Cambridge University Press.

Whiten, A. (In press). The dissection of socially mediated learning.

Whiten, A., Custance, D. M., Gomez, J., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children *(Homo sapiens)*and chimpanzees *(Pan troglodytes)*. *Journal of Comparative Psychology, 110*(1), 3-14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, V., et al. (1999). Culture in chimpanzees. *Nature, 399*, 682-685.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (2001). Charting cultural variation in chimpanzees. *Behaviour, 138*, 1484-1516.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer & M. Milinski (Eds.), *Advances in the Study of Behaviour* (pp. 239-283). New York: Academic Press.

Whiten, A., Horner, V., & Marshall-Pescini, S. (2003). Cultural Panthropology. *Evolutionary Anthropology, 12*(2), 92-105.

Whiten, A., Horner, V., & Marshall-Pescini, S. (In press). Selective Imitation in Child and Chimpanzee:

A Window on the Construal of Others' Actions. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: from cognitive neuroscience to social science*: MIT Press.

Zentall, T. (2001). Imitayion in animals: Evidence, function, and mechanism. *Cybernetics and Systems, 32*.

APPENDIX A

NGAMBA CHIMPANZEES: HISTORIES BEFORE ARRIVAL AT NGAMBA

JUVENILE GROUP			
NAME	**SEX**	**~ DATE OF BIRTH**	**CONFISCATION LOCATION**
Ajore	F	1996 († June 2001)	Arua, Northern Uganda
Asega*	M	1998	Arua, Northern Uganda
Born in the bush - Lubara			
Baluku*	M	1998	Mponde, QENP
Name of ranger rescued him			
Bili*	F	1997	DRC
Town in DRC			
Ikuru*	F	1995	Arua, Northern Uganda
Happy one - Lubara			
Indi*	M	1999	Bwera, QENP
Independent one			
Kalema*	M	1996	Army border-post, Kampala
Dr Gladys Kalema			
Kisembo	M	1998	Arua, Northern Uganda
Mawa*	M	1996	Arua, Northern Uganda
Has faced problems - Lubara			
Mukisa*	F	1998	Bwera, QENP
Nkumwa*	F	1996	Cook at US Marine HQ, Kampala
I am protected - Luganda			
Pasa*	F	1999	Arua, Northern Uganda
Named after PASA			
Umugenzi*	M	1997	Burundi
Friend - Kirundi			
Umutama*	M	1996	Burundi
Old one - Kirundi			
Yiki*	M	1998 († June 2002)	Bwera, QENP
Survivor - Lubara			
Yoyo*	F	1998	Kasese

* Took part in one or more experiments.

Italics: How the chimpanzees were named

ADULT GROUP			
NAME	**SEX**	**~ DATE OF BIRTH**	**CONFISCATION LOCATION**
Bahati	F	1990	Kibale area, Western Uganda
Becky	F	1991	Kampala area
Cindy*	F	1993	Masindi, Western Uganda
Connie	F	1989	Army raod-block near Mbarara
Eddy	M	1989	Akefs Egyptian Circus, Kampala
Katie	F	1987	Entebbe airport
Kidogo	F	1984	Entebbe airport
Maisko	M	1984	Entebbe airport
Megan	F	1984	Entebbe airport
Mika	M	1992	Akefs Egyptian Circus, Kampala
Nagoti	F	1986	Kampala area
Natasha	F	1990	Arua, Northern Uganda
Peace	F	1986	Colleen Hotel, Mukono, Uganda
Robbie	M	1986	Kyambura village
Sally	F	1991	Kampala area
Sophie	F	1986	Malaba, Kenya borber
Sunday	M	1987	Entebbe airport (Ex-circus chimpanzee)
Tumbo	M	1989	Entebbe airport

APPENDIX B: LETTER OF PARENTAL CONCENT

UNIVERSITY OF ST ANDREWS
SCHOOL OF PSYCHOLOGY
ST ANDREWS, FIFE, SCOTLAND, U.K., KY16 9JU

Victoria Horner

Switchboard: (+44) 1334 462072
Direct line: (+44) 1334 462096
Fax: (+44) 1334 463042
E-mail: vkh1@st-and.ac.uk

Dear Parent / Guardian

I am a PhD student at St Andrews University studying some aspects of normal development in young children. My work focuses on how children learn to solve a puzzle-game by watching someone else.

I am writing to ask if you would permit your child to participate in this study.

The game involves using a tool to retrieve a cartoon-sticker from a plastic box. Each child would be shown how to solve the puzzle, and then allowed to retrieve the sticker 6 times. I am interested in the extent to which children copy the demonstrated technique, in comparison to exploring alternative methods. There is no wrong or right answer.

The study is designed to look at the development of children as a group, and therefore not to single out individual differences between children. Your child will be allowed to choose on a daily basis whether they participate or not. However, in the past it has been more problematic to persuade children that they can only participate 6 times!

The game would be video recorded, but the camera would focus mainly on the hands, and the tape would remain within the School of Psychology, and be viewed only for scientific analysis. In the event of the findings being published, no child will be identifiable from the rest of the group.

I would be extremely grateful if you would permit you child to participate in this study. Please complete the form below and return it to the nursery as soon as possible.

Yours sincerely

Victoria Horner

Please tick the relevant box:

I give permission for my child to participate in this study ☐

I do not wish my child to participate in this study ☐

Name of child.. Date of birth..............................

Signature of parent / guardian...

UNIVERSITY OF ST ANDREWS
SCHOOL OF PSYCHOLOGY
ST ANDREWS, FIFE, SCOTLAND, U.K., KY16 9JU

Victoria Horner

Switchboard: (+44) 1334 462072
Direct line: (+44) 1334 462096
Fax: (+44) 1334 463042
E-mail: vkh1@st-and.ac.uk

Dear Parent / Guardian

I am a psychology student studying intelligence in chimpanzees. Chimps are the most closely related animal to humans, and many scientists believe that by studying chimpanzees, we may learn a lot about why we are the way we are.

My work involves giving puzzle games to infant chimps to seeing how well they can solve them. To decide how cleaver the chimps are, I then compare them to children of the same age. I am therefore writing to ask if you would permit your child to participate in a puzzle game study. The children would be part of a group against which chimpanzees can be compared.

The puzzle game involves using a stick to push a toy out of a plastic tube that is open at both ends. Each child will be shown how to solve the task, then encouraged to retrieve the toy. I am interested in how children try to get the toy, not whether they succeed or fail, so there is no wrong or right answer.

The study is designed to look at children as a group, and not to single out individual differences between children. Your child will be asked to choose on a daily basis whether they wish to participate or not. The game would be video recorded, but the tapes will be locked inside the university and viewed only as part of this study. No child will be identifiable by name. Many scientific journals require that researchers keep raw data for 5 years after the study is published. The tapes will therefore be destroyed 5 years after the first publication.

Having undergone a Fife Police background check, I have been cleared to work with children.

If you wish your child to participate in this study, please could you fill out the form attached and hand it to Mrs Edwards.

Thank you

Victoria Horner

Please tick the relevant box:

I give permission for my child to participate in this study ☐

I do not wish my child to participate in this study ☐

Name of child.. Date of birth..............................

Signature of parent / guardian..

UNIVERSITY OF ST ANDREWS

SCHOOL OF PSYCHOLOGY ETHICS COMMITTEE

PROPOSAL FOR RESEARCH

Please submit 8 copies of the completed Proposal Form, which **must** include (if applicable) Participant Information Sheets, Debriefing Form, Consent Forms and any Advertisements for subjects to: Tracy Niven, Committee Secretary. Alternatively submit 1 copy by email attachment to tlm1@st-and.ac.uk, clearly labeled 'Ethics Application' (you must however submit 1 paper copy of the signed signature sheet).

Name and Status of Proposer:
Victoria Horner, Postgraduate Student

Name of Supervisor:
Prof. Andrew Whiten

Title of Proposed Project:
Observational Learning about Causality in Tool-use

Does this Study involve the participation of children and/or vulnerable adults?

YES

Please give a summary of the proposed project, including the questions to be answered, full details of the participants, the procedures to be used, and how the data will be analysed. Explain in plain words why this particular investigation is important: what is it going to contribute to our knowledge in the field? Use this page, and not more than one additional page.

The proposed study will use a trap-tube task to assess whether children are able to extract causal information about a tool-using problem by observing an adult demonstrator. It seems likely that the way in which an individual learns to use a tool by social learning will be directly related to his/her understanding of the causal relationships that they observe. One way to determine whether an observer monitors the causal significance of a demonstrator's behaviour is to determine what is learned from the observation of mistakes. It would be expected that if children are able to extract causal information by observation, they might benefit more from observing both the incorrect and correct way to solve a task, than from observing only the correct solution. Seeing both correct and incorrect responses might enable an individual to avoid making the same mistake as the demonstrator as well as providing additional visual information from which causal relationships could potentially be inferred. The aim of the trap-tube task is to insert a tool into the correct end of the tube so as to retrieve the reward (a plastic dinosaur) without pushing it into the trapping-hole located in the center of the tube. The reward is placed either on the left or right side of the trapping hole; therefore the correct end of tool insertion is dependent on the position of the food relative to the trap (see Fig. 1). This experiment has recently been run with juvenile chimpanzees in Uganda using food rewards. The purpose of the proposed study is to repeat this experiment with children of approximately the same age.

The proposed participants are 20 children aged between 3- and 4-years-old. The children will be divided into four groups. The *correct only* group will observe the demonstrator successfully retrieve a plastic dinosaur from the trap-tube. The *incorrect + correct* group will see the demonstrator fail by trapping the dinosaur then succeed. The remaining two groups will act as controls. They will observe the demonstrator move the tool along the top of the apparatus in the same direction as the demonstration groups, but without the tool having a causal effect on the reward inside the tube. Each child will receive a block of 10 trials with a demonstration before each trial in accord with which group they are in. Children will be asked to retrieve as many of the 10 dinosaurs as possible over the block of 10 trials. At the end of the block, regardless of whether the child has succeeded, they will be asked to choose their favourite dinosaur toy, which they can take home.

If children are able to learn causal relationships by observation, it would be expected that the demonstration groups will retrieve significantly more dinosaurs than the control groups. Additionally, it would be expected that children in the *incorrect + correct* group will be more successful than the *correct only* group.

Each child will be asked individually if they wish to participate in the study, and no child will be made to feel obliged to take part. Children can withdraw from the study at any point. All demonstrations and trials will be video recorded. The tapes will be analysed later to determine the number of successes and failures, the side of tool insertion and any occurrence of interesting qualitative data, such as particular strategies.

6. *Please describe how the participants will be selected, and how informed consent will be obtained.*

Participants will be selected on the basis of age from St Andrews Nursery School, St Andrews. Informed consent has already been obtained from the head teacher, Mrs Edwards. Informed consent forms have already been distributed to parents, and a poster giving information about some of the comparative research carried out with chimpanzees has been put up in the nursery foyer for parents to read.

7. *Will there be difficulty in obtaining informed consent due to participants' age, mental illness or communication difficulties?*

YES

The participants are too young to give informed consent. Therefore a letter has been circulated to the children's parents to ask for informed consent on their behalf.

8. *Will the participants receive the standard payment of £4 per hour* NO

The children will not receive payment for their participation in the study. Instead children will be given a toy dinosaur at the end of the experiment, regardless of their performance.

9. *Starting date of project:*
   The project is ready to start, pending the return of parental consent forms and ethical approval.

   Duration of project:
   The project will hopefully be completed over a period of 3 to 4 weeks.

   Duration of involvement for individual participant:
   Each participant will be involved in the study for no more than 20 minutes.

   Location of testing of participants:
   Children will be tested in a playroom at the nursery that is not used during the afternoons. The child will be separated from the rest of the class, but the door will be left open so that children can hear their classmates in the adjoining room and do not feel isolated.

10. *Please state who will have access to the data, and what steps will be taken to keep data confidential.*

The data tapes will be kept in the School of Psychology, and viewed only for the purposes of the current study. Written reports of the results will not contain any information about the participants except for their age and sex. No child will be identifiable by name or by any other means.

11. a. *Are there any potential hazards to either the investigator(s) or participant(s). If YES, please explain what these are.*

NO

b. *Will the procedures cause discomfort or distress? If Yes, please explain what these are, and what steps will be taken to minimize them.*

NO

c. *What training has the investigator received in order to of set any negative consequences resulting from the experiment?*

The investigator has no formal training to off-set any negative consequences. However, the investigator does have history of working with young children in both a professional and research setting.

12. *Are any of the participants in a dependent relationship with the Investigator, (e.g. student). If YES, explain why this is necessary.*

NO

13. a. *Will participants be kept naïve to the purpose of the experiment?* NO

b. *If YES, why is participant naivety necessary for achieving the aims of the research? Please justify your answer.*

c. *If NO, how will the participants be debriefed?*
Participants will be told that they are playing the same game as the chimpanzees in the poster. The participants are thought to be too young to be fully debriefed about the results. However, a poster of the results of the study will be put up on the notice board at the school, so that teachers and parents can be debriefed in full. The poster will also contain contact information if parents have any particular questions or concerns.

14. Please note and justify any other aspect of the research that in your view requires special ethical consideration.

All trials will be recorded on video camera. The children will not be specifically alerted to the presence of the camera, as this may change their behaviour. However, the camera will not be hidden, and its presence will not be denied if a child asks about it. Most journals requite that raw data is available for 5 years following publication. Tapes will therefore be destroyed 5 years after the date of first publication.

15. Where in the application have the following key points been addresses?

Confidentiality: 10

Withdrawal: 5

Informed Consent: 6

Debriefing: 13

I have had a Fife police check, which is clear and finds no reason to question my ability to work with children

For Undergraduate Supervisors (only)

Why do you consider this project requires special ethical consideration?

For All Supervisors

Please specify the particular aspects of the project you wish the committee to consider.
Have you read the statement by the British Psychological Society on Code of Conduct and Ethical Principles

YES/NO

Applicant's Signature .... Date........................

Supervisor's Signature .... Date........................

APPENDIX C

PILOT STUDY: IMITATION AND EMULATION SWITCHING IN CHIMPANZEES

Introduction

The rational behind this study is the same as for Experiment 1. For details see Chapter 6.

Methodology

Study-site

Data collection took place at Ngamba Island Chimpanzee Sanctuary, Uganda. See Chapters 5 and 6 for more details.

Participants

Subjects were 15 members of the juvenile group at Ngamba Island. Subjects ranged in age from 2- to 8-years-old and were of both sexes (see Table 1).

Apparatus

The experimental apparatus was a $16cm^3$ polycarbonate box, that was presented in either an opaque or clear condition (see Figure 1). On the top of the box was a square hole 3cm x 3cm, covered by a sliding lid. The hole could be opened by sliding the lid back using a protruding handle. On the front face of the box was a circular opening to a sloping tube concealed inside the box. A food reward, in the form of raisins, was placed at the bottom of this tube. The reward could be obtained by inserting the aluminium tool (22cm x 1cm) in the front hole and pulling the raisins out. Insertion of the tool into the top hole was not necessary to retrieve the reward. Manipulation of the box could therefore be divided into *irrelevant actions* directed at the top of the box, and *relevant actions* directed at the front. The apparatus was secured onto a wooded board that was bolted to a bench inside the research room.

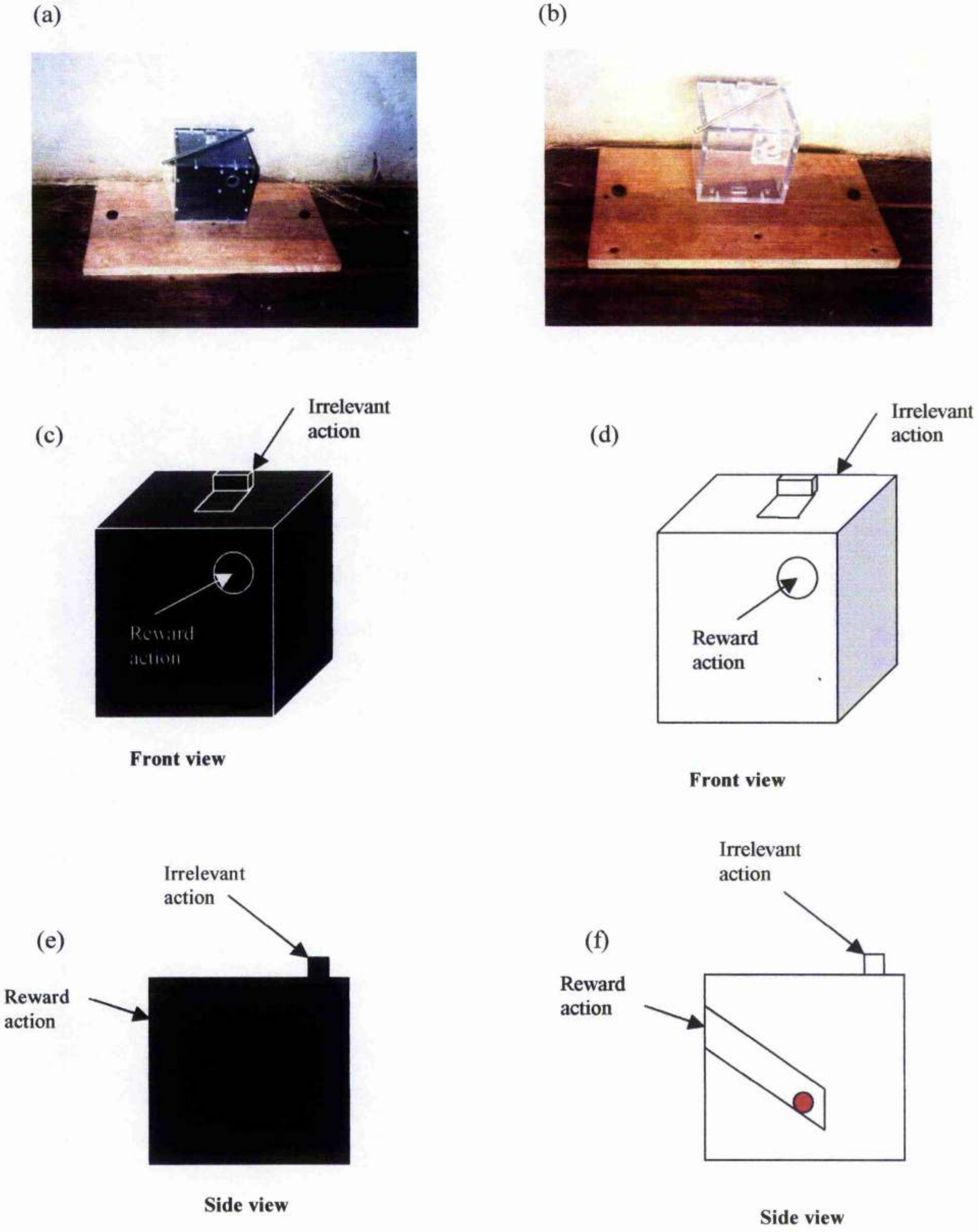
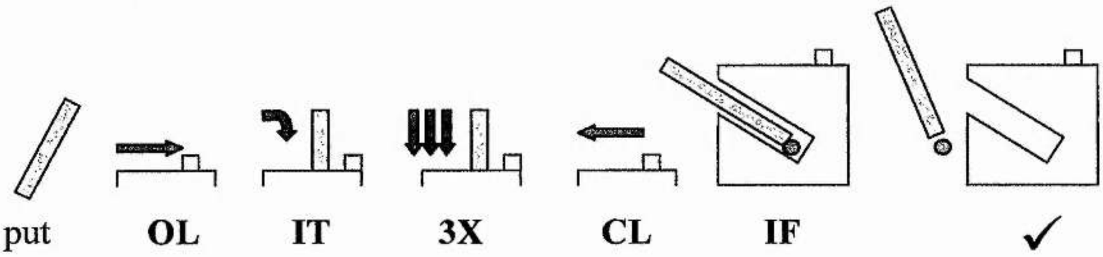


Figure 1. (a, c, d) Opaque Box - Subjects cannot see the location of the reward inside the tube, and therefore cannot determine which actions are relevant to task solution. (b, d, e) Clear box - Subjects can see the location of the reward, and can therefore have the potential to determine that the first action is irrelevant. (d) Clear box viewed from the side. Subjects can determine the location of the reward.

Subjects observed a human demonstrator use the tool to retrieve a food reward from one of the boxes. Each demonstration always involved two parts: (i) *irrelevant actions* – slide back top lid, insert tool and move up and down three times, and (ii) *relevant actions* – insert tool into front hole, retrieve reward. This can be seen more clearly in Figure 2.



Code	*Description*	
Put	- pick up tool	Irrelevant actions
OL	- open lid on top with index finger	
IT	- insert tool into opened top hole	
M3X	- move up and down to hit bottom 3 times	
CL	- close lid	
IF	- insert tool in front hole	Reward actions
✓	- Retrieve reward	

Figure 2. Schematic representation of demonstration.

The apparatus was presented in two conditions, opaque and clear (see Fig 6.1). In the opaque condition, causal information was unavailable since the surfaces of the box were black so that subjects could not see the location of the food tube, or the effect of the tool within the apparatus. It was predicted that when the causal information was restricted in this way, subjects would selectively include both irrelevant and relevant actions in their own later efforts, consistent with imitation.

In the clear condition, causal information was available, as the effect of the tool inside the box could be viewed. It was therefore possible to perceive that actions in the top of the box had no causal link with the reward. It was predicted that when causal information was available in this way, subjects would be inclined to develop an alternative, more efficient strategy by selectively excluding the irrelevant top actions, consistent with emulation.

Procedure

Subjects observed a human experimenter demonstrate how to retrieve the reward from the box in either the opaque or clear condition. Subjects were tested individually within the holding facility (see Chapter 5). Prior to each trial the experimenter would enter the research room and play with or groom the subject for approximately five minutes to reaffirm the relationship with the experimenter. Testing would begin as soon as the subject was calm. The experimenter would then move to the apparatus, which was bolted to a bench in the room, and demonstrate how to retrieve the reward (see Fig. 3). The chimpanzee would typically sit close beside or on the lap of the experimenter. In this respect the methodology was naturalistic in that the subject observed the demonstration from the same perspective as it was performed, and the proximity of the experimenter and subject was analogous to a mother infant pair.

During the majority of demonstrations, the experimenter would eat rewards which she had retrieved, but on some occasions tolerated scrounging, as would be typical of a mother infant pair. Following a demonstration, the chimpanzee could interact with the apparatus for approximately four minutes. The actions of the subject were recorded on a Sony Hi-8 hand-held video camera operated by the experimenter (see Figure 3). This cycle of demonstrations and trials was repeated every four minutes for 30 minutes. Each subject received 30 demonstrations and trial periods in total. For subjects in the Opaque > Clear group, the black card was then removed from the apparatus, and they received a further 30 trials in the clear condition.

(a) (b)

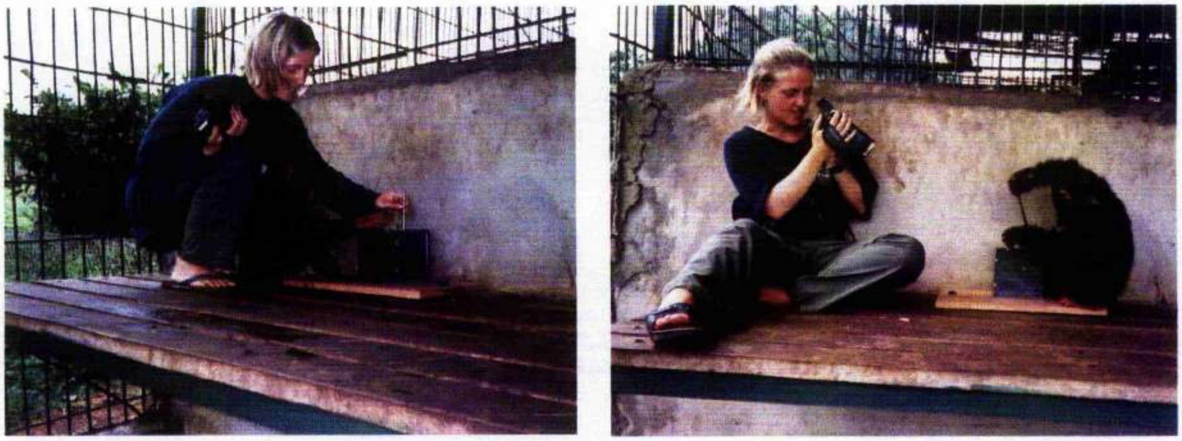


Figure 4. (a) The experimenter demonstrates how to retrieve the food reward using both the irrelevant and relevant act. (b) The subjects can then interact with the apparatus freely for four minutes.

Subjects were divided into 3 groups, Group A - 6 individuals, Group B - 5 individuals and Controls - 4 individuals (see Table 1). Unfortunately subjects were not allocated to 3 equal groups, as 2 potential subjects, one from Group B and one from the control group, broke into the enclosure during testing, and interacted with the apparatus. They therefore had to be excluded from the study, due to possible knowledge gained from this prior experience.

GROUP A Opaque > Clear			**GROUP B** Clear box only			**CONTROLS** Opaque & Clear		
Name	**Age**	**Sex**	**Name**	**Age**	**Sex**	**Name**	**Age**	**Sex**
Indi	2	M	Kisembo	2	M	Billy	3	F
Yiki	2	M	Asega	2	M	Umugezi	3	M
Baluku	2	M	Yoyo	2	F	Nkumwa	5	F
Pasa	2	F	Mukisa	2	F	Mawa	5	M
Kalema	5	M	Cindy	8	F			
Ikuru	6	F						

Table 1. Name, age and sex of subjects who took part in the experiment. Subjects were divided into 3 groups which were age and sex matched as much as possible.

(i) *Group A*

Group A received 30 demonstrations and trials with the opaque box, then an additional 30 demonstrations and trials with the clear box. The purpose of this contrast was to determine whether different social learning strategies were employed by the same individual depending on the availability of causal information.

(ii) *Group B*

It is possible that the actions of subjects from Group A with the clear apparatus would be influenced by prior experience with the opaque condition. Group B therefore received 30 demonstrations with only the clear box to control for learning or perseverance effects from the opaque box phase.

(iii) *Controls*

Control subjects received no demonstration in order to investigate the influence of individual learning alone. Each subject was allowed to interact with the apparatus for 30 minutes. Two subjects were given the opaque box, and two subjects the clear box.

In order to keep the experimental and the control conditions the same, without a demonstration every four minutes to break up each trial, control subjects would have to be presented with the apparatus 30 separate times in four minute blocks. This would involve either removing the apparatus or the subjects from the research room every four minutes. As the experimenter was working alone, this was logistically impossible. Alternatively, the apparatus would have to be presented to the control subjects for a four minute block on 30 consecutive days. Unfortunately, the time frame of the pilot study did not allow for this methodology to be employed. However, this method may have had a deleterious effect on the motivation of the subjects and therefore affected the results.

Experimental Hypotheses

(i) *Group A* – Opaque box

Subjects cannot perceive the causal mechanisms, so are therefore more likely to imitate the demonstrated technique, reproducing the irrelevant act more than controls.

(ii) *Group A* – Clear box

When the same subjects are transferred to the clear apparatus they can perceive the causal role of the tool and are therefore more likely to ignore the irrelevant act than controls, developing their own technique by emulation.

(iii) *Group B* – Clear box only

The performance of Group A with the clear box will not affected by prior experience with the opaque apparatus; there will therefore be no significant difference in the performances of Group A and B with the clear box.

Data analysis

The performance of each subject was recorded using a hand held video-camera. The tapes were later analysed, and the behaviour of the subject was recorded using the following categories taken from Figure 2:

Code	*Description*	
Put	- pick up tool	Irrelevant actions
OL	- open lid on top with index finger	Irrelevant actions
IT	- insert tool into opened top hole	Irrelevant actions
M3X	- move up and down to hit bottom 3 times	
CL	- close lid	Reward actions
IF	- insert tool in front hole	Reward actions
✓	- Retrieve reward	

In addition to the demonstrated actions, it was necessary to create a number of new codes which corresponded to behaviours that were not included in the demonstration. These were as follows:

H – hit outside of box around hole (top or front), but not insertion of tool into hole.
h – insert digit into hole (top or front).
m – use mouth to explore hole / open lid (top or front).

The coded behaviour of each subject was then entered into SPSS for analysis. The very first action has been omitted from the analysis, as none of the subjects performed experimental actions to the box. Instead, they were extremely excited by the new objects, and all first actions involved playing with the tool (biting, trying to snap it, using it to hit the bars), or trying to pull the box off the wooded board.

Results

The behaviour of subjects was coded for all actions performed within each 4-minute trial. However, analysis focused on the first action that was performed by a subject following each of the 30 demonstrations.

Group A (Opaque box) versus *controls*

The results suggests that subjects from group A in the opaque condition performed the irrelevant act following a demonstration more than controls, although as yet there are too few control subjects to perform a statistical test (see Fig. 5). An 'emulative' understanding of the causal features involved in task solution would predict that subjects should ignore the irrelevant act. Reproduction of the irrelevant act is therefore most consisted with imitative learning.

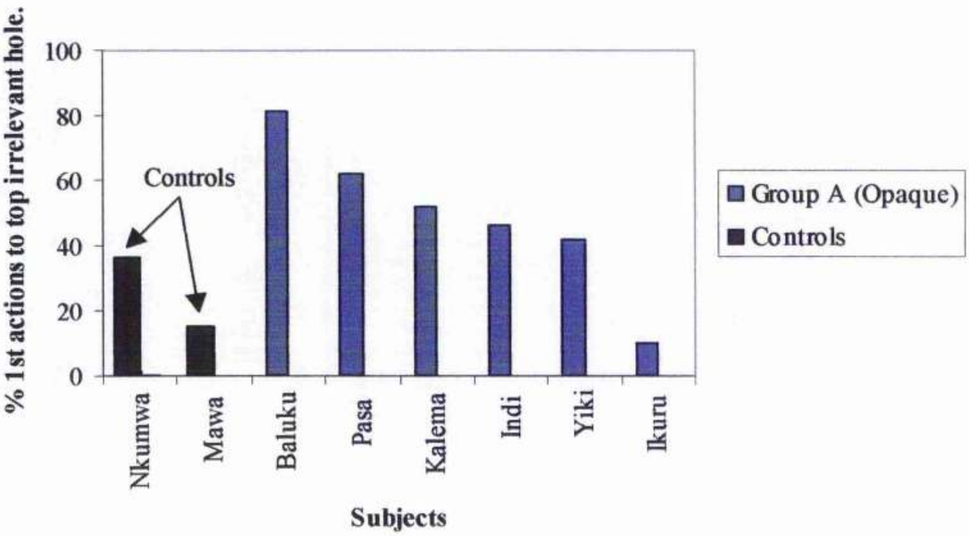


Figure 5. First actions of Group A following a demonstration with the opaque box averaged over 30 trials, in comparison to the total number of actions directed to the irrelevant hole by non-observing controls.

Group A: Opaque > Clear

With the exception of Baluku, all subjects in Group A ignored the irrelevant action following a demonstration with the clear box significantly more than with the opaque box ($t = 3.051$, $df = 5$, $p = 0.028$, two-tailed, see Fig. 6). This result was significant even with the inclusion of Baluku. Although Baluku's actions go in the opposite direction, his continued reproduction of the irrelevant actions, even when given the opportunity to perceive that such actions are causally irrelevant to task solution, strongly suggests imitative learning.

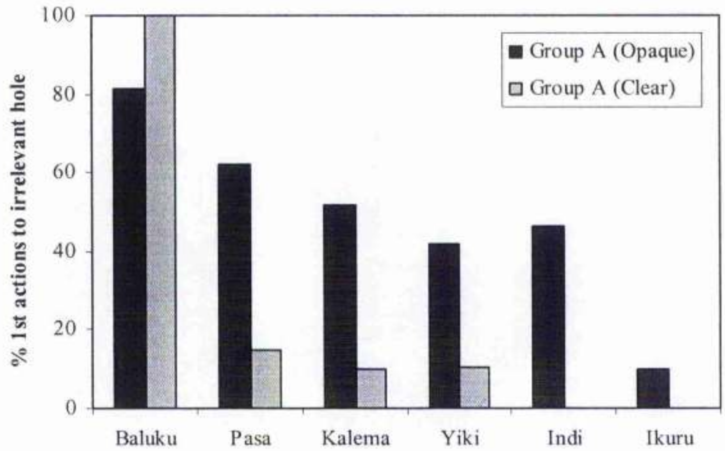


Figure 6. Percentage of first actions performed following a demonstration by subjects from Group A with the opaque box and then the clear box.

Figure 7, illustrates that when the subject was presented with the opaque apparatus, he showed a preference to reproduce the demonstrated strategy, performing the irrelevant action first, following a demonstration. However, when the same subject was tested with the clear box, he soon came to demonstrate a preference to reproduce only the reward action, therefore using his own technique and ignoring the irrelevant act. This strategy is most consistent with emulative learning. It is important to note that the subjects had ample opportunity with the opaque apparatus to learn that actions to the top were irrelevant (front hole was used first on 11 occasions).

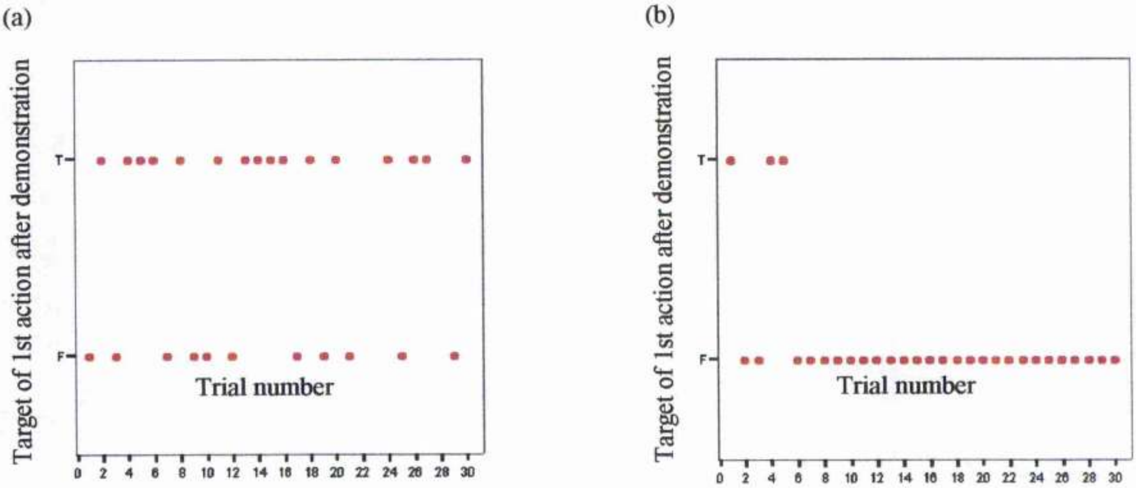


Figure 7. Target of first action following a demonstration for Kalema, a 5-year-old male. 'T' indicates actions to the top, irrelevant hole. 'F' indicates actions to the front reward hole. (a) Opaque box. (b) Clear box.

The performance of subjects from Group A and B was not significantly different with the clear box (t = 0.239, df = 10, p = 0.819, two-tailed, see Fig. 8). The performance of Group B with the clear box was significantly different from Group A with the opaque box (t = 2.641, df = 10, p = 0.032, two-tailed, see Fig. 8). The data therefore suggest that the chimpanzees changed their social learning strategies when interacting with the opaque and clear boxes, and was not a result of prior experience with the opaque apparatus.

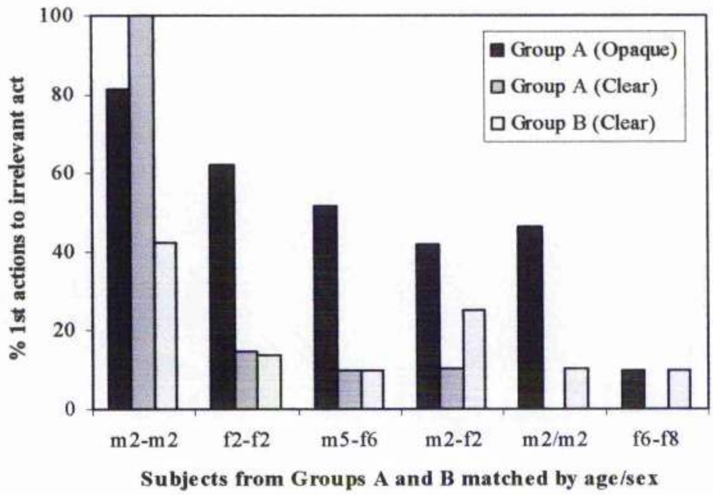


Figure 8. Subjects from Groups A and B were matched as much as possible for age and sex. The x-axis refers to subjects from group A and B respectively (e.g. 'm5-f6' corresponds to a male aged 5 from Group A, paired with a female aged 6 from Group B).

Degree of copy fidelity

The best copy of the demonstrated actions was chosen for each subject. This set of actions was judged for the match of (i) the sequential structure, and (ii) the details of the observed actions. These scores were then compared to the demonstration to get an overall measure of fidelity using the following criteria:

(i) *Sequence structure*

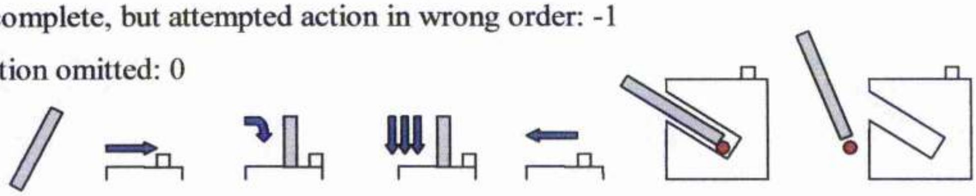
Action in same order as demonstration: +1

Action in wrong order to demonstration: -1

Incomplete, but attempted action in same order: +1

Incomplete, but attempted action in wrong order: -1

Action omitted: 0



put	**OL**	**IT**	**3X**	**CL**	**IF**	✓
+1	+1	+1	+1	+1	+1	+1

The demonstrated strategy would therefore score a maximum of +7

(ii) *Detail of behaviour*

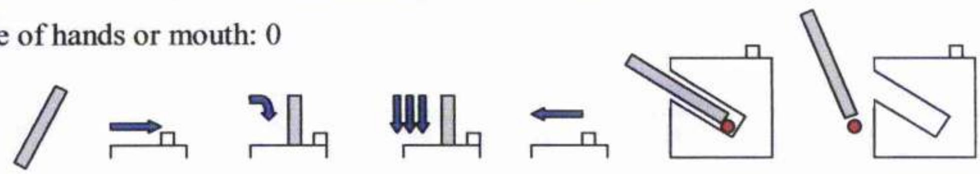
Complete action: +1

Incomplete actions (e.g. 'hit top' but not 'insert top'): + 0.5

Hit bottom of box 3 times: +3

Hit bottom multiple times (excluding 3 times): +2

Use of hands or mouth: 0



put	**OL**	**IT**	**3X**	**CL**	**IF**	✓
+1	+1	+1	+3	+1	+1	+1

The demonstrated strategy would therefore score a maximum of +9. These scores do not represent a linear interval measurement of fidelity, but are intended to provide approximate measures, which can be used for comparative analysis.

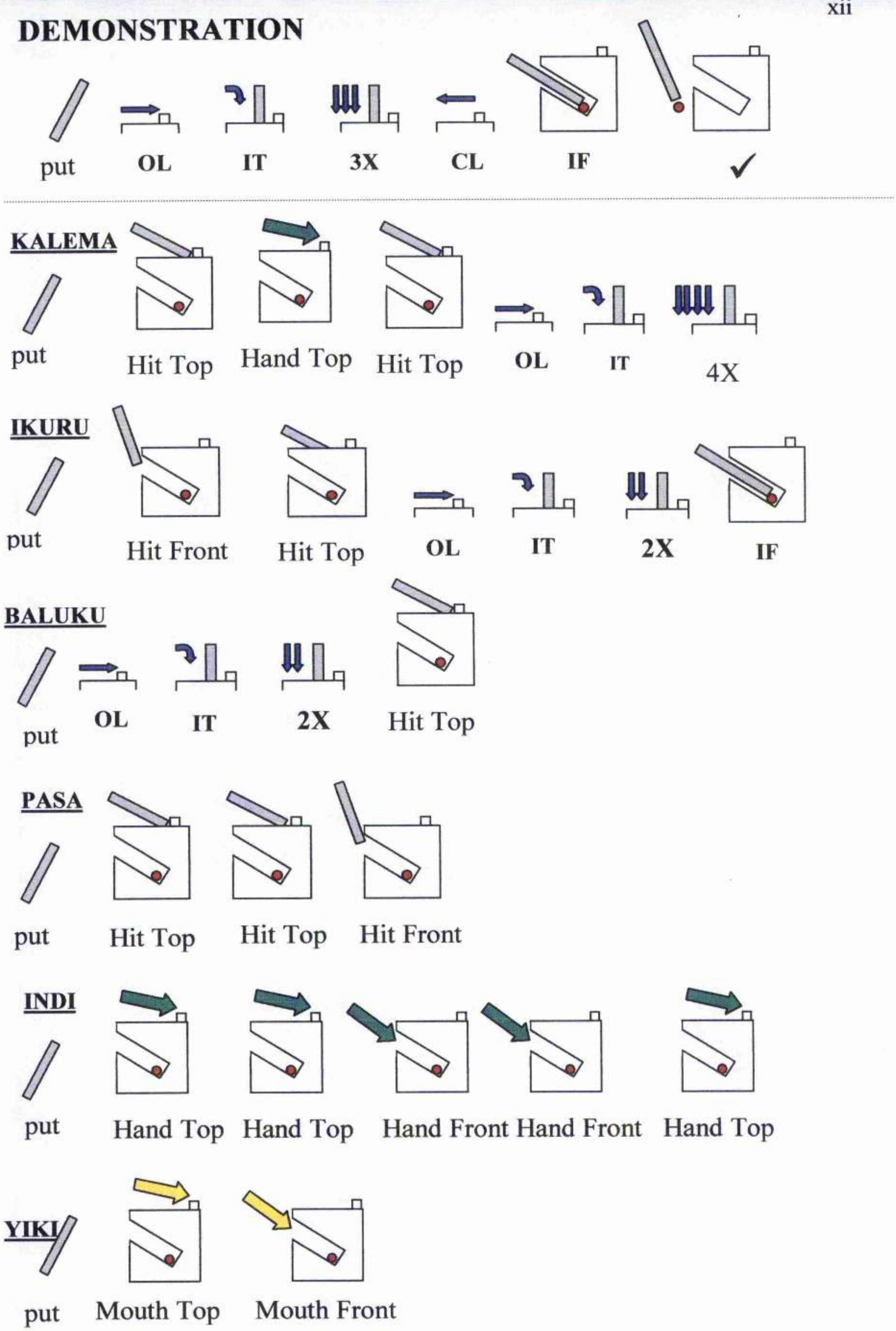


Figure 9. Schematic representation of ***first action on trial 1*** by subjects from Group A with the opaque apparatus.

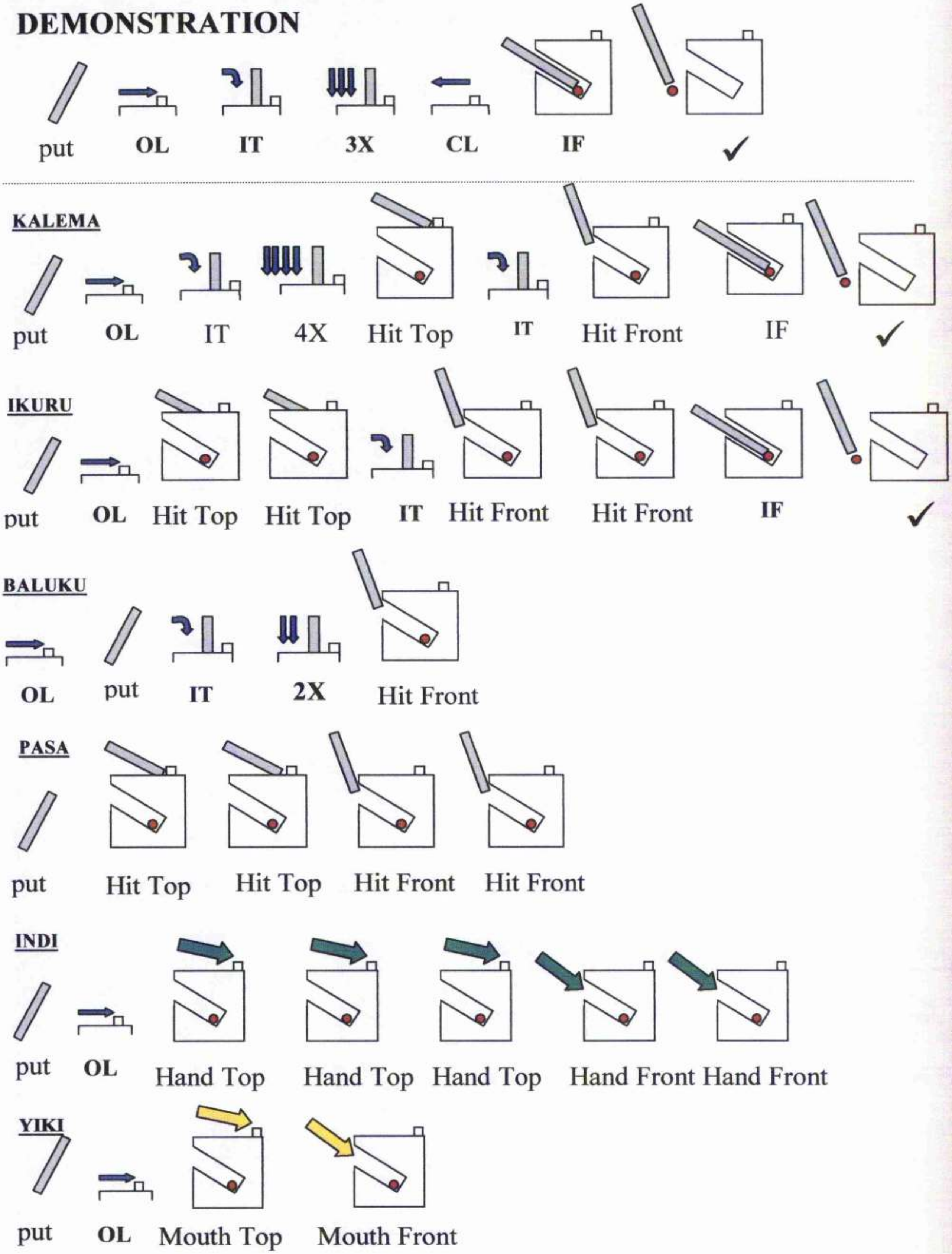


Figure 10. The closest behavioural match to the demonstration during a single trial for subjects from Group A - opaque box: Kalema trial 16; Ikuru trial 2; Baluku trail 17; Pasa trial 6; Indi trial 4; Yiki trial 14.

(i) *Sequence structure* – maximum score = 7

Kalema:	1 + 1 + 1 + 1 + 0 + (-1) + 1 + 1 = 5	(71.43%)
Ikuru:	1 + 1 + 1 + 0 + 0 + 1 + 1 = 5	(71.43%)
Baluku:	(-1) + 1 + 1 + 0 + 0 + 1 + 1 = 3	(42.86%)
Pasa:	1 + 0 + 0 + 0 +1 + 1 + 0 = 3	(42.86%)
Indi:	1 + 1 + 1 + 0 + 0 + 1 + 0 = 4	(57.14%)
Yiki:	1 + 1 + 1 + 0 + 0 + 1 + 0 = 4	(57.14%)

(ii) *Detail of behaviour* – maximum score = 9

Kalema:	1 + 1 + 1 + 2 + 1 + 1 = 7	(77.78%)
Ikuru:	1 + 1 + 1 + 1 + 1 = 5	(55.56%)
Baluku:	1 + 1 + 1 + 2 + 0.5 = 5.5	(61.11%)
Pasa:	1 + 0.5 + 0.5 = 2	(22.22%)
Indi:	1 + 1 = 2	(22.22%)
Yiki:	1 + 1 = 2	(22.22%)

(iii) *Total fidelity*

The total fidelity can be calculated by combining the score for sequence and detail. The maximum score possible for a perfect replication of the demonstration is 7 + 9 = 16.

Kalema:	5 + 7 = 12	(75%)
Ikuru:	5 + 5 = 10	(62.5%)
Baluku:	3 + 5.5 = 8.5	(53.12%)
Pasa:	3 + 2 = 5	(31.25%)
Indi:	4 + 2 = 6	(37.5%)
Yiki:	4 + 2 = 6	(37.5%)

During the first 5 trials with the opaque apparatus, subjects from Group A tended to perform the irrelevant top action following a demonstration from the very first trial (see Fig. 11). This, in conjunction with the irrelevant nature of the top action, makes it highly unlikely that learned contingencies were used to reproduce the demonstrated behaviour.

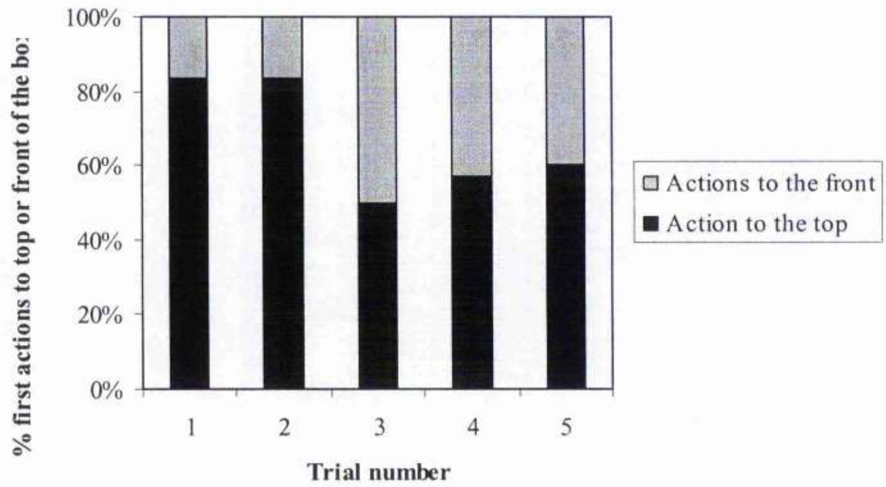


Figure 11. The percentage of subjects from Group A performing actions to the top or front of the box following a demonstration, during trial 1 to 5, with the opaque box.

Discussion

Subjects from Group A who observed demonstrations with the opaque box, tended to perform the irrelevant actions more than controls who had received no demonstration (see Figure 5). This would suggest that reproduction of the irrelevant action was directly influenced by social learning. When the same subjects from Group A then transferred to the clear apparatus, they ignored the irrelevant actions significantly more than with the opaque apparatus. The exception to this trend is Baluku, a 2-year-old male. Baluku showed the greatest tendency to reproduce the irrelevant action following a demonstration with the opaque box. This tendency increased with the clear apparatus. Although Baluku's actions go against the predicted trend, his continued reproduction of the irrelevant act, even when he can potentially perceive that this action is having no causal effect on the reward, strongly suggests social learning.

It may be argued that the behavioural change of subjects from Group A between the opaque and clear apparatus was the result of prior experience with the opaque box. It might be possible that subjects had learned specific features of the task during the previous 30 trials. Group B therefore received demonstrations only with the clear box to control for any carry-over effects. The results indicate that there was no significant difference in the performances of Group A and B with the clear box. This suggests that subjects employed two different social learning strategies in each experimental condition.

Different social learning strategies

When presented with the opaque box, subjects from Group A showed a tendency to reproduce the irrelevant actions more than controls who received no demonstration (see Figure 5). Subjects from Group A also reproduced the irrelevant action significantly more with the opaque box than with the clear box, or than Group B with the clear box.

Figures 9 and 10, illustrate the most faithful behavioural match to the demonstration by subjects from Group A, with the opaque box, during a single trial. Although the individual performance of each subject is varied, every subject reproduced at least one element of the irrelevant action. Kalema, Ikuru and Baluku appear to have reproduced a number of the irrelevant actions to the top part of the box, including opening the lid by hand, inserting the tool, and moving it up and down. These subjects reproduced over 50% of the detail of the demonstration. The remaining 3 subjects, Pasa, Indi and Yiki, although they did not produce a very faithful reproduction of the demonstration, did include at least one element of the irrelevant action, including opening the lid and actions to the top of the box.

It is difficult to explain the reproduction of a causally irrelevant action following a demonstration by any other means than imitation. It could be argued that since the apparatus did not incorporate a two-action design (Dawson & Foss, 1965), stimulus enhancement may be responsible for the results. Stimulus enhancement would draw the attention of subjects to specific areas of the box. However, attention should be equally drawn to both the top and front holes. Therefore stimulus enhancement cannot account for the preference to select the top hole over the front hole. Furthermore, three of the subjects, Kalema, Ikuru and Baluku showed fidelity of both the sequence and detail that exceeded 50%. It is difficult to see how stimulus enhancement could account for the order of actions, and detailed replication of specific elements of the demonstration. The behaviour of chimpanzees with the opaque apparatus therefore seems to be most consistent with imitative learning.

Once the black plastic cover had been removed from the apparatus, the box was completely transparent (see Fig. 1). Subjects could therefore potentially perceive that demonstrated actions to the top of the box were causally irrelevant to task solution. Subjects from both Group A and Group B ignored the irrelevant action significantly more than subjects who were tested with the opaque apparatus. The omission of the irrelevant action was not the result of prior experience with the opaque box (see Figure 8).

An objection to this interpretation might be that the attention of the subjects was perhaps simply drawn to the reward (which was now visible inside the box), and that they therefore did not attend to the demonstration, and retrieved the reward in the most direct way. However, although the reward was located at the end of the transparent tube, from the outside the reward looked as if it was located in the middle of the box, equidistant from all six sides (see Figure 12).

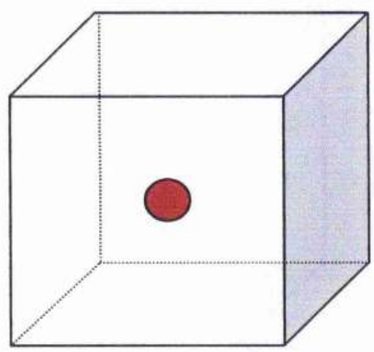


Figure 12. Viewed from the outside, the reward is equidistant from all 6 sides. It is therefore not apparent whether the insertion of the tool into the top or front will retrieve the reward.

The distance from the top and reward hole was therefore equal, and it was not obvious which hole would result in the retrieval of the reward. The omission of the irrelevant action must therefore have been influenced by social learning. The results therefore suggest that when the box was clear, subjects learned by observation the causal features of the task, and therefore that only the front action was necessary. The results therefore suggest that subjects switched to a strategy of emulation learning.

Causal reasoning

The ability of chimpanzees to employ different social learning strategies in the conditions described above, hinges on an ability to understand the causally relevant features of the task. Data from the present study suggest that chimpanzees are able to differentiate causally relevant and irrelevant features. These results are in accordance with recent publications by Daniel Povinelli and colleagues at Louisiana State University, who have performed a series of experiments with chimpanzees designed to investigate causal understanding. They concluded that although chimpanzees are capable of extracting patterns of regularity in a task, and generalising these to different environmental conditions, they are not capable of representing unobservable variables that mediate a causal sequence. Their understanding of the environment is based on directly perceivable action sequences, such as 'contact' (Povinelli & Reaux, 2000; Povinelli, et al., 2000).

Conclusions

The results from Experiment 1 suggest that when chimpanzees cannot perceive the causal features of a task, they employ a social learning strategy that is most consistent with imitative learning. However, when the causal mechanisms can be perceived, and the individual can potentially bring about the same result using their own technique, chimpanzees change to a strategy that is most consistent with emulation.

The results are consistent with the hypothesis that chimpanzees are capable of imitative learning, but that they do so only when emulation is not possible. However, further data will be required from control subjects before more confident conclusions can be drawn.

PILOT STUDY: IMITATION AND EMULATION SWITCHING IN CHILDREN

Introduction

This experiment was carried out as a direct replication of the previous study.

Methodology

Participants

Subjects were 16 human children of mixed sex, aged between 2 and 3 years old (mean: 2 yrs 10 mo; range: 2 yrs 1 mo - 3 yrs 11 mo). All subjects were recruited from St Andrews Under Fives day-care nursery, UK. Parental consent was sought before a child was included in the investigation (see Chapter 5). Although 21 children participated when the investigation began, only 15 children completed the experiment over a three-week period, due to illness or irregular attendance at the playgroup.

Apparatus

The apparatus used in this experiment was the same as the previous study. However, certain features were modified to make the task more suitable for children (see Fig. 13):

i. The end of the tool was covered in Velcro
ii. The reward was a Velcro-backed cartoon sticker

The reward could therefore be retrieved by inserting the Velcro-tip of the tool into the front hole, where it could adhere to the Velcro backed cartoon sticker and be removed.

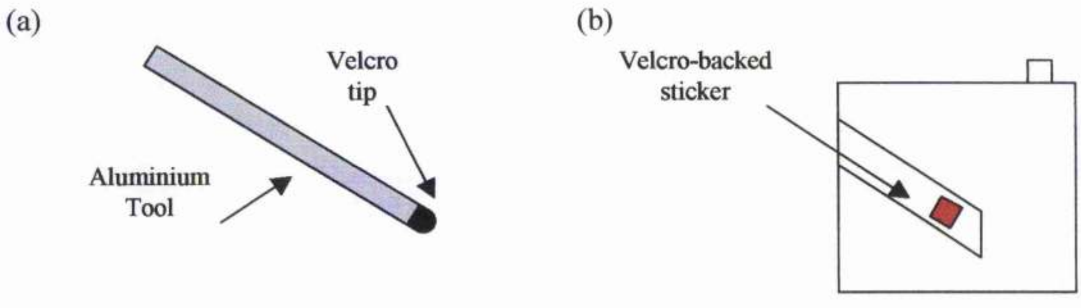
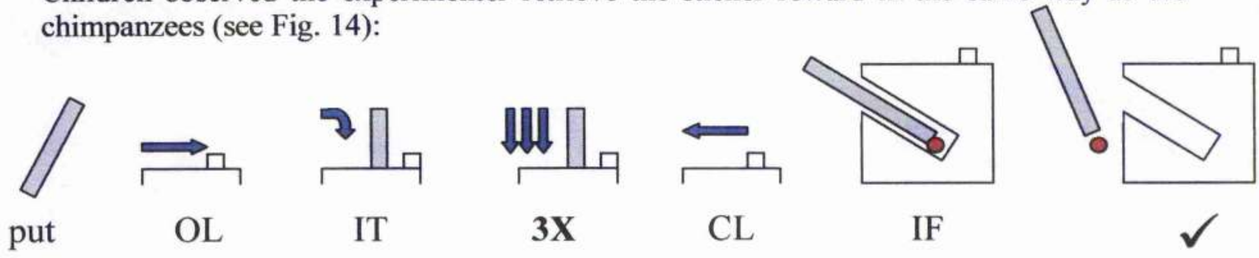


Figure 13. (a) Aluminium tool with Velcro tip, which can be used to retrieve the sticker reward. (b) Velcro-backed sticker concealed within the apparatus.

Procedure

The experiment was conducted following the same procedure as the previous experiment. Subjects were tested individually in a separate room within the nursery. The experimenter spent time at the playgroup for three weeks prior to the investigation, so that the children would feel comfortable participating in the experiment. The apparatus was set up on a small table, and the children sat in a chair behind the table to observe the demonstration.

Children observed the experimenter retrieve the sticker reward in the same way as the chimpanzees (see Fig. 14):



Put- pick up tool; **OL** - open lid on top; **IT**- insert tool in top hole; **3X**- hit bottom 3 times; **CL**- close lid; **IF**- insert tool in front hole; ✓ - Retrieve reward

Figure 14. The method used by the demonstrator to retrieve the sticker reward. The demonstration has been divided into 7 actions for coding.

In order to remain consistent with the methodology used with chimpanzees, minimal verbal information was given to the children about the task. They were told that the experimenter had a 'special box' that contained a cartoon sticker. The experimenter then retrieved the sticker using the same technique as the previous study. The children were then asked if they would like to try to retrieve the sticker. They were not asked to reproduce the method of the experimenter, or given any other indication of what they should do in order to obtain the reward.

	Romy	Finl	Lewi	Josf	Ande	Ryan	Conn	Emma	Thom	Megn
Age	2.1 f	2.11 f	3.5 m	3.9 m	3.11 f	2.9 m	2.9 m	2.10 f	2.10 m	2.8 f
OPAQUE BOX										
1	T	T	T	T	T	T	T	T	F	F
2	T	T	T	T	T	F	F	F	T	F
3	T	T	T	T	F	F	F	F	T	F
CLEAR BOX										
4	T	T	T	T	T	F	T	F	T	F
5	T	T	T	F	F	F	F	F	T	F
6	T	T	T	F	T	F	F	F	T	F

Table 2. The first action performed by subjects from Group A following a demonstration. 'T' = irrelevant actions to the top of the box. 'F' = reward actions to the front of the box. 'm' and 'f' indicate male/female.

The children were divided into 2 groups. Group A received demonstrations with the opaque box and then the clear box. As with the previous experiment, there was a danger that the actions of subjects from group A with the clear apparatus would be influenced by prior experience with the opaque apparatus. Group B therefore received demonstrations only with the clear box.

This study was conducted within a three-week time window before commencing data collection in Uganda for the previous study. Therefore in contrast to the chimpanzee data, time constraints prevented 30 demonstrations and trails with each child. Each subject received three demonstrations and trial sessions. Children succeeded in retrieving the sticker in every trial. Subjects were therefore rewarded regardless of the technique that was used.

Group A - Variance is not age/sex related

Trial 1, 8/10 children used irrelevant act following demonstration. x^2=3.6, df=1, p=0.058

9/10 children performed irrelevant act during trials 1-6. x^2=6.4, df=1, p=0.011

Trails 1-3, 6/10 children maintained the same strategy. $x^2 = 0.4$, df = 1, p = 0.527

Trials 4-6, 7/10 children maintained the same strategy. $x^2 = 1.6$, df = 1, p = 0.206

Trials 1-6, 5/10 children maintained the same strategy. $x^2 = 0.0$, df = 1, p = 1.00

Irrelevant act trial 1 > ignore by trial 6, 3/10 children. $x^2 = 1.6$, df = 1, p = 2.06

Ignored irrelevant act trial 1 > gained by trial 6, 1/10 children $x^2 = 0.0002$, df =1, p=0.989

	Sam	Claire	Lucy	Erien	Lois
	4.4 m	4.6 f	2.10 f	2.5 f	3.3 f
CLEAR BOX ONLY					
1	T	T	T	F	F
2	T	T	T	F	F
3	T	T	T	F	F

Table 3. The first action performed by subjects from Group B following a demonstration. 'T' = irrelevant action to the top of the box. 'F' = reward actions to the front of the box. 'm' and 'f' indicate male/female.

3/5 children used irrelevant action $x^2 = 0.2$, df = 1, p = 0.655

2/5 children ignored the irrelevant action $x^2 = 0.2$, df = 1, p = 0.655

5/5 children maintained the strategy through trials 1 - 3.

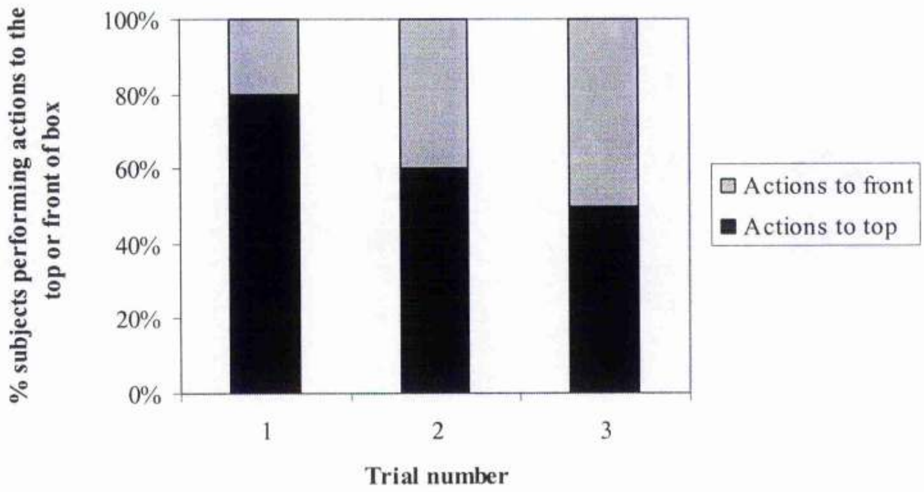


Figure 15. Percentage of subjects from Group A who performed action to the top or front of the box following a demonstration with the opaque apparatus.

Children initially tended to reproduce the irrelevant action following a demonstration with the opaque apparatus, but that this tendency decreased to 50% by trial 3 (see Fig. 15). Children therefore seemed able to both reproduce the irrelevant action and ignore it when the causal role of the tool could not be directly perceived. However, repeated trials would be required before comparisons can be made with chimpanzees.

Degree of copy fidelity

The fidelity of the closest behavioural match to the demonstrated strategy was analysed for subjects from Group A. The behavioural responses illustrated in Figure 18, were categorised using the following criteria:

(i) *Sequence structure*

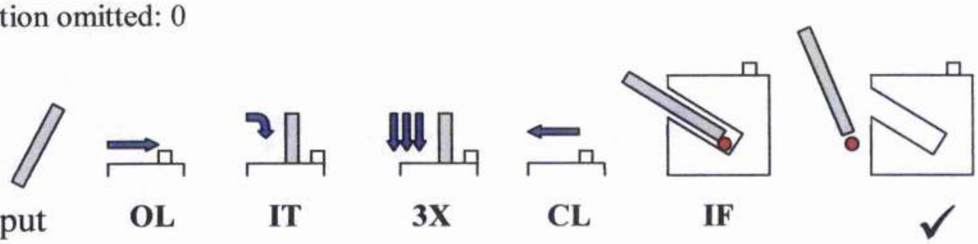
Action in same order as demonstration: +1

Action in wrong order to demonstration: -1

Incomplete, but attempted action in same order: +1

Incomplete, but attempted action in wrong order: -1

Action omitted: 0



+1 +1 +1 +1 +1 +1 +1

The demonstrated strategy would therefore score a maximum of +7

(ii) *Detail of behaviour*

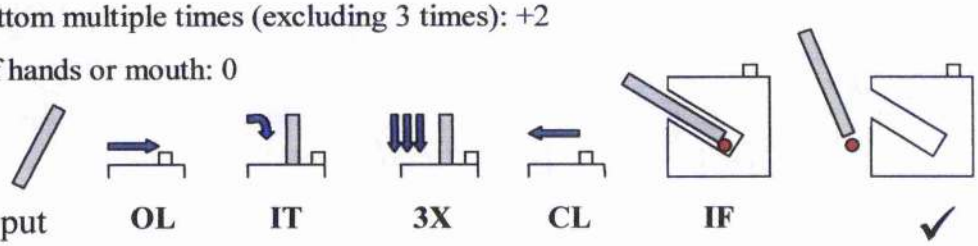
Complete action: +1

Incomplete actions (e.g. 'hit top' but not 'insert top'): +0.5

Hit bottom of box 3 times: +3

Hit bottom multiple times (excluding 3 times): +2

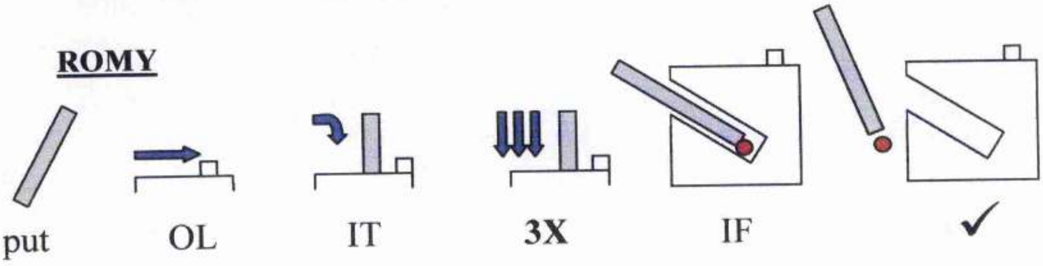
Use of hands or mouth: 0



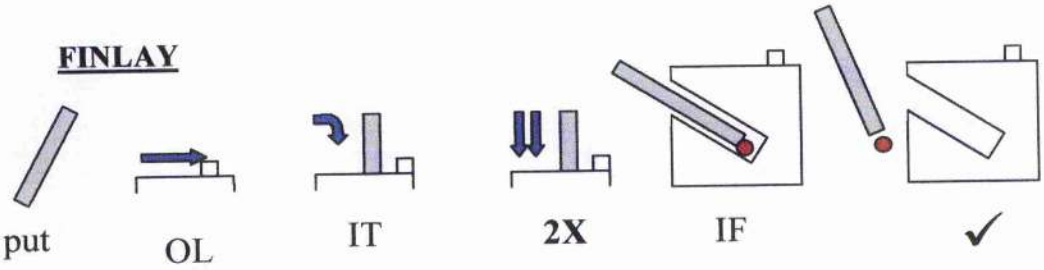
+1 +1 +1 +3 +1 +1 +1

The demonstrated strategy would therefore score a maximum of +9

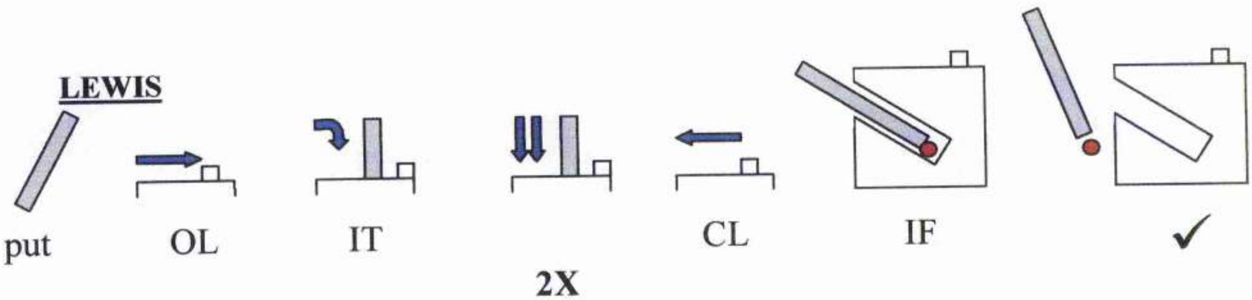
ROMY



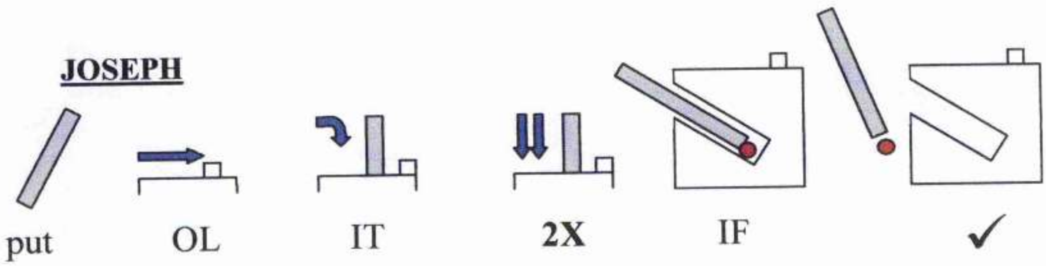
FINLAY



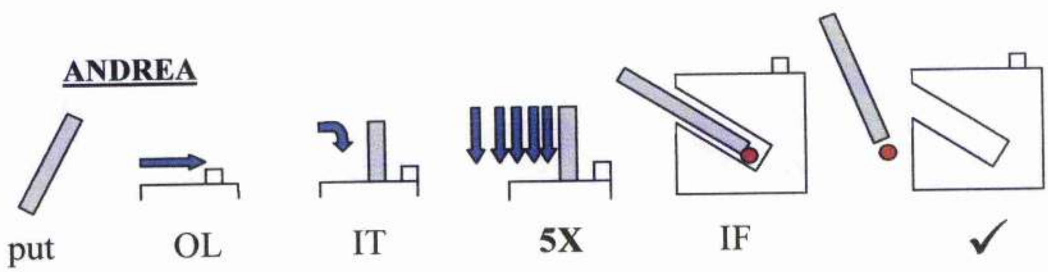
LEWIS



JOSEPH



ANDREA



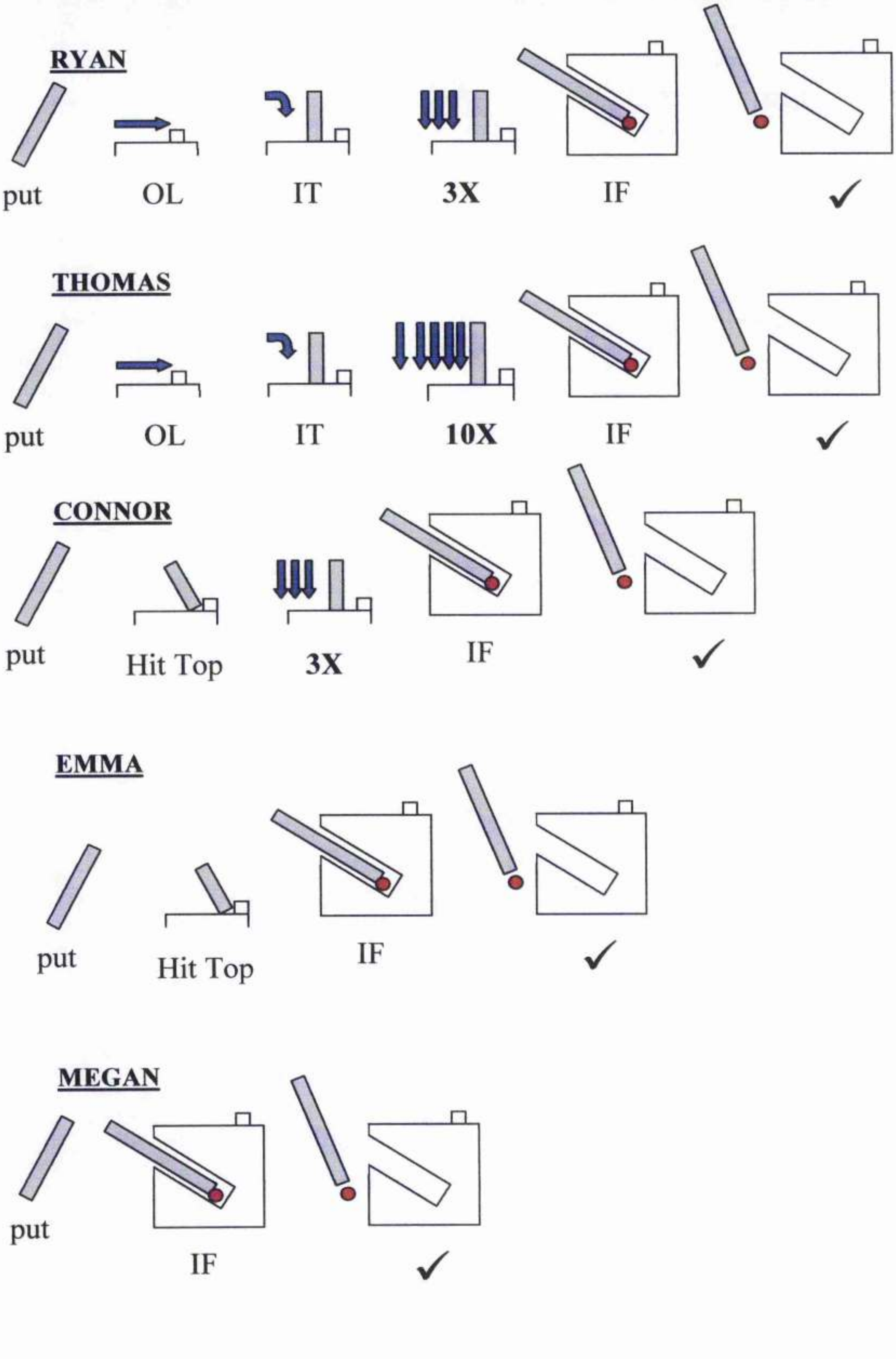


Figure 16. The closest behavioural reproduction of the demonstration during a single trial for each subject from Group A with the opaque apparatus.

(I) *Sequence structure* – maximum score = 7

Romy:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Finlay:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Lewis:	1 + 1 + 1 + 1 + 1 + 1 + 1 = 7	(100%)
Joseph:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Andrea:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Ryan:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Thomas:	1 + 1 + 1 + 1 + 0 + 1 + 1 = 6	(85.71%)
Connor:	1 + 0 + 1 + 1 + 0 + 1 + 1 = 5	(71.43%)
Emma:	1 + 0 + 0 + 0 + 0 + 1 + 1 = 3	(42.86%)
Megan:	1 + 0 + 0 + 0 + 0 + 1 + 1 = 3	(42.86%)

(ii) *Detail of behaviour* – maximum score = 9

Romy:	1 + 1 + 1 + 3 + 1 + 1 = 8	(88.89%)
Finlay:	1 + 1 + 1 + 2 + 1 + 1 =7	(77.78%)
Lewis:	1 + 1 + 1 + 2 + 1 + 1 + 1 = 8	(88.89%)
Joseph:	1 + 1 + 1 + 2 + 1 + 1 = 7	(77.78%)
Andrea:	1 + 1 + 1 + 2 + 1 + 1 = 7	(77.78%)
Ryan:	1 + 1 + 1 + 3 + 1 + 1 = 8	(88.89%)
Thomas:	1 + 1 + 1 + 2 + 1 + 1 = 7	(77.78%)
Connor:	1 + (0.5) + 3 + 1 + 1 =6.5	(72.22%)
Emma:	1 + (0.5) + 1 + 1 = 3.5	(38.89%)
Megan:	1 + 1 + 1 = 3	(33.33%)

(iii) *Total fidelity*

The total fidelity can be calculated by combining the score for sequence and detail. The maximum score possible for a perfect replication of the demonstration is 7 + 9 = 16.

Romy:	6 + 8 = 14	(87.5%)	Ryan:	6 + 8 = 14	(87.5%)
Finlay:	6 + 7 = 13	(81.25%)	Thomas:	6 + 7 = 13	(81.25%)
Lewis:	7 + 8 = 15	(93.75%)	Connor:	5 + 6.5 = 11.5	(71.87%)
Joseph	6 + 7 = 13	(81.25%)	Emma:	3 + 5 = 8	(50%)
Andrea:	6 + 7 = 13	(81.25%)	Megan:	3 + 3 = 6	(37.5%)

Discussion

Variability in performance

The performance of subjects was extremely varied. Variability in the data may be the result of social factors that were not relevant with chimpanzees, i.e. differences in the way in which subjects perceived the task. It is possible that some children perceived the task as a game whereby they were supposed to reproduce the actions of the experimenter. In contrast, other children may have thought that they should retrieve the reward in the quickest possible way. As children never failed to retrieve the reward, their actions were reinforced irrespective of the technique that was used. In addition, the expression of imitation may be a function of task difficulty. Children have been shown to preferentially imitate actions that are similar to, or just beyond their own abilities (Harnick, 1978). Actions that are too easy are attempted by emulation or trial and error (Russon & Waite, 1991). Therefore the perceived difficulty of the task may have varied between subjects.

Social learning strategies

Figure 16, indicates that on at least one occasion, following a demonstration with the opaque box, 9/10 subjects performed a recognisable attempt to replicate some aspects of the irrelevant actions of the demonstration. As discussed in the previous experiment, imitation is the most likely explanation for the replication of irrelevant behaviour, as alternative forms of social learning cannot account for the order, and detail of the behaviour. This conclusion is consistent with previous investigations which suggest that children of this age are capable of imitating novel object actions (Nagell, et al,. 1993; Tomasello, et al,. 1993; Meltzoff & Moore, 1994; Meltzoff, 1995; Call & Tomasello, 1995; Carpenter, et al,. 1998; Whiten, 1999; Whiten, in press). However, non-observing controls would be required before confident conclusions could be drawn.

Subjects also demonstrated an ability to ignore the irrelevant action. As with the previous experiment, emulation appears to be the most likely explanation. However, inclusion or exclusion of the irrelevant action during trials 1 to 6 does not appear to be related to the opaque or clear condition of the box. Therefore children's ability to ignore the irrelevant actions of the task was not dependent on the availability of causal information.

Causal reasoning

The continued reproduction of the irrelevant action with the clear apparatus would suggest that subjects had a poor understanding of the causal mechanisms which were involved in task solution. However, social differences in the way subject perceived the task (i.e. whether it was to imitate the demonstrator, or retrieve the reward with the most efficient technique), may mask any underlying trend in the results. Six out of ten children ignored the irrelevant action during at least one trial with the opaque apparatus. Children therefore seem able to extract causally relevant features of a task on the basis of unobservable elements. The literature supports the conclusion that 2-year-old children are capable of understanding causal relationships between objects (Shultz, et al,. 1986; Bates, et al,. 1980; Hauser, 1997; Carpenter, et al,. 1998; Want & Harris, 2001; Want & Harris, in press). It therefore seems likely that although children understood that there was an alternative, more efficient way to retrieve the reward, they continued to imitate the demonstrated technique for social reasons.

At the end of each block of 3 trials, the children were asked why they performed the top irrelevant action. The answers ranged from arbitrary explanations like 'because you have to' to 'because that's what you did'. It was not therefore possible to use verbal explanations to analyse the behaviour of subjects, as it was felt they were giving answers which they thought the experimenter wanted to hear, or they felt like they were being criticised and refused to co-operate. Future experiments should incorporate a less ambiguous questioning method.

Conclusions

The data therefore suggest that children aged between 2 and 3 years of age have the ability to imitate and emulate, but which strategy they chose to employ may be dependant on their perception of the task.

General discussion

The results from the first experiment suggest that chimpanzees have the ability to alter their social learning strategy from emulation to imitation depending on the availability of causal information. As subjects reproduced the irrelevant act significantly more with the opaque box than with the clear box, although the outcome was the same, the data also suggest that the ability to differentiate causally relevant features is dependant on directly observable elements. The ability to differentiate relevant and irrelevant actions has important implication for chimpanzee cultures, as only selective reproduction of the intentional actions of others can support cultural proliferation (Carpenter, et al,. 1998).

The results from the second experiment indicate that children also have the ability to alternate between emulation and imitation. However, the choice of strategy does not seem to be linked to the availability of causal information, as children were able to ignore the irrelevant act equally with the opaque and clear boxes. In contrast to chimpanzees, children therefore seem able to extract the causal mechanisms of a task on the basis of unobservable elements. Children were also influenced by social factors, which may not have been applicable to chimpanzees.

The data are consistent with a study by Nagell, et al (1993), who found that in a tool using task, chimpanzees used emulation to achieve the most efficient solution to the task, in contrast, 2-year-old children continued to imitate the less efficient demonstrated technique.

Conclusions

The combined results of experiments of these two studies suggest that both chimpanzees, and 2 to 3 year old children are capable of altering the social learning strategy that is used to solve a task. However, the conditions under which each ability is expressed are different. Chimpanzees appear, where possible to use the most efficient technique. If chimpanzees can perceive the causal mechanisms involved in a task, they will seek to use their own technique to bring about the same causal outcome. This may be an extremely adaptive strategy, as it allows socially learned behaviours to be generalised to different environmental conditions. However, in contrast, children may continue to imitate even when emulation may be more efficient. This may be the result of social factors that are not relevant to chimpanzees.

Those subjects who took part in the first experiment were wild born chimpanzees, raised with conspecifics, but who had considerable human contact, and a close affiliation with the experimenter. It has been argued that extensive human contact can lead to a fundamental change in the socio-cognitive development of great apes (Call & Tomasello, 1996; Premack, 1983). It might therefore be disputed that the results of this experiment are an artefact of the rearing history of the subjects, and cannot be extrapolated to wild chimpanzees. However, it seems unlikely that evolution has favoured a dormant cognitive capacity that is not expressed under natural conditions. An opposing view is that human contact simply replaces the rich social and physical environment which would be experienced in the wild (Boesch, 1996b). In addition, Great Apes have been reported to imitate humans with whom that have a close affiliation (Russon & Galdikas, 1993; 1995). For this reason, the results of this experiment are not believed to be an anomaly caused by the rearing history of the subjects.

In the first study, 50% of chimpanzee subjects reproduced the demonstrated behaviour with a total fidelity score that exceeded 50%, and with a maximum of 75%. In the second experiment, 90% of human subjects reproduced the demonstrated behaviour with a total fidelity score that exceeded 50%, and a maximum of 93.75%.

The data suggest that while both species demonstrated an ability to imitate, the fidelity of imitation was greater for children than for chimpanzees. This conclusion is consistent with a number of publications that indicate chimpanzees and children are qualitatively similar in their imitative abilities, but that there are quantitative differences in the fidelity of structural and detail matching (Whiten, et al,. 1996; Whiten, 1999; Whiten, in press).

EXPERIMENTAL SHORTCOMINGS AND REASONS FOR EXCLUSION FROM MAIN THESIS

Study 1: Chimpanzees

Although the irrelevant nature of the task makes it unlikely that stimulus enhancement was responsible for the observed results, a two-action design would allow this possibility to be ruled out.

The food-tube should be opaque so that the location of the reward cannot be determined in the clear condition.

A group should be included to counter balance the order in which the apparatus is presented, i.e. instead of the groups being *Opaque > Clear*, and *Clear only* they should be chance to *Opaque > Clear*, and *Clear > Opaque*

Subjects in this experiment found it difficult to manipulate the tool. Future designs should incorporate a more appropriate size of tool, and a non-tool use experiment as wild chimpanzees do not start to habitually use tools until the age of 3 or 4 (Goodall, 1986).

Study 2: Children

The methodology of this experiment was originally designed for chimpanzees. Therefore a number of problems came to light throughout the course of the experiment.

Children were rewarded after every trial. This may have caused inadvertent reinforcement of the first action that was used. Children should therefore only be rewarded once the trails are complete.

Children may have perceived the experiment differently, and thought that they were required to reproduce the actions of the demonstrator, irrespective of their understanding of the causality of the task. In future the experimenter should leave the room after each demonstration, to record the actions of subjects without the social influence of the experimenter watching.