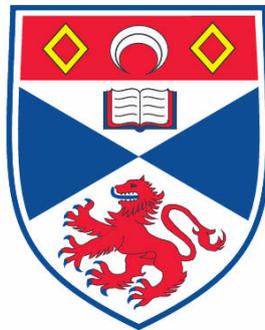


**DISSECTION OF OBSERVATIONAL LEARNING AMONG
CHIMPANZEES (*PAN TROGLODYTES*) AND CHILDREN (*HOMO
SAPIENS*)**

Lydia Meriel Hopper

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



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**Dissection of Observational Learning among
Chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*)**

Lydia Meriel Hopper

**Corrected thesis submitted to the School of Psychology of the
University of St Andrews for the degree of Doctor of Philosophy**

January 2008

I, Lydia Meriel Hopper, hereby certify that this thesis, which is approximately 60,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a previous degree.

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Abstract

In the wild, a variety of inter-group behavioural differences have been reported for chimpanzees (*Pan troglodytes*) and it has been suggested that these may have resulted from social learning. To determine whether chimpanzees show the necessary propensity for social learning, groups of captive chimpanzees were tested in a series of experiments involving the use of two-action and bidirectional apparatuses. For comparison, and to shed light on any contrasts between our own and chimpanzee learning strategies, similar tests were also conducted with children (*Homo sapiens*) to ascertain the nature of their observational learning when watching conspecifics. Through the use of open diffusion and diffusion chain techniques, it was shown that both species learnt how to operate different foraging devices from observing an expert conspecific and this learning was strong enough for the generation of behavioural traditions which passed along multiple test 'generations'. Additionally, ghost conditions were used to distinguish imitative and emulative learning by both species. With one of the two test devices used (the Slide-box) the first evidence for emulation learning by chimpanzees, through the use of a ghost condition, was shown. Children in this condition also showed apparent emulation; a contrast to previous research which has concluded that children tend to rely on imitation. Additionally, to test its potential for use in future social learning experiments, the ability of chimpanzees to learn from video-footage of an unknown conspecific was tested. It was found that the chimpanzees not only learnt how to operate two devices from observing this footage but also used the same alternative method used by the model chimpanzee.

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Chapter 1: Social Learning: A Focus on Chimpanzees

1.1. What is social learning?

When the English speak of 'passing down' something from one generation to another, it is only that. A son passes nothing back up
(Thomas Pynchon 1961, p. 204)

The above quote, although a familiar concept to many, belies the complexity of social learning between individuals. As will be discussed, it is a more fluid process and one which is not necessarily unidirectional. Put simply, social learning involves an individual learning a new behaviour from observing another's actions.

In the Seventies, Bandura (1977) developed his 'social learning theory', in which he stated that social learning allows "people to acquire large, integrated patterns of behaviour without having to form them gradually by tedious trial and error" (p. 12). Social learning is of particular interest because it describes a process through which information is transmitted between individuals and down generations by a process of learning, rather than traits inherited genetically (Mesoudi & Whiten 2004).

Social learning can increase the fitness of an animal by allowing it to avoid potential health, reproductive, and feeding costs (Galef & Giraldeau 2001; Chittka & Leadbeater 2005; Galef & Laland 2005; Kendal *et al.* 2005). Additionally, these learnt behaviours may allow for adaptation to a particular environment (Boyd & Richerson 1985), the development of local traditions and for information learnt by a

previous generation to be transmitted to a later one, as opposed to the behaviour or information being learnt afresh with each generation.

Under certain circumstances however, it should be noted that blindly copying others could be maladaptive, for example when the environment changes and the information gained from social learning is 'out of date' (Galef & Laland 2005; Laland 2004; Boyd & Richerson 2005). However, evidence is also emerging that some animals are capable of selectively copying others, choosing which information is useful, and which is not, depending on the circumstance and their own personal information about it (van Bergen *et al.* 2004; Kendal *et al.* 2005). A second condition that renders social learning as potentially costly for an animal is if a group were to consist of entirely, or a high proportion of, individuals learning from one another with no innovation. In such a scenario no new information could be learned, leaving the group stagnant and vulnerable to environmental change (Giraldeau & Caraco 2000).

So when is social learning efficient? Boyd and Richerson (1985) stated that cultural transmission would evolve under the assumption that individual learning was not perfect. They set out two conditions under which social learning would be favoured over individual learning. The first of these was when the costs accrued from individual learning outweigh those of social learning. The second is when the environment is relatively stable. This second stipulation has been supported experimentally by Galef & Whiskin (2004). Boyd & Richerson concluded from their models that "when individual learning is inaccurate, increasing the importance of cultural transmission reduces the variance in the population; when environments are predictable, a weak force is adequate to keep the mean of the population near the optimum" (p. 117).

Put simply, the transmission of information can be ‘vertically’ or ‘obliquely’ down generations, for example from parent to child, or ‘horizontally’ among peers. In the wild, when adult chimpanzees (*Pan troglodytes*) perform subsistence behaviours such as nut-cracking (Boesch & Boesch 1982; Boesch 1996a), young chimpanzees often sit in close proximity to these adults and closely watch what they do. These observations have provided possible evidence suggesting transmission of information between group members (Biro *et al.* 2003). Biro *et al.* noted that these young chimpanzees in Bossou, Guinea, would only select proficient individuals who were their own age, or older, to observe, never younger individuals. This vertical transmission is certainly a familiar concept for humans, but horizontal transmission also plays an important role in the transmission of information among peers and siblings (Bartlett 1932; Mesoudi & Whiten 2004; Horner *et al.* 2006). Studies conducted to test for these empirically will be discussed in greater detail below.

Much work has been conducted investigating social learning among both captive and wild vertebrates (Tomasello *et al.* 1987; Custance *et al.* 1999; Templeton *et al.* 1999; Hirata & Morimura 2000; Maestripieri *et al.* 2002; Hirata & Celli 2003; Stoinski & Whiten 2003; see Whiten & Ham 1992 for a review). Nicol (1995) also provides a comprehensive review, considering not only the various vertebrate species that have been tested but also the mechanisms that have been suggested to underlie the observed behaviours.

The experiments described in this thesis focus on chimpanzees and human children. It is worth noting, however, that in addition to the corpus of research conducted with vertebrates, studies have also focused on social learning among invertebrates (Webster & Fiorito 2001; Chittka & Leadbeater 2005; Coolen *et al.* 2005; Leadbeater *et al.* 2006; Leadbeater & Chittka 2007). Webster & Fiorito applied

Whiten & Ham's (1992) model in which Whiten & Ham distinguished 'social learning' and 'social influence' as two umbrella terms to include the various mechanisms by which socially mediated learning occurs (see Whiten & Ham 1992, p. 247, Figure 1). Whiten & Ham defined social learning as "B learns some part of the mimicry from A" (p. 247) and social influence as "B is influenced by A but does not learn any part of mimicry from A" (p. 247).

From one review, it was concluded that the taxa Gastropoda, Cephalopoda and Crustacea displayed long-term memory retention and independent learning, while the Arthropoda showed no such abilities (Webster & Fiorito 2001). From their analysis Webster & Fiorito drew the conclusion that Whiten & Ham's model could be usefully applied to invertebrates as well as to vertebrates and that if an invertebrate was capable of social learning it should also be susceptible to social influence, whereas the reverse was not always the case.

Certain primates display inter-group differences in their behaviours, notably chimpanzees (Whiten *et al.* 1999), orangutans (*Pongo pygmaeus*; van Schaik *et al.* 2003), capuchins (*Cebus capucinus*; Perry 2007), macaques (*Macaca fuscata*, McGrew 1998) and bonobos (*Pan paniscus*; Boesch, *et al.* 2002). More detailed examples will be given below, but it has been suggested that these group differences possibly represent socially learnt behaviours. However Boyd & Richerson (1996) proposed that "cumulative cultural evolution is rare. Most culture in non-human animals involves behaviours that individuals can, and do, learn on their own" (p. 78). However, referring to these inter-group differences in nonhuman animals as 'cultures' is contentious (Laland & Janik 2006). Laland & Hoppit (2003), who defined culture as "those group-typical behavior patterns shared by members of a community that

rely on socially learned and transmitted information” (p. 151), judged that there is not yet enough evidence to show that cultures exist among wild chimpanzees.

Due to the uncertainty in explaining the behaviour of wild chimpanzees (Laland & Hoppit 2003) further investigation of social learning among chimpanzees is required. The great apes are, genetically, are closest living relative namely the chimpanzee (*Pan troglodytes*, Wildman *et al.* 2003) and bonobo (*Pan paniscus*, Hacia 2001, but see Gagneux & Varki 2001) and it is partly because of this link and a long-standing interest in behavioural variants among chimpanzees in the wild that here I compare chimpanzee social learning with that of human children. Humans also evidence behavioural traditions which are proposed to have arisen from social learning (Uzgoris 1991, 1993). The overall aim of this thesis therefore was to study the social learning shown by both captive chimpanzees and children. A series of experiments has been designed and conducted to establish similarities and differences between the two species in forms of social learning that can explain their observed behaviours.

a. Behavioural traditions among wild chimpanzees

The fascination with the chimpanzee lies not only with the study of their behaviour for its own interest but also because of the possible insights that such investigations may provide with regard to ourselves and our evolutionary history. The study of chimpanzee behaviour in the field has a relatively long history. Such studies commenced in earnest in the late 1950s and early 1960s by researchers including Jun'ichiro Itani, Jane Goodall and Adriaan Kortlandt in study sites across Africa (Goodall 1994). Through the course of this research on chimpanzees in the wild it was

noted that a number of distinct behavioural patterns were evidenced at some locations but not others, and these were inferred to be socially transmitted traditions (Boesch & Boesch 1993; McGrew 2004).

The study of traditions among wild chimpanzees culminated in a collaboration between many primatologists describing their long-term findings in the field, from which it was concluded that there were 39 different behavioural variants (Whiten *et al.* 1999). A second reason why it has been suggested that these behavioural variants have arisen from social learning is the observation of wild juvenile chimpanzees closely observing their mothers (Biro *et al.* 2003; Lonsdorf *et al.* 2004; Lonsdorf 2005). Additionally, the study of behavioural traditions has broadened to include fish, birds and mammals, further illuminating the similarities and differences to human cultures (Fragaszy & Perry 2003; Mesoudi *et al.* 2006; Whiten & van Schaik 2007).

McGrew (1992; 2004) concluded that the material 'culture', as he termed it, of wild chimpanzees is associated with four main functions which are subsistence, defense, self-maintenance and social relations. Although captive chimpanzees are the primary focus of this thesis, it is important to provide an overview of traditions observed in the wild because it is from a desire to further elucidate the transmission mechanisms of such behaviours that has spurred much research on social learning among captive chimpanzees. For brevity, two of the forms of behavioural tradition identified by McGrew will be detailed here: subsistence and social relations.

Local behavioural variants associated with subsistence, often involving the use of tools, are possibly the best documented and include the various forms of nut-cracking, termite fishing and ant dipping demonstrated by some of the communities of wild chimpanzees (Whiten *et al.* 1999). Ant dipping is a useful example of the caution required when inferring traditions from behavioural variants among groups of wild

chimpanzees. Ant dipping has often been cited as a clear example of chimpanzee traditions, because different populations been observed to use different dipping techniques to collect and eat ants. Chimpanzees in Tai, Cote d'Ivoire, use the one-handed, long-tool (mean length 66 cm) termed the 'mouth-sweep' technique (Boesch 1996a). The chimpanzee holds the tool in the path of ants and once they climb up the stick, and collect on the tool, the chimpanzee pulls it directly through its mouth. Conversely, at Gombe, Tanzania, the chimpanzees use the two-handed, short-tool, method, For this, a tool (mean length 24 cm) is used to collect ants and is then drawn through the chimpanzee's remaining hand, collecting the ants in a ball, before being put directly into the chimpanzee's mouth (Boesch 1996b). McGrew (1974) termed this the 'pull through' technique.

A more recent study of the tool use by chimpanzees in the Ngotto Forest, Central African Republic, found four main tool types (Hicks *et al.* 2005). Two different tools were created for the extraction of honey ('honey hammer/club' and 'honey probe') and two for gathering driver ants ('ant-dip tool' and 'ant club'). Hicks *et al.* inferred from a comparison with the tool-use by chimpanzees at Gombe, that the chimpanzees in Ngotto must employ the pull-through method for ant dipping, as the tools used had an average length of 85 cm. Such a conclusion however may be premature, as behaviour cannot be inferred merely from the associated physical artifacts. Such a study highlights the need for further, detailed, observations of tool-use among wild chimpanzees and the experimental testing of captive chimpanzees to learn how, and why, chimpanzees use certain tools. Such caution is highlighted by the findings of Humle & Matsuzawa (2002).

The inter-group differences of tool-using behaviours by wild chimpanzees have been considered to have arisen from social learning rather than from environmental

differences between the two sites (Whiten *et al* 1999). However, in 2002 Tatanya Humle found that at Bossou, Guinea, chimpanzees exhibit both these ant-dipping techniques and that which they use is dependent on both the ant sub-species and location of foraging (Humle & Matsuzawa 2002). Black *Dorylus* ants were found to be more aggressive and give more painful bites compared to the red *Dorylus* ants on which the chimpanzees fed. When dipping for the black ants, chimpanzees employed longer tools (average length greater than 50 cm) than for the red ants for which they used a shorter tool (average length less than 50 cm). Additionally, when foraging for ants at the nest site, where both red and black ants were more aggressive and more gregarious, the chimpanzees used longer tools to maintain a greater distance from the ants whilst dipping.

The findings of Humle & Matsuzawa (2002) highlight the possibility that the inter-group behaviour differences, such as ant-dipping techniques, may be a result of ecological differences, rather than a product of social learning (Galef & Laland 2005). Additionally, findings have suggested that potential tool-use, observed by woodpecker finches (*Cacrospiza pallida*) in the Galapagos Islands, is learnt by individual trial-and-error, not by social learning (Tebbich *et al.* 2001). Both these, highlight the prudence required when interpreting the behaviour of wild chimpanzees.

The behavioural differences observed between groups of wild chimpanzees involved in the maintenance of social relations, however, seem harder to explain by differences in local ecology. An example of this is the 'grooming hand-clasp' which was observed by McGrew & Tutin (1978). Chimpanzees in the Mahale Mountains, Tanzania, performed this grooming hand-clasp, the like of which McGrew had not seen when previously studying the chimpanzees at Gombe, Tanzania (McGrew 2004). During the grooming hand-clasp, a pair of chimpanzees, engaged in reciprocal

grooming, each have an arm raised above their heads with their hands joined. The resulting symmetry of their bodies has come to represent one of the iconic symbols of chimpanzee culture in the wild. In the wild, this grooming hand-clasp has only been observed in one other study site in Kibale Forest, Uganda (Ghiglieri 1984) and its spread within each group has been attributed to cultural learning rather than environmental influence (McGrew 1992). McGrew (2004) also noted that along with the grooming hand-clasp, the chimpanzees at Mahale have added another elaboration to their reciprocal grooming, the 'social scratch', which has also not been observed at Gombe despite both groups living in Tanzania in similar habitats.

These examples represent only a few of those reported behaviours which are found to be unique to one, or a few, wild populations of chimpanzees (Whiten *et al.* 1999) and wild orangutans (van Schaik *et al.* 2003). These putative 'cultural variants' sometimes appear to have no direct survival value attached to them and even when there does appear to be a functional value it is hard to discern why one group should adopt one method and another group use a second, however the true effect of genetic influences cannot be ruled out.

Although fascinating, these behavioural variants must not be accepted at face-value, as discussed (Laland & Hoppit 2003; Galef & Laland 2005; Laland & Janik 2006; Byrne 2007). The differences that arise between communities of chimpanzees may be a result of, as yet, unknown environmental and/or genetic differences that exist between communities as the work of Humle highlights (Humle & Matsuzawa 2002). Therefore, in addition to the observational work of field researchers, work with captive groups of chimpanzees offers a greater level of control, which allows for the more detailed dissection of how such traditions may have arisen and spread within a group. It must be acknowledged, however, that the capacities of captive and wild

chimpanzees may differ greatly, rather, studying captive chimpanzees allows us to answer the ultimate cognitive potential of the species.

b. History of interest in social learning by captive chimpanzees

Studying chimpanzees in their natural environment provides rich and detailed information about their wild behaviour but it does not allow for control of all the variables that may allow for the emergence of these behavioural variants. Studying chimpanzees in captivity, in contrast, provides an opportunity to discover whether chimpanzees show a tendency to learn socially, and if so how such learning occurs. Additionally, the use of captive groups of chimpanzees also provides the opportunity to ascertain whether chimpanzees have the potential to maintain behavioural traditions.

(i) Self-seeded traditions

Inter-group behavioural differences have been documented between communities of wild chimpanzees but comparable traditions have also been noted among captive groups of chimpanzees (de Waal & Seres 1997; Bonnie & de Waal 2006).

Additionally, de Waal (1989) noted differences in the hand-clapping behaviour of bonobos to gain conspecifics' attention between different groups of bonobos housed at San Diego Zoo.

The grooming hand-clasp observed between wild chimpanzees at certain study sites has also been noted in captivity (Bonnie & de Waal 2006). Its propagation within

a group of captive chimpanzees at the Yerkes Regional Primate Research Center (from now on termed ‘Yerkes’) was monitored by de Waal & Seres (1997). From their observational study of these captive chimpanzees, de Waal & Seres concluded that the custom had been derived from one specific chimpanzee and the behaviour spread throughout the group with its occurrence increasing in frequency over a five-year period. They also noted that this behaviour continued to be shown by members of the group even after the ‘inventor’ chimpanzee was removed. These observations provided a unique opportunity to study the propagation of a behaviour within a captive group of chimpanzees, which can assist our understanding of comparable processes among wild populations of chimpanzees.

(ii) Artificially-seeded traditions

The interest of the self-propagation of the grooming hand-clasp at Yerkes (de Waal & Seres 1997; Bonnie & de Waal 2006) is that it demonstrates the possibility of the emergence of behavioural traditions among captive chimpanzees which reflect those observed in the wild. However the observational study of such behavioural variants does not allow for control over the possible ecological causes nor to elucidate the potential social learning mechanisms that allowed the reported transmission.

To answer such criticisms Whiten *et al.* (2005) investigated the spread of a tool-use tradition within captive groups of chimpanzees housed at Yerkes using an ‘open diffusion’ technique. The methodology underlying such an experiment will be discussed in detail below (Section 1.3b), but the importance of an open diffusion design is that control over the seeded behaviour and its spread throughout a group is

under the control of the experimenter and can be documented in detail throughout. This method has been used with continued success with chimpanzees housed at a second facility, the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M. D. Anderson Cancer Center, Bastrop, Texas, U. S. A. (from now on termed ‘MDACC’; Hopper *et al.* 2007; Whiten *et al.* 2007).

1.2 Forms of social learning

From the wealth of studies with both wild and captive chimpanzees it does appear that social learning occurs between chimpanzees and this was the conclusion of Whiten *et al.* (2004). Whiten *et al.*’s review aimed to answer the question ‘How do apes ape?’ from the premise that apes *do* ape. Many classifications have been proposed to describe the various forms of social learning and for clarity in future discussions an overview of the major classifications will be presented here. This overview does not aim to cover all the distinctions that have been proposed but merely the major ones that will be later referred to throughout this thesis (see also Whiten & Ham 1992; Heyes 1993; Byrne & Russon 1998; Call & Carpenter 2002, 2003; Zentall 2003; 2006).

a. Contagion and mere presence effect

Contagion describes the phenomenon by which species-typical behaviours are elicited from an animal when it observes another (Thorpe 1963). An example of contagion is when an animal eats after observing a conspecific feeding, even if the observing animal is satiated (Tolman 1964).

Mere presence effect, and social facilitation (Zajonc 1965), have similarities with contagion. It describes how the presence of a conspecific can affect the ability and speed with which an observer can acquire a new behaviour. Zajonc believed that the presence of a conspecific was detrimental to the observer, however more recently Caldwell & Whiten (2003) found that the presence of a conspecific scrounging facilitated social learning by marmosets (*Callithrix jacchus*).

b. Response facilitation

Response facilitation is a term introduced by Byrne (1994) to describe the increased probability of an animal to also do a familiar act they have observed a conspecific do. Crucially, Byrne noted, response facilitation differs from imitation because the actions done are already in the repertoire of the observing animal, however, more commonly this latter aspect of response facilitation is considered to be less crucial (Hoppitt 2007).

c. Local and stimulus enhancement

Local and stimulus enhancement occur when an individual's attention is drawn to a particular locale or object merely by the presence of another animal, or the change in the environment as a result of such an interaction (Whiten & Ham 1992; see also Zentall 2001 for a review). In local enhancement the animal's attention is drawn to a particular location, while in the more specific stimulus enhancement, it is a particular part of an apparatus or object to which the observer's attention is focused.

Tomasello *et al.* (1993a) advocated that local enhancement cannot allow for cumulative culture because, although learning occurs in a social environment, the specific behaviours of the model are not copied, instead the observer relies on individual, trial-and-error learning. Boyd & Richerson (1996) concur with Tomasello *et al.* and proposed two models under which such a mechanism could evolve. Only within their ‘continuous trait model’, which led to behaviours that could not be learnt individually, could cumulative cultural change occur, further suggestive of the importance of imitative learning for such a process.

One example of local enhancement is the milk-bottle-top piercing behaviour observed among blue-tits (*Parus caeruleus*), which spread across Britain (see Bonner 1980; Reader & Laland 2003 for reviews). Sherry & Galef (1984, 1990) replicated the social learning of this behaviour with black-capped chickadees (*Parus atricapillus*) and found that exposing the birds to bottles previously opened (by the experimenter) was sufficient for the naïve birds to learn how to pierce the bottle tops themselves. These findings suggest, that at least for a simple behaviour, local and stimulus enhancement are sufficient for the spread of a behaviour and the emergence of a new tradition. However, as proposed by Tomasello *et al.* (1993a) such a tradition is distinct from cumulative culture.

d. Emulation, affordance learning and object movement re-enactment

Regarding chimpanzees, emulation was first defined by Tomasello (1990) to refer to a form of learning about changes in the environment as a result of a fellow chimpanzee’s behaviour. Latterly, Tomasello (1999) provided the following example to define emulation:

“For example, if a mother rolls a log and eats the insects underneath, her child will very likely follow suit. This is simply because the child learned from the mother's act that there are insects under the log - a fact she did not know and very likely would not have discovered on her own. But she did not learn from her mother how to roll a log over to eat insects; these are things she already knew how to do or could learn how to do on her own. (Thus, the youngster would have learned the same thing if the wind, rather than the mother, had caused the log to roll over and expose the ants.) This has been called *emulation learning* because it is learning that focuses on the environmental events involved - the changes of state in the environment that the other produced - not on a conspecific's behavior or behavioral strategy” (Tomasello 1999 p. 29)

Tomasello's (1990) definition of emulation arose from an earlier study conducted by him and colleagues. Tomasello *et al.* (1987) presented young chimpanzees with a T-bar shaped tool to retrieve an out-of-reach food item. The chimpanzees were exposed to either (i) a chimpanzee who could use the tool in one of two specific ways to retrieve the food or (ii) a chimpanzee not using the tool. The younger chimpanzees (aged 4-6 years) were able to use the tool to get the food but did not do so imitatively as they did not “copy the demonstrator's precise behavioral strategies” (Tomasello *et al.*, p. 175). These findings are suggestive of emulation because the observing chimpanzees learnt the affordances of the tool, that it could be used to retrieve the food, but not necessarily the precise manner with which the model used it.

The definition of emulation given by Tomasello refers to the observer replicating changes in the environment. A second concept which is often used synonymously with emulation, but which has a distinct meaning is that of affordance learning as used by Klein & Zentall (2003). From affordance learning the observing animal learns

about the properties of the environment from the changes that occur. Byrne (1998) distinguished four aspects of emulation learning, which were (i) setting a goal, (ii) learning the physical properties of objects, (iii) learning relationships among objects and (iv) learning what can be done with an object, all of which relate to learning the affordances of an object (see also Byrne 2002a; Whiten *et al.* 2004).

An example of affordance learning was proposed by Zentall & Akins (2001) when describing the study of Bugnyar & Huber (1997). Bugnyar & Huber recorded the responses of marmosets that had observed cage mates entering a box to retrieve food through a door which could either be pulled or pushed to pass through it. The observers showed a tendency to use the same method as that which they observed. Zentall & Akins however concluded that the marmosets might have learnt about the affordances of the door ('it can be pulled' or 'it can be pushed') rather than imitating the action of the model marmoset. These learnt properties relate to the last three of Byrne's (1998) four sub-categories of emulation.

In their review of observational learning, Whiten *et al.* (2004) were careful to distinguish imitation from object movement re-enactment (OMR; Cusance *et al.* 1999). Whiten *et al.* defined OMR as "copying what the object does" (p. 39), distinct from imitation (introduced in next section) which requires the observer to replicate the bodily movements of the demonstrator (as well as its intentions, according to some definitions). OMR should not be thought of as less 'beneficial' than imitation however because "it may reflect adaptive choices, where it can be more efficient to replicate object movement through actions that do not match those of the model" (Whiten *et al.* 2004, p. 41).

e. Imitation

Whiten & Ham (1992) defined imitation as a process in which “B learns some aspect(s) of the intrinsic *form* of an act from A” (p. 250). However since this somewhat raw definition can be contrasted with more elaborate ones (Whiten *et al.* 2004) some now consider that imitation should involve not only matching the behaviours involved in an act, but also an *understanding* of the model’s intentions (Tomasello 1999; Zentall 2003).

Boyd & Richerson (1996) stated that perspective-taking by the observer is an essential element of true imitation, which therefore requires this level of ‘theory of mind’ by the observer. However Zentall (2001) disagrees with this conclusion, because he believes that as imitation has been shown in “species as varied as rats, pigeons, and Japanese quail...the responsible mechanism is not likely to be theory of mind or perspective taking. But in cases in which stimulus matching is inadequate to account for imitation, some precursor of perspective taking is likely to be involved” (p. 85).

Care should be taken when concluding that the responses of a subject are imitation rather than object movement reenactment as highlighted by Tomasello (1996). Tomasello suggested that the imitation by chimpanzees found by Whiten *et al.* (1996) could also be explained by OMR. Whiten *et al.* (1996) presented chimpanzees and children with an ‘artificial fruit’ apparatus on which were three defences that could be opened in two different ways. It was reported that although the chimpanzees, and to a lesser extent the children, used their own methods to open the artificial fruit, they also copied some of the model’s specific actions. An example of this matching is the removal of one of the defenses, the bolt. Models either removed the bolt defense by

twisting it and pulling it out ('twist') or poking it out ('poke'). Whiten *et al.* reported that those chimpanzees who had seen twist went on to do more twist than poke actions themselves and concluded that this was evidence for imitation. Tomasello (1996), in contrast, suggested that the observers might have been copying the movement of the bolt itself (OMR) rather than the action of the demonstrator (imitation).

(i) Contextual and production imitation

In his review of social learning strategies, Byrne (2002*b*) introduced two forms of imitation; contextual and production. In the former the introduced behaviour (such as a tool-use task) does not require an action novel to the subject, but rather the subject learns how to apply a behaviour already in its repertoire to this new situation. He concluded that the fitness of the animal may increase in many cases when contextual imitation is evidenced but no new learning necessarily occurs. In contrast, in production imitation "the result of observation is to learn a new action" (p. 85), and for which, Byrne believes there is less conclusive evidence amongst animals.

To provide a brief overview of imitation, three domains of imitative learning, adapted from Call & Tomasello (1996), are given here:

(i) Arbitrary actions and 'do-as-I-do'

Both in the wild and captivity, as indicated above, chimpanzees have been observed to show local behavioural traditions, of which some relate to the maintenance of social relations. These behaviours, such as the grooming hand-clasp (McGrew & Tutin 1978; Ghiglieri 1984; de Waal & Seres 1997; Bonnie & de Waal 2006), appear to be arbitrary in their nature, serving no obvious functional purpose, yet are performed by many chimpanzees. However, due to the constraints detailed previously, one cannot be certain how such behaviours are learnt by chimpanzees and so whether actions like the grooming hand-clasp arise from imitative learning cannot be ascertained.

With captive chimpanzees, researchers have adapted the children's game 'Simon says' to study further the imitative capabilities of apes and other animals through an experimental paradigm named 'do-as-I-do' (Hayes & Hayes 1952). The chimpanzee is taught a number of actions and trained to match those to the same actions when performed by the demonstrator (usually a human). Once the chimpanzee understands the concept of imitating actions, the experimenter performs novel gestures and body movements to determine whether this elicits a corresponding action by the observing animal.

Successful matching to a demonstrator during a do-as-I-do test has been demonstrated with chimpanzees on a number of occasions (Hayes & Hayes 1952; Tomasello *et al.*

1993b; Custance *et al.* 1995; Myowa-Yamakoshi & Matsuzawa 1999) and also orangutans (Miles *et al.* 1996; Call 2001). However, a recent study of a captive gorilla (*Gorilla g. gorilla*, Byrne & Tanner 2006) reported that although the gorilla copied the demonstrated actions, notably without reward, the matching was not consistently exact. Furthermore, Byrne & Tanner likened this to the generally poor consistency of matching by apes in previously reported do-as-I-do studies. They concluded that a more parsimonious explanation of the social learning mechanism was response facilitation, rather than imitation.

Aside from the method of copying, it should be noted that Zentall & Akins (2001) distinguish gestural imitation, arising from do-as-I-do tests, from other imitation because the demonstrator's physical appearance is often quite distinct from that of the test subject, for example human models with species diverse as dolphins (*Tursiops truncatus*, Herman 2002), dogs (*Canis lupus familiaris*, Topal *et al.* 2006) and parrots (*Psittacus erithacus*, Moore 1992). However, that these animals can relate their body to that of a human and show bodily imitation, could be regarded as more impressive than that shown by apes.

(ii) Object manipulations and spontaneous imitation

Hayes (1951) described how the home-reared chimpanzee, Viki, would spontaneously perform actions on familiar household objects that she had apparently observed her carers using. Examples of such actions include attempting to apply lipstick and brushing her teeth with a toothbrush. However as the account of Hayes is purely observational it is questionable that the behaviours shown by Viki were learnt through

imitative learning; it remains possible that stimulus enhancement, response facilitation or emulation may explain them.

(iii) Problem-solving and tool-using tasks

Tomasello *et al.* (1987) presented young chimpanzees with a tool-using task in order to determine whether, and how, they were able to learn it from observing a conspecific. However, as described earlier, it was concluded that the chimpanzees learnt by emulative, rather than imitative learning, because they did not use the tool in the *exact* manner as the model, but rather used the tool in their own manner to achieve the same goal (see Tomasello 1999). Many recent studies have concluded that chimpanzees tend to show emulation, rather than imitation (Whiten *et al.* 2004; Call *et al.* 2005) while Horner & Whiten (2005) proposed that chimpanzees switch between both imitation and emulation depending on the particular situation.

f. A note on deferred imitation

Deferred imitation has been defined as “the ability to reproduce a previously witnessed action or sequence of actions in the absence of current perceptual support for the action” (Courage & Howe 2002, p. 257). Studies describing deferred imitation include a delay between the demonstration and the response period which has the benefit of reducing the likelihood of behaviours resulting from response facilitation, providing possibly greater evidence for evidence. Despite the potential interest that

deferred imitation might encourage, only a few studies have been conducted with apes, and the majority of these have focused on enculturated¹ chimpanzees (Tomasello *et al.* 1993b; Bering *et al.* 2000; Bjorklund *et al.* 2002; Bjorklund & Bering 2003).

Tomasello *et al.* (1993b) compared the levels of deferred imitation shown by mother-reared chimpanzees to enculturated chimpanzees and found that the enculturated chimpanzees out-performed the mother-reared chimpanzees. This finding prompted Bjorklund *et al.* (2002) to test enculturated chimpanzees further and concluded that three enculturated juvenile chimpanzees tested showed deferred imitation after a delay period of ten minutes. However each chimpanzee performed ‘approximate target’ or ‘target’ behaviours on one or more of the tasks during a baseline phase and secondly, not all of the target stimuli were truly novel to the chimpanzees as they had been utilized in previous experiments. If novelty of action (Thorpe 1963) is a key component for demonstrating imitation, the findings of Bjorklund *et al.* appear less compelling, but this is only so if describing production, rather than contextual, imitation (Byrne 2002b).

Two observational studies of rehabilitant orangutans (*Pongo pygmaeus*) used three criteria to identify imitation in the wild (Russon & Galdikas 1993, 1995). Russon & Galdikas (1993) concluded that many of the actions displayed by these orangutans, such as hanging up a hammock and painting with a paintbrush, must have been observed at an earlier point in time from a human model. It was concluded that the observations provided examples of deferred imitation by the orangutans.

¹ Enculturation is the term used to describe apes that have been reared by human caregivers in an intensive environment resembling the upbringing of a human infant (Tomasello *et al.* 1993a; Call & Tomasello, 1996).

However, the past history of these orangutans was not known, nor was information provided about the degree to which these orangutans had been seen to observe the acts done, and so the conclusion of deferred imitation has to be taken with caution.

The ability of apes to generalise across different stimuli in a deferred imitation paradigm has also been assessed (Bjorklund *et al.* 2002; Yunger & Bjorklund 2004). Bjorklund *et al.* tested three enculturated chimpanzees on their ability to transfer an action across seven pairs of stimuli after a delay of 10 minutes from the demonstration. However some of the pairs of stimuli were perceptually very different and so to transfer actions might have been opaque to the apes tested. Despite the apparent ambiguities of the seven pairs of test stimuli selected by Bjorklund *et al.*, two of the three enculturated chimpanzees deferred imitation by the transfer of actions across the stimuli. However, the level of imitation was less than that displayed when the test stimuli remained constant. It is interesting to note that it was the older two chimpanzees (aged 9 years, 1 month and 7 years, 2 months respectively) that showed significant levels of generalised imitation while the younger (aged 5 years, 9 months) did not.

It should be emphasised that little work has been conducted to determine these abilities in mother-reared apes in comparison to enculturated apes. This apparent bias appears to have possibly been borne from the findings of Tomasello *et al.* (1993b). They concluded that for both immediate and deferred imitation, enculturated chimpanzees outperformed both children and mother-reared chimpanzees due to their rearing history. Indeed, Bjorklund & Pellegrini (2001) concluded in their review of enculturation that its impact is due to chimpanzees being reared in an environment where shared joint-attention is encouraged. They argued that enculturated apes actually understand the referential pointing involved rather than just learning it as a

conditioned response. It is this reasoning which they use to explain the greater abilities of deferred imitation shown by enculturated chimpanzees and orangutans. However the conclusions of Bjorklund and colleagues are based on no direct comparisons made between enculturated and mother-reared chimpanzees (see also Whiten 1993). A second criticism of these previously-run studies is that many only incorporate short delays between observing and response periods which is not distinct from the methods of general social learning experiments. Deferred imitation studies testing the abilities of children (discussed in Chapter 2) provide more convincing evidence of deferred imitation as they have included delays of up to 6 months (Barr *et al.* 1996) and such factors should be incorporated in the planning of future studies testing for deferred imitation in non-human animals.

1.3 Testing how apes ape

In order to determine *how* apes ape a number of experiments have been conducted, including those documented in this thesis, which have employed a variety of experimental paradigms and apparatuses. An overview of the methods used will be detailed here for clarity in later discussions.

a. Apparatus used

(i) Tool-use

Many experimental studies with chimpanzees involve apparatuses that require the use of a tool in order to reach the ultimate goal, reflecting the behaviour of wild chimpanzees which have been observed to use tools for a variety of functions (McGrew 1992; Whiten *et al.* 1999, 2001). A variety of these studies have concluded that tool-use is more evident among captive primates than among those in the wild (Westergaard & Fragaszy 1987; Westergaard 1988; Visalberghi *et al.* 1995; Mulcahy *et al.* 2005). Brent *et al.* (1995) found that among captive chimpanzees, those that were wild-born chimpanzees showed a greater success rate when using tools, than did groups comprising of captive-born chimpanzees regardless of their prior experience with tools.

As an interesting aside, further to the use of single tools by wild chimpanzees is their documented use of ‘tool-sets’ – the use of more than one tool in succession to achieve a goal (Bermejo & Illera 1999; Brewer & McGrew 1990). Bermejo & Illera concluded that the use of tool-sets showed that “chimpanzees used the tools in a flexible, insightful way...[recognising] the functions of the tools and the hierarchical nature of the multiple action involved in the use of the tool-set” (p. 626). That chimpanzees can manipulate and use tools in such a complex manner gives some indication of the familiarity that they must have with the raw materials as well as an understanding of the task in hand. Huffman & Quiat (1986) suggested that such familiarity and practice were the precursors that allowed the development of

successful tool use by chimpanzees and this explains why the study of tool-use by chimpanzees is particularly pertinent.

(ii) Two-action method

To test for imitation, Dawson & Foss (1965) developed a 'two-action method' in which the goal of the task was always the same, but the behaviour required to achieve it could be demonstrated in more than one way. Imitation could then be determined if the observer used the same body movement as the model observed, to complete the task. In the original task, budgerigars (*Melopsittacus undulates*) observed conspecifics remove a square of card (lid) from a dish containing food using one of three methods; 'edged off by the beak', 'lifted off by the beak' or 'used foot to dislodge the square'. The budgerigars tended to use the same method as that demonstrated, but due to the paucity of detail provided in the report, the conclusion should be regarded with caution (see also Galef *et al.* 1986).

However Zentall & Akins (2001) criticised the two-action method in general, focusing on the conclusions drawn by Galef *et al.* (1986) who replicated Dawson & Foss's design. Zentall & Akins stated that as the lid moved in different ways (slide off vs. lift off) the observing birds may have actually learnt about the affordances of the lid rather than matched the model's behaviour. To overcome such limitations, Zentall and colleagues designed experiments in which a pedal could be depressed by either a bird's beak or foot. In this, the resultant movement of the target object was the same for both actions (Akins & Zentall 1996; Zentall *et al.* 1996; Kaiser *et al.* 1997). Kaiser *et al.*, for example, advised that imitation could only be inferred when a two-action

method was used, if a control group was also included and that the level of responses of both methods were higher for each respective experimental group compared to the control animals, however it should be noted that the results of Kaiser *et al.* could also be explained as resulting from response facilitation and that only a substantial delay between demonstration and response can rule this out (Hoppitt *et al.* 2007).

(iii) Bidirectional method

A bidirectional task is composed of an apparatus with a manipulandum that can be moved in one of two directions; left/right or up/down, for example, and was developed by Heyes & Dawson (1990). Such an apparatus has the advantage of being able to control against stimulus enhancement insofar as there is always interaction with the same device. Despite this benefit over the two-action method, Zentall & Akins' (2001) criticisms of the two-action method could also apply here to the bidirectional method as the manipulandum moves in two distinct ways.

Heyes & Dawson (1990) recorded that the rats (*Rattus norvegicus*) which observed a bar moved either to the left or right by a conspecific pushed the bar in the same direction when allowed access. More recently, however, Mitchell *et al.* (1999) concluded that the rats were responding to olfactory cues left on the bar by the demonstrating rats. This would need to be controlled for to test for imitation (Klein & Zentall 2003).

(iv) Ghost condition

When testing for the use of emulation learning directly, one method that has been suggested to be suitable for this is the ghost control, or ghost condition (Heyes *et al.* 1994; Fawcett *et al.* 2002). A ghost condition provides a ‘demonstration’ of the test task through a hidden or discrete mechanism

When describing emulation, Byrne (2002*b*) stated that “the important distinction from other kinds of imitation is that motor behavior *per se* is not copied. Thus, in principle, emulation could be as effective if the behavior were not seen” (p. 90). It is from this kind of rationale that the ghost method was developed, as it allows for the demonstration of the movements of an apparatus without a conspecific demonstrator present (Whiten *et al.* 2004; Tennie *et al.* 2006; Hopper *et al.* 2007).

Ghost conditions have now been used with a variety of species and these have produced both positive and negative evidence for emulation, discussed in full in *Chapters 4-7*.

b. Test scenario

Testing chimpanzees in captivity allows the experimenter maximal control over the experimental variables when investigating social learning. There are a numerous ways of testing chimpanzees and a brief review of the main four is given here.

(i) Field 'laboratory'

Matsuzawa and colleagues created a 'field laboratory' to study the nut-cracking and other behaviours of chimpanzees at Bossou, Guinea. At this site, a clearing in the forest, the chimpanzees have been provided with nuts and the chimpanzees observed (Biro *et al.* 2003). Although useful and interesting, such an approach does not allow for direct comparison with other groups or provide direct control over key variables; in particular, no control condition can be applied.

(ii) Captive dyads

In captivity, chimpanzees have often been tested in a dyadic context when investigating the process of social learning where one naïve individual observes a model and their behaviour compared to that of a control or baseline phase (see Whiten *et al.* 2004 for a review). Although such a method has been widely used, and allows for close control over many experimental variables, testing chimpanzees in a dyadic setting is limited because it does not provide information about how novel behaviours might spread among multiple individuals. Additionally, human models have often been used rather than conspecifics

(iii) Diffusion chains and the replacement method

In order to give experimenters more information about how behavioural traditions may develop and be transmitted within a group of animals three paradigms have been used; (i) diffusion chains, (ii) the replacement method and (iii) the open diffusion method. The first of these two are similar in design and so shall be discussed together first.

Diffusion, or transmission, chains were originally used by Bartlett (1932) when studying the transmission of folk tales and human memory (Kashima 2000) and have been applied more recently to testing chimpanzees (Horner *et al.* 2006). In a diffusion chain, an individual (A) is trained in a particular behaviour which it then demonstrates in the presence of a second conspecific (B). After observing the behaviour, individual B is allowed to attempt the task themselves. If proficient, B then performs the behaviour in front of a third conspecific (C). This chain of transmission continues until all individuals have acted both as models and observers. The diffusion chain method, in addition to the work with chimpanzees, was previously successfully used with blackbirds (*Turdus merula*, Curio *et al.* 1978) and rats (Laland & Plotkin 1990, 1993).

Somewhat similar to the diffusion chain is the replacement method (Menzel *et al.* 1972). In this method a trained individual (A) is introduced to a group of naïve conspecifics (e.g. B, C, D) who are able to observe the trained model perform the target behaviour. Ultimately, when all group members can perform the behaviour the model is removed from the group and replaced with a new naïve individual (E) so the group now comprises of individuals B, C, D, and E. Then later individual B will be removed and replaced with yet another naïve individual (F) leading the group to

comprise of individuals C, D, E and F. This method allows the transmission of a behaviour to be traced along a series of individuals but in a more naturalistic way than the 'dyadic' diffusion chain. It represents a half-way house between the diffusion chain and the open diffusion method. The replacement method has been used successfully with rats (Galef & Allen 1995) and fish (*Poecilia reticulata*, Laland & Williams 1998).

(iv) Open diffusion

The open diffusion method allows a most 'natural' way of studying the spread of behavioural traditions (Whiten *et al.* 2005; Bonnie *et al.* 2007; Hopper *et al.* 2007; Whiten *et al.* 2007). In this method a trained model is allowed to perform a target behaviour in the presence of their cage-mates. Whether this new behaviour spreads throughout the group can be documented by the experimenter. When this method is combined with the use of a two-action task a model from one group can be trained in one method while a second chimpanzee from another group can be shown the second. From following this procedure Whiten *et al.* (2005) found that two distinct behavioural traditions emerged with the majority of members of each group using the method they observed used by their seeded model despite both options being available to them.

1.4 Conclusions

Whether or not chimpanzees evidence ‘culture’ in the wild is a contentious issue (Laland & Hoppit 2003), however that they show social learning is more certain (Boesch 1996*b*, Whiten *et al.* 1996, 2004). Studies with captive chimpanzees allow us to shed light on whether chimpanzees have the propensity to maintain traditions within a group (Whiten *et al.* 2005; Hopper *et al.* 2007; Whiten *et al.* 2007) and what forms of social learning chimpanzees use (Tomasello *et al.* 1993*b*; Horner & Whiten 2005; Hopper *et al.* 2007). *Chapter 2* will provide an additional and comparable review to the one provided here, but with a focus on research pertaining to social learning by children. From both these chapters, conclusions will be drawn and the aims of this thesis outlined in greater detail.

Chapter 2: Social Learning: A Focus on Children

The imitative abilities of young children have been traditionally studied by developmental psychologists (Want & Harris 2002) and since the early 1990s research conducted by comparative and evolutionary psychologists has gathered pace examining similarities and differences between the behaviour exhibited by children and apes (Nagell *et al.* 1993; Whiten 2002*a, b*; Call *et al.* 2005; Horner & Whiten 2005; Tennie *et al.* 2006). Following in this tradition and with an aim of expanding it, the focus of this thesis is concerned with social learning among children, as well as chimpanzees.

Chapter 1 provided an overview of the various social learning processes along with the numerous ways in which one can test for them with a particular focus on chimpanzees. This chapter will provide an overview of the history of studying social learning by children. Additionally, to complement *Chapter 1*, the experimental methods that have been used to test for social learning in children will be described.

2.1. History of interest of social learning among children

Social interactions, and resultant observational learning, are observed among humans from an early age (see Meltzoff 1988*d*; Uzgiris 1991; Want & Harris 2002 for reviews). Boyd & Richerson (1996) believe that observational learning by humans has evolved because it allows for the development of cultures, an advantageous adaptation for humans. This view was supported by Uzgiris (1991, 1993).

A formal interest in observational learning by children began in earnest with the early observational recordings made by Guillaume (1926/1971) and Piaget (1962). The work of Piaget was pioneering, and indeed Barr *et al.* (1996) stated that “the most extensive developmental theory remains the one originally proposed by Piaget” (p. 159). Piaget documented the behaviour of his own children and, although these accounts lack modern scientific rigor, they still provide a useful insight into the development of imitative abilities by children. It was from these reports that Piaget developed his stage theory of infant development, in which infants are not born with the ability to imitate, but learn to do so along with the development of their sensory-motor abilities.

Piaget (1962) proposed that imitation developed linearly, in stages throughout a child’s early development and that by 9-months-old an infant’s imitation would show high fidelity. By around the age of 12-months-old an infant was able to locate out-of-sight regions of their body when imitating others. Barr (2002) concurred with Piaget, suggesting additionally, that the onset of mimicry, imitation and emulation followed a developmental progression along with the ability to use tools.

Meltzoff (1995) also advocated the idea that the imitative abilities of children develop in a linear fashion with regard to understanding the intentional acts of others, from copying simple body acts, to actions on objects and finally to using tools with objects. However, in contrast to Piaget (1962), Meltzoff and colleagues found evidence from a series of experiments on neonatal imitation that suggest infants younger than 6-months-old can imitate facial expressions such as tongue protrusions and head movements (Meltzoff & Moore 1977, 1983; Meltzoff 1988*d*; Meltzoff 1995).

Recent work by Jones (2007), however, calls into question the findings of Meltzoff & Moore (1977). In the study, infants aged 6, 8, 10, 12, 14, 16, 18 and 20 months of age observed their parent perform a battery of facial gestures and body movements, each for up to three minutes. Throughout, the infants were encouraged to imitate their parents. Each action was either silent (e.g. waving hands “bye bye”) or had an associated sound (e.g. clapping hands). Jones determined that infants do not start imitating until sometime between their eighth and twelfth month and these first behaviours to be imitated were actions already within the child’s repertoire. It was additionally shown that infants were most likely to imitate behaviours incorporating a sound at a younger age than those behaviours which did not. Jones found that it was not until children were well into their second year that they imitated behaviours, such as sequential finger movements and tongue protrusion, identified by Meltzoff and colleagues as the hallmarks of neonatal imitation. Further support for Jones’ criticisms come from Anisfeld and colleagues (Anisfeld 1996, 2005; Anisfeld *et al.* 2001).

Social interactions that facilitate observational learning are common within the daily experiences of children. In a day-to-day scenario, children may often observe adults, such as their mother and also their peers, for example when at nursery (Uzgiris 1991). The former interaction represents a time for the potential vertical transmission of information, while the latter a context for the possible horizontal transmission of information (as introduced in *Chapter 1*). Pigeon-holing such transmission between is obviously simplistic as it is not simply horizontal *or* vertical, but more complex, including oblique transmission (e.g. aunt to niece) and collaboration (Ashley & Tomasello 1995; see Flynn in press for an overview). Indeed, it is this complexity that makes social learning among children so interesting, providing further avenues for

future research. But as the experiments reported in this thesis focus on vertical and horizontal transmission alone, for brevity, they are the terms that shall be referred to throughout. Much developmental research, as that presented here investigated what might be regarded as only vertical or oblique transmission, insofar as the experimental paradigm involved infants and children observing adult models demonstrating target acts, body movements and interactions with tools and artifacts (but see Hanna & Meltzoff 1993; Horner *et al.* 2006; Flynn & Whiten in press).

Whom the child imitates and why may shed light on what a child gains from such an interaction. Uzgiris (1991) suggested that imitation has four main functions which are; (i) a mode for social interaction, (ii) a way to gain new skills, (iii) a way to gain knowledge about the culture and views of the society within which the child lives and (iv) that it has an affiliative function. However, in reality children copy relentless and often when there is no apparent benefit or reinforcement which could be costs and non-functional. Secondly, Uzgiris encouraged studying imitation within a wider social context and although she raised important issues within her work, she continually used observational learning and imitation as interchangeable terms, and when describing imitation had no controls for stimulus and local enhancement, mimicry, nor emulation. This lack of dissection of forms of social learning was a general failing within the work of early developmental psychologists, as highlighted by Want & Harris (2002).

Social learning by children is not purely dependent on the person with whom they interact and observe but also on the context within which that interaction takes place. As was noted for non-human animals by Nicol (1995), Want & Harris (2002) suggested that the form of a child's social learning may also be context- and task-specific. They proposed that "instead of thinking of children's social learning as, at

any one time, bound to one particular form (albeit one that may change *over* time), the alternative hypothesis is that children of a given age are capable of both imitation and emulation, and that the form that their social learning takes is determined by their knowledge of the actions they witness” (p. 11).

Despite the potential concurrence of both imitation and emulation there is a general consensus within the literature that children, in contrast to chimpanzees, use imitation predominantly rather than emulation (Call & Carpenter 2002; Call *et al.* 2005; Horner & Whiten 2005). Despite this, experiments have tested for, and evidenced, potential emulation among children (Thompson & Russell 2004; Tennie *et al.* 2006). Bauer & Kleinknecht (2002) concluded that emulation was not determined solely by the age of a child, but children are able to emulate under the age of 4-years-old. Ultimately, Bauer & Kleinknecht agreed with Want & Harris (2002) in their proposal that the learning strategy employed by children is dependent on the complexity and demands of the task with which they are presented with.

The context-dependency of children’s imitation and emulation was highlighted by a cleverly designed experiment by Gergely *et al.* (2002), a replication and extension of previous study by Meltzoff (1988*b*). Meltzoff, when testing deferred imitation, presented 14-month-old infants with a series of novel actions. One of these tasks involved the adult model turning on a light in a box by leaning forward and depressing a button on the top of the box using their forehead. The infants imitated this act, also using their forehead. To determine why the infants in Meltzoff’s study imitated, rather than emulated by using their hand to activate the light, Gergely *et al.* extended upon this experiment with two conditions. In both, the adult turned on the light with their forehead. The first condition followed the same procedure as described by Meltzoff (hands free), while in the second, the adult had a rug around

their shoulders (the adult feigned being cold) and so was *unable* to use their hands to switch on the light (hands occupied). Gergely *et al.* found that, after observing the first condition, 69% of the infants imitated and used their forehead, while in the second in which the adult was unable to use their hands, only 21% imitated the head action.

Gergely *et al.* (2002) concluded from their findings that children were capable of, what they termed, ‘functional imitation’ because they inferred intentions to the model and only copied faithfully when there was a logical rationale for the behaviour. The flexible imitation by children, identified by Gergely *et al.*, has recently also been identified in enculturated chimpanzees (Buttelmann *et al.* 2007). The authors proposed that this parallel between the abilities of human infants and enculturated chimpanzees could be due to the way such chimpanzees are reared. Buttelmann *et al.*, citing the work of Tomasello & Call (2004) and Gergely & Csibra (2006), argue that as a result of enculturation, such chimpanzees are more attuned to ‘human pedagogical cues’ and more motivated to attend to them. However, the case of enculturated chimpanzees may not be unique as comparable ‘inferential imitative selection’ has been shown by the domestic dog when observing a conspecific (Range *et al.* 2007). Demonstrator dogs modeled a behaviour with their paw, instead of their mouth. Following Gergely *et al.* in the equivalent of the ‘hands occupied’ the dog had a ball in its mouth, while in the ‘hands free’ equivalent the dog’s mouth was free to use but it still demonstrated with its paw. As found by Gergely *et al.* and Buttelmann *et al.*, Range *et al.* noted greater imitation in the ball-in-mouth condition.

a. A note on deferred imitation

Piaget (1962) initially proposed that deferred imitation developed in human infants at around 16-24-months. He theorised that the maturity of mental representation allowed the infant to encode an internal representation of an object or act, which could then be retrieved at a later date, and thus generate deferred imitation. He concluded that the infant by this stage was imitating not an external model, but an internal representation (the 'internal model').

More recently, researchers have utilised the principle of deferred imitation to investigate the development of declarative memory in pre-verbal infants (Bauer *et al.*, 2000; Hayne *et al.* 2000; Hayne & Herbert 2004). Eichenbaum (1997) defined declarative memory as involving "representations of facts and events that are subject to conscious recollection, verbal reflection, and explicit expression" (p. 548); the parallels between Piaget's (1962) internal representation and declarative memory are apparent. Abravanel & Gingold (1985) believed that the study of deferred imitation could not only shed light on mental representations and long-term memory, but also on how such information is perceived and encoded.

The recent research has challenged previously held ideas about the onset of deferred imitation among human infants and the constraints by which it is bound. It has been found that infants begin to show deferred imitation from the ages of 6- to 9-months of age (Barr *et al.* 1996; Meltzoff 1988c) and that by 14-months-old, infants show deferred imitation of multiple acts after a delay of up to a week (Meltzoff, 1988b). It has also been demonstrated that infants are able to exhibit deferred imitation after changes in context and stimulus material (Barnat *et al.* 1996; Hanna & Meltzoff 1993; Hayne *et al.* 2000; Herbert & Hayne 2000a). In addition, 14-month

old infants have been reported to be able to imitate an act demonstrated on a television screen when presented with the 3D stimulus after a delay of 24 hours (Meltzoff 1988a).

Herbert & Hayne (2000b) found that there was a positive correlation between the infant's age and length of delay after which an infant showed deferred imitation. It was found that 18-month old infants displayed imitation after delays of up to 14 days while 24-month olds were able to exhibit deferred imitation after delays of 56 days. They concluded that, for 24-month olds, forgetting was complete after a period of six months, after which no deferred imitation was shown.

Kuczynski *et al.* (1987) conducted a longitudinal study that aimed to investigate the development of deferred imitation in a more natural setting by observing its occurrence among infants in their own homes. Incidents of immediate and deferred imitation were recorded by the infant's mothers over a period of between four and eight months. Two age groups of infants were studied with a mean age (at the start of data collection) of 16- and 29-months-old. This study stands apart from the previously discussed work as the imitation recorded included social interactions such as making noises, play behaviours and imitating tones of voice. Kuczynski *et al.* found that the numbers of incidences of deferred imitation were significantly greater within the group of older children than the younger children. In addition, the acts imitated after a delay were found to be different from those exhibited immediately².

² The behaviours that were imitated significantly more after a delay were defined as 'task/care taking/self-care behaviours', 'discipline/control behaviours' and 'mannerisms/expressive behaviours' whilst those imitated significantly more after no delay were defined as 'affective behaviours'.

b. Theories proposed to explain imitation

Meltzoff (2002) stated that, for an infant to match the observed physical movements of an external object (e.g. the demonstrator's hand) to their own actions (e.g. moving their own hand), requires the use of visual guidance. The reason this process is non trivial, according to Meltzoff, is that the infant is able to copy the demonstrated movement despite differences in orientation and size between what they see and their own body, and their perspective of it. Additionally, an infant's ability to imitate facial movements (Meltzoff & Moore 1977) cannot rely on the visual guidance employed when matching hand actions, as they are unable to see their own face and match its movements to the movements that they see on the demonstrator's face.

Meltzoff & Moore (1977) proposed a model involving 'active intermodal mapping' (AIM) to describe the underlying mechanisms. In this, positive feedback helps an infant to shape their behaviour in line with that which they observed. More recent research which has identified 'mirror neurons' may possibly lend support to the AIM hypothesis³ (di Pellegrino *et al.* 1992; Fadiga *et al.* 1995; Rizzolatti *et al.* 1996). The finding of mirror neurons supports AIM because they are "visually activated when the monkey observes another individual (the experimenter or another monkey) making a goal-directed action either with the hand or, in some cases, with the mouth" (Rizzolatti *et al.* 2002, p. 249) thus providing neural feedback to the observed action.

³ Mirror neurons have been identified in the inferior frontal gyrus (F5 region) and the inferior parietal lobule of the rhesus macaque brain. These neurons have been found to fire both when a monkey performs a particular act and also when it observes a conspecific do the same act, even if the observing monkey remains stationary. These neurons therefore 'mirror' the observed behaviour as if the observing animal were doing it itself.

Others, however, suggest that AIM is too limited and cannot take into account the complexity of human imitation (for a review see Bekkering *et al.* 2000). Additionally, the findings of Bekkering *et al.* suggest that children's imitation is mediated by perceived goals rather than merely mapping a pattern as proposed by Meltzoff & Moore.

In the study conducted by Bekkering *et al.* (2000) an adult performed ipsilateral and contralateral⁴ gestures in front of children. The series of demonstrations were that the adult reached for, and touched, (i) their ears, (ii) dots marked on a table ('dot' condition) and (iii) comparable locations on the table but not marked by dots ('no-dot' condition). These latter two conditions enabled the experimenter to control the presence or absence of a goal. When the dot was present, the children would touch the correct dot but often made errors in hand-selection, yet in the no-dot condition this error disappeared. Bekkering *et al.* concluded that this highlights the confusion of goals for the children in the dot condition ('hand used' or 'dot touched') whilst in the no-dot condition the goal ('hand used') is clear to them.

From the work of Bekkering *et al.* (2000), and that of Gleissner *et al.* (2000), Wohlschlager *et al.* (2003) developed a theory of goal-directed imitation (GOADI). According to their GOADI theory a "similarity between the movement of the model and the imitator is only superficial and incidental: the underlying similarity is a similarity of action goals" (Wohlschlager *et al.* p. 512). The GOADI theory helps to explain the findings of Bekkering *et al.* (2000) and why in some instances the children imitated (no-dot) and emulated in others (dot).

⁴ An example of an ipsilateral movement is the adult using their *left* hand to touch their *left* ear, while an example of a contralateral movement is the adult using their *left* hand to touch their *right* ear.

Another theory to explain imitation is the associative sequence learning theory (ASL), which unlike AIM, states that imitation is highly dependent upon experience (Heyes 2001). Heyes acknowledges that at present this theory lacks true empirical support from direct testing, however, she cites much contemporary support available in the literature. Finally, Byrne & Russon (1998) argued, from observational data, that all great apes, not just humans, are capable of showing program-level imitation and from which Byrne (1999; 2002*b*) proposed, and described, an entirely mechanistic model of program-level imitation which he termed 'string parsing'. Byrne (1999) stated that such a theory is sufficient to account for imitation of the underlying hierarchical structure as well as the surface form of a novel, complex behavior. Brass & Heyes (2005) provide a comprehensive review of these current theories including AIM, ASL and the ideomotor theory (IM) and concluded from their review that the evidence to date supports the generalist view with no specific brain region dedicated to imitation.

2.2 Forms of social learning

The various forms of social learning that can be distinguished were defined in *Chapter 1*. In contrast to the field of comparative psychology, the research conducted by developmental psychologists concerning children, has less of a tradition of identifying the specific social learning mechanisms and instead describes most social learning as 'imitative' (Want & Harris 2002). In their review, Want & Harris attempted to redefine previous research in terms of the underlying social learning mechanisms that could be identified from the experimental paradigms used.

Instead of merely re-writing Want & Harris's (2002) review, and also because space was dedicated to defining the forms of social learning in the previous chapter, the second half of this chapter is concerned with the various experimental designs that have been employed when testing social learning among children, whilst making reference to how they can be used to identify particular forms of social learning.

2.3 Experimental tasks and apparatus

a. Action imitation

(i) Neonatal imitation

Piaget (1962) suggested that this pre-verbal imitation (for example tongue protrusion) was an early indicator of a child's intelligence. Neonatal imitation has been observed by children less than 48-hours-old (Meltzoff & Moore 1983) but these findings have been called into question by later research which suggests imitation develops at a later age, as discussed above (Anisfeld 1996, 2005; Anisfeld *et al.* 2001; Jones 2007).

Meltzoff & Moore (1983) reported that newborn infants as young as 42-minutes-old imitated facial movements, including tongue protrusion and mouth opening. Using a cross-target comparison design, comparable to the two-action method, Meltzoff & Moore found that significantly more mouth opening movements were shown by newborns in response to the mouth opening display of the adult model than to the tongue display, with the reverse being true for the tongue protrusion condition.

Later, Meltzoff & Moore (1989) concluded that such imitative behaviour is not automatically triggered like a Moro reflex⁵. It is interesting to note that comparable neonatal imitation has also been shown by infant chimpanzees (Myowa-Yamakoshi *et al.* 2004; Bard 2007) and rhesus macaques (Ferrari *et al.* 2006; Gross 2006).

Prior to these studies with newborn infants, Meltzoff & Moore (1977) had conducted similar studies with older infants, showing them various facial gestures from which they concluded imitation was shown. Ultimately, Meltzoff (1988*d*) concluded “this imitation far outstrips that predicted by standard theories” (p. 331). Despite this long-held interest in neonatal imitation, Bard (2002) noted that there has not been enough investigation into the underlying mechanisms of such imitation.

A second criticism of neonatal imitation has come from Tomasello and colleagues who argued that it does not represent true imitation because no new skill is learnt (Tomasello *et al.* 1993*a*). Despite this, they recognized the importance of neonatal imitation as a possible precursor for later cultural learning. It is this latter component of neonatal imitation that Uzgiris (1993) thought made it such an interesting and important avenue of research. She stated that it was “precisely because the acts being matched in these early imitative exchanges are familiar to the infants, their mutual enactment can result in a shared experience” (p. 536).

⁵ The Moro reflex, also termed the ‘Startle reflex’, is a primitive reflex seen in young babies until around the age of 4 months. When a baby is moved downwards sharply, as though about to be dropped, it will extend its arms and legs, stiffen the body and make a clinging movement.

(ii) *Body movements and facial gestures*

Testing the imitative abilities of children through the use of body movements and facial gestures precludes both local and stimulus enhancement because no object or location is enhanced by the demonstrated action (Want & Harris 2002). A number of studies have shown that young children are quite capable of imitating gestures (Abravanel *et al.* 1976; Rodgon & Kurdek 1977; Abravanel & Sigafos 1984).

Bekkering *et al.* (2000), who defined imitation simply as “performing an act after perceiving it” (p. 153) showed that a child’s fidelity of imitation of another’s body movements is dependent on the goals that the child perceives regarding the observed action (see also Gleissner *et al.* 2000; Wohlschlager *et al.* 2003), as discussed earlier.

b. Object manipulation

A number of studies with young children have involved the demonstration of (simple) actions associated with an object, or the manipulation of that object. This was employed by Tomasello *et al.* (1993b) to investigate, and compare, the imitative abilities of mother-reared and enculturated chimpanzees and children. Both the children and enculturated chimpanzees showed immediate imitation of the demonstrated acts while the mother-reared chimpanzees did not.

Killen & Uzgiris (1981) studied the propensity of infants to copy actions involving familiar objects and found that those aged between 10- to 17-months-old were more likely to reproduce ‘appropriate’ acts with related objects than they would with ‘inappropriate’ acts on the same target objects. An example of this would be

pretending to drink a liquid from a cup compared to a toy car. In contrast, older infants (aged 22-months-old) were more able to reproduce both forms of action. That infants were more likely to reproduce relevant-actions conducted on every-day objects may possibly be explained as 'functional imitation' as described earlier (Gergely *et al.* 2002).

Other age-dependent effects have also been identified when children observe interactions with objects. Barr *et al.* (1996) showed children a puppet and then performed a series of specific actions with it. Regarding the replication of these target acts, Barr *et al.* found an age effect (18- and 24-month-olds reproduced more target acts than the 12-month-olds) when a delay of 24-hours was imposed. However when there was no delay between the demonstration and the test period, 12- and 6-month-old infants performed at the same level.

Hayne (2002) stated that when testing infants and young children, it is very important to keep the child's interaction with the test object very short so that they do not have the opportunity to 'discover' the task through trial-and-error learning but, rather, use observational learning.

c. Transfer tasks

One aspect of tool-using tasks has been to learn whether children are able to transfer knowledge learnt about a particular object or tool to another, comparable, test apparatus. Indeed, studies conducted by Chen *et al.* (1997) have shown that children can indeed transfer knowledge about tools from one task to the next (see also Brown 1990). In Chen *et al.*'s first study, for example, children were presented with a series

of three tasks in which a toy had to be pulled towards them using two aids (a length of string and a piece of cloth) with the specific toys, string and cloth differing between all three scenarios. Despite the changes in the appearance of the target objects, the children (12-months-old) were able to transfer knowledge across the three conditions.

The above studies refer to tests which require a child to transfer their knowledge about one object to another. In contrast to this, Hanna & Meltzoff (1993) investigated whether children would be able to transfer knowledge from one location to another. Children observed a fellow child perform specific actions on target objects and when tested in another context (e.g. the laboratory *versus* their home) the observing child would imitate the actions, despite a change in location and a delay of up to 2 days.

Barnat *et al.* (1996) also proposed that infants should show the ability to transfer information learnt in one context/manner to another. The ability of 14-month-old infants to generalise was tested with changes in target objects/actions and context. Children were shown, either the same target object in the demonstration and response period (no change group) or a different target object in the response period to that which had been demonstrated on (change group). Infants imitated even when changes made to the context and characteristics of the target objects and did a significantly greater number of target actions than did children in a control group provided with no information. However, children in the change group showed lower levels of imitation than those children in the no change group and this effect was heightened with increasing alterations to the target object (context, size and colour). Barnat *et al.* concluded that “infants this age seem to hypothesise that if objects have the same form they may have the same function” (p. 249).

Herbert & Hayne (2000a) found evidence for both immediate and deferred imitation with 18-, 24- and 30-month-old children. However, when the stimuli were

altered, both age-related and delay-related affects were reported. Children in all the three age categories displayed immediate imitation even after the stimuli had been changed, supporting the findings of Barnat *et al.* (1996). However Herbert & Hayne also found that if a 24-hour delay was imposed *and* the stimuli altered, only the 24- and 30-month-old children were capable of deferred imitation. Similarly, Hayne *et al.* (2000) found that 6-month, but not 12- and 18-month-olds, were unable to display deferred imitation when the test context was changed. While the deferred imitation of both 6- and 12-month-old infants, but not 18-month-olds, was inhibited when the object was altered. Hayne *et al.* concluded that “infants apparently begin to generalise across contexts sometime between 6 and 12 months of age” (p. 81) and proposed that this is due to the development of declarative memory.

d. Problem-solving and tool-using tasks

As with studies investigating social learning in chimpanzees and other non-human primates, a number of studies with children have involved the use of problem-solving tasks and/or those which require the use of tools. Despite this trend, a problem with utilizing tool-using tasks to test children, according to Barr (2002), is that they require more complex motor skills than other imitative tasks. Barr concluded that an “inability to imitate tool use may reflect motor incompetence, rather than imitative difficulty *per se*” (p. 16). The limitations of tool-use tasks highlighted by Barr should not be taken as a reason to halt all such research because the use of tools forms such an integral part of the human culture which is afforded by the social learning investigated in such studies.

Goldenberg & Haggmann (1998), with regard to human understanding of the use of an unfamiliar tool, proposed an “inference of function from structure can identify both the possible motor actions associated with a tool and the kinds of objects it can be combined with” (p. 581-582). If children were indeed able to ascertain the use of a particular tool from its physical properties, one would suspect that they would show affordance learning, rather than imitation, when presented with a new task. However a common consensus is that children show a tendency towards imitative learning, while chimpanzees are classed as emulators. This discrepancy from Goldenberg & Haggmann’s suggestion could be due to the unfamiliar nature of the tool-using tasks children are presented with in experimental situations. Often, these tasks are designed specifically in order that they are novel to the child to preclude the child employing previously-held knowledge and thus rely instead on social learning.

From their observations of children engaged in a tool-use task, Nagell *et al.* (1993) concluded that children blindly imitate rather than emulate. The children, unlike the chimpanzees also presented with the task (detailed in *Chapter 1*), copied the specific motor actions used by the model with the rake-like tool. The rake was either turned over before being used to retrieve the out-of-reach reward (‘flip’ condition) or was used in the starting orientation (‘no-flip’ condition). The children would rotate the tool in the flip condition but not in the no-flip, condition which differs from the chimpanzees who used the tool but made distinction between the conditions, as in neither did they reorient the tool.

A simplified conclusion of child social learning, that they imitate with greater fidelity than chimpanzees, has support (for example Whiten *et al.* 1996; Horner & Whiten 2005; see also *Chapter 1*). From their findings, Horner & Whiten concluded that children use imitation as a ‘rule of thumb’. Call & Tomasello (1995) provide

further evidence that children are better able to take advantage of observing others than are great apes. Both children and orangutans were tested, but it was only the children who were able to replicate the actions of a demonstrator in order to open an apparatus which opened through a hidden mechanism. Call & Tomasello suggest that the lack of observational learning evidenced by the orangutans was maladaptive, as it meant they were unable to gain the reward frequently. Conversely, the children made use of what they had seen in order to solve the task, despite not necessarily understanding how it worked. However, contrasting evidence also shows that children are capable of emulating too (McGuigan *et al.* 2007).

These findings, and the suggestion that children should be able to infer the use of a tool from its physical properties (Goldenberg & Hagmann 1998) means that both imitation and emulation could allow for the acquisition of tool-use by children. Generally, the field of developmental psychology reveals a paucity of research aiming to distinguish, and identify, emulation and imitation. Some inferences from previously conducted studies can still be made; for example, Murphy & Wood (1981, 1982) conducted a series of experiments to assess from what form of media children, aged 4- to 8-years-old, could learn how to solve a problem.

The children in Murphy & Wood's (1981, 1982) studies were presented with either video footage or still photographs depicting a method for constructing a wooden pyramid and the responses of the children were compared to a group provided with no information. Interestingly, it was found that, when shown photographs, the girls used the information provided and constructed the pyramid in the method described, while the boys tended to use their own method to reach the same end-state. It might be suggested that the boys evidenced end-state emulation (Whiten *et al.* 2004) consistent with Wood's (1989) original definition of emulation in

which he said that children try to emulate others “by achieving similar ends or objectives” (p.71).

(i) The two-action method

The two-action method has been used, since it was pioneered in the 1960s (Dawson & Foss 1965), to distinguish imitation from simpler forms of social learning. In this method, either of two distinct methods can be employed to reach an ultimate end-state. Despite its use with non-human animals (*Chapter 1*) there has been much less use of it with children as many studies have involved single target objects or merely gestures (but see Bekkering *et al.* 2000; Gleissner *et al.* 2000; Wohlschläger *et al.* 2003). Whiten (2002*b*) noted that the cross-target method, as employed by Meltzoff & Moore (1977) when testing neonatal imitation, is comparable to the two-action method as referred to by comparative psychologists.

A small corpus of studies have employed two-action tasks with children (Whiten & Custance 1996; Horner *et al.* 2006; Flynn & Whiten in press) and adults (Horowitz 2003; Custance *et al.* 2006). These studies with children have identified a general trend of children to use the particular method that they saw demonstrated. This ability to use the information that they observe, rather than learning by trial-and-error, meant that children continued to copy one another along a diffusion chain (*Chapter 1*) of eight children (Horner *et al.* 2006) suggesting imitative, rather than emulative learning by the children.

(ii) *A note on the trap-tube task*

Want & Harris (2002) proposed that presenting children with a novel and unfamiliar task would reduce the possibility of the child learning about the affordances of the apparatus, and hence emulative learning. For this, they suggest using the ‘trap-tube’ task. The trap-tube task was originally used by Visalberghi & Limongelli (1996) with capuchins, but has also been used to test children (Want & Harris 2001; Horner & Whiten 2007) and great apes (Mulcahy & Call 2006; Horner & Whiten 2007). The trap-tube has also been used to test children’s understandings of ‘failed attempts’ and these are discussed in greater detail later.

The trap-tube task consists of a horizontal tube with open ends into which a tool can be inserted. At either end are two vertical tubes, one of which (the trap) has a sealed bottom while the second has no bottom. A reward is placed into the centre of the horizontal tube. If the tool is inserted into the horizontal tube and pushed toward the trap the reward will fall in and cannot be retrieved. However if the tool is inserted from the trap end then it can be used to push the reward *away* from the trap and out of the bottomless tube. Want & Harris (2001) found that 2- and 3-year-old children were unable to solve the task by themselves but performed better after having observed a demonstration.

Want & Harris’s (2002) rationale for employing the trap-tube task when testing social learning among children was that “a novel task may preclude certain types of learning” (p. 6). This should be questioned. A variety of studies have presented children, and other animals, with novel tasks, but their novelty alone did not control for the child learning by emulation (for example Tomasello *et al.* 1987, 1993b)

2.4 Experimental design

a. Observer-model interaction

To investigate observational learning among children, they can be tested in a number of experimental situations. A number of comparable test scenarios were identified in *Chapter 1* that have been employed with chimpanzees and these same experimental paradigms will be examined here with regard to the literature concerning children.

(i) Dyadic situations

The majority of experiments in the literature have tested children in dyadic situations, and most often with the child or infant observing the adult experimenter (Meltzoff 1988*d*; Barr *et al.* 1996; Wohlschlager *et al.* 2003). Using an adult model in a dyadic scenario with children or infants, although it does not test for possible horizontal, peer-to-peer transmission, can represent day-to-day experiences of children who often imitate adults, such as their parents (Uzgiris 1991). However no studies, as yet, have investigated the relationship and emotional connection between the observer and model which could certainly affect the level of learning evidenced.

In contrast to conventional child-adult interactions, Hanna & Meltzoff (1993) used children models. They found that peers represented reliable models for children as the observers reliably matched the demonstrated actions, even after a delay, when compared to control children who saw no demonstration. Uzgiris (1991) stressed the

importance of child-child imitation for their social and cultural development, citing the study of Nadel-Brulfert & Baudonniere (1982). Nadel-Brulfert & Baudonniere found that those children, who were imitated by others, engaged in greater imitative play themselves. These findings suggest that using child models is important, however, to my knowledge; no study has directly compared the efficacy of adults or children as models for children and infants.

(ii) Diffusion chains and the replacement method

The history of the use of diffusion chains was discussed in *Chapter 1*, citing the early studies of Bartlett (1932), Menzel *et al.* (1972) and Curio *et al.* (1978). Only more recently have diffusion chains been used successfully with children (Horner *et al.* 2006; Flynn & Whiten in press; Whiten *et al.* under review).

In the study conducted by Horner *et al.* (2006) two diffusion chains, each comprising of eight children, were seeded with one of two methods for solving a two-action task. The method that each chain was started with, by showing the first child a particular method, spread down each chain with 100% fidelity. This faithful replication of the method observed by children has been replicated again in more recent studies (Flynn & Whiten in press; Whiten *et al.* under review).

The replacement method, also introduced in *Chapter 1*, a sister to the diffusion chain and has been used successfully with adults (Baum *et al.* 2004). Indeed Baum *et al.* concluded that “the procedure succeeded as an experimental model of cultural evolution. Traditions of two sorts evolved” (p. 321). Diffusion chains and the replacement method offer a more fluid way of testing observational learning among

children with ecological validity, which relates to the everyday experiences of children when interacting with their friends and siblings.

However it should be noted that the artificial nature of these tests may be too rigid for use with children. Who each child observes, and models for, is dictated by the experimenter; the successive dyads are not spontaneously self-selected by the children themselves. In reality, for example in a nursery setting, children may only play with particular children and so being forced to work with those with whom they are not friends may hinder their performance. However it is probable that such a concern is unfounded, or at least does not impact on the children's performance, as the studies cited above demonstrate that children when tested in diffusion chains show strong observational learning.

b. Form of demonstration

(i) Irrelevant actions and unintentional actions

Horner & Whiten (2005) presented children and chimpanzees with a tool-using task which was presented both in a transparent form ('clear box') and also in an opaque form ('opaque box'). The human model initially demonstrated irrelevant actions with a tool and then used the tool to perform a relevant action to retrieve the reward from the box. That the first action was irrelevant to gaining the reward was only apparent with the clear box, but not so with the opaque box (see also McGuigan *et al.* 2007).

Both boxes and demonstrations were presented to the subjects in succession with a response period directly after. The boxes were presented in one of two conditions;

(i) the clear then the opaque box or (ii) the opaque then the clear box. It was predicted that when the clear box was presented first the subject would learn that the first action was irrelevant and so would not replicate it in their response period. However, when the opaque task was presented first no such information could be learnt and so it was expected that the subjects would copy both the irrelevant and relevant actions.

Contrary to these predictions the children reproduced both the irrelevant and relevant actions in both conditions. The chimpanzees did follow the predicted pattern however, only reproducing the irrelevant actions when presented with the opaque box first (Horner & Whiten 2005). Horner & Whiten suggest that when the subjects replicated all the actions when having seen the opaque box first, this cannot be explained by emulation as they used the same method as demonstrated, not a novel method to achieve the same end-state; so from this we infer imitation. However as the children copied all actions despite having seen the clear box first, this suggests that they were not influenced by the available information, and Horner & Whiten concluded that they defer to the use of imitation. McGuigan *et al.* (2007) confirmed this result, finding the blanket imitation to be even stronger with 5-year-old children.

The finding of Horner & Whiten (2005) seems initially in opposition to previous research with children which has concluded that children *do* use information they observe to solve tasks presented to them (for example Call & Tomasello 1995). However, the majority of these previous studies have only given children demonstrations comprising of relevant actions and so, as with Horner & Whiten, the children copied all the actions and solved the task. It may appear that if children imitate all the actions demonstrated, unlike the chimpanzees, that it may affect their ultimate success as they blindly copy irrelevant, time-consuming, actions where an emulative may have been more efficient.

A further proposed reason for why the children may have copied the relevant and irrelevant actions was a result of the complexity of the task. Harnick (1978) demonstrated irrelevant actions within a demonstration repertoire and the children imitated all actions, irrelevant and relevant, like those of Horner & Whiten (2005). However when the children were presented with a simpler task, the children were more selective in their imitating (Harnick; see also Sibulkin & Uzgiris 1978).

Horner & Whiten (2005) demonstrated both relevant and irrelevant acts to determine what children understand when observing such demonstrations. Determining what a child understands about the intention of the demonstrator has been argued to be important because “to engage in imitative learning the child must understand the demonstrator in terms of his intentions towards things (i.e. as an intentional agent) in order to distinguish the relevant and irrelevant aspects of the demonstrator's behavior” (Tomasello *et al.* 1993a, p. 503). To learn how much children understand about other's intentions, the experimenter can show the child what they intend to do, but not achieve their goal, to ascertain whether the child can still understand the intended goal.

This ‘failed attempt’ technique was originally used by Meltzoff (1995). Meltzoff's original study included two experimental conditions and two controls. The conditions were (i) a full demonstration (ii) a ‘failed attempt’, in which the adult tried, but failed, to complete the task, (iii) a control with no demonstration and finally (iv) a ‘manipulation control’ in which the adult manipulated the target object as a control for stimulus enhancement.

Children in the two control conditions failed to replicate the test behaviours, but those in the two experimental conditions replicated the test behaviours and to a comparable degree. Meltzoff (1995) concluded that the children in the failed attempt

group “did not re-enact what the adult literally did, but rather what he intended to do” (p. 846) and thus that the children, aged 18-months-old, were capable of ‘intention reading’. In a second experiment, the same conditions were replicated by a mechanical arm instead of a human demonstrator. It was reported that the children did not show the same responses as they were unable to recreate the acts to the level that they did with a human model.

Bellagamba & Tomasello (1999) replicated Meltzoff’s (1995) experiment with 12- and 18-month-olds. With the 18-month-olds their findings replicated those of Meltzoff’s; however for the 12-month-olds the failed attempt was not sufficient for such learning, while the full demonstration was. Bellagamba & Tomasello concluded from their findings that this failure was a result of developmental trajectory, and that only by 18-months of age are infants capable of intention-reading.

Charman & Huang (2002) raised two criticisms of Meltzoff’s (1995) failed attempt method which led Huang *et al.* (2002) to create a third experimental condition (the ‘emulation condition’) as an extension to Meltzoff. Charman & Huang suggested that the manipulation control did not adequately control for stimulus enhancement because in such a condition the adult would handle the object in a quite a different manner to that in the experimental conditions; for example, they may make less contact with the ‘target-relevant parts’. The second criticism was that the failed attempt condition itself might give the observing child an insight into the affordances of the task. It is perhaps from these learned affordances that the children were able to solve the task, rather than from intention reading.

In the emulation condition, designed to answer these criticisms, Huang *et al.* (2002) showed children the objects in their start position but just before the experimenter began the demonstration a cardboard screen was lowered between the

child and the objects and experimenter. The screen was raised at the end of the demonstration so that the child could see the final end-state. Huang *et al.* reported that the children were equally successful in the full demonstration, failed attempt and emulation condition. That children were equally adept in the emulation condition was suggested by Huang *et al.* to contradict the theory that the children were showing intention reading (Meltzoff 1995; Bellagamba & Tomasello 1999). Huang *et al.* propose that it is more likely that the behaviour is explained by emulation learning and stimulus enhancement.

Huang *et al.* (2006) replicated Huang *et al.* (2002) with 31- and 41-month-old infants and found matching to the full demonstration. However only the 41-, but not the 31-month-olds reproduced the actions in the failed attempt condition. Huang *et al.* (2006) concluded that although children are able to read the intentions of others by a certain age (which Huang *et al.* do not stipulate) other forms of social learning can affect their behaviour and this interplay is situation-dependent.

Carpenter *et al.* (1998) developed a new approach to the investigation of intention-reading by infants aged 14- to 18-months-old. In the test there were six objects on which the experimenters either demonstrated an intentional or accidental action, the former followed by the utterance 'There!', the latter with 'Whoops!'. The children saw both intentional and accidental actions on different objects in a counterbalanced manner. Overall, infants imitated more of the intentional than accidental actions, suggesting an understanding of intentions.

A further experimental paradigm design to assess children's understanding of another's intentions was described by Behne *et al.* (2005). In this, an adult interacted with a child and initiated play with a toy. However in a third of the conditions the adult was unable to play with the child, in another third they were unwilling, whilst in

the final set they were able, and did play with the child. Behne *et al.* reported that the children showed much more patience and less frustration to those adults who were unable rather than unwilling to play with them. However, Heyes & Ray (2002) do not believe that there has been adequate evidence to show reliably *when* children show ‘intentional-sensitive’ imitation.

(ii) End-state and ghost conditions: testing for emulation

As noted, the failed attempt paradigm was designed originally to test children’s ability to interpret, and respond to, the intentions of others, namely the adult experimenter. Through the course of these experiments Huang *et al.* (2002) drew attention to the interplay between emulation learning, mimicry and intention-reading. As children in many of these studies may possibly have relied on emulating to complete the task, the study of emulation learning for its own sake is of great interest. It is further of interest because many previous studies have suggested that children, unlike chimpanzees, are predominantly imitators, not emulators. To this end, two experimental paradigms have been used; the ‘end-state’ and the ‘ghost condition’.

In the end-state condition, similar to the emulation condition (Huang *et al.* 2002), the subject is shown the initial state of the target object, it is then manipulated out-of-sight, and the subject is shown the resultant form of the object. For example, Meltzoff (1985) showed 14-month-old infants a dumbbell-shaped toy, the ends of which could be removed. The initial-state was the intact dumbbell and the end-state was the central shaft separated from the two end pieces. When shown a full demonstration of this action, infants were able to reproduce it, even after a 24-hour delay. However when

infants were shown *only* the initial-state and the resultant end-state, a non-significant number of children could re-enact the action to create the same end-state when presented with an intact dumbbell. The failure of the infants suggests that they are not capable of emulation learning.

In an extension of the end-state paradigm, Call *et al.* (2005) gave children and chimpanzees one of four demonstrations; either a full demonstration (Full Demo), showing only the actions (Action Only), showing the end-states (End State) or a baseline control. The apparatus used was a tube, either transparent or opaque, with a reward inside. To retrieve this reward one of two demonstrations was provided; (i) twist the ends off or (ii) pull the tube apart, breaking it in the middle; thus both methods resulted in distinct end-states.

Regardless of method demonstrated, there was no significant difference in the number of tubes opened by the chimpanzees between the three experimental conditions, or between those and the baseline. However, more clear, than opaque, tubes were opened suggesting possible nonsocial enhancement. Chimpanzees in the End State were more likely to match the method demonstrated than those in the Action Only condition. In fact, the chimpanzees often attempted the *other* method when having seen only the action demonstrated, possibly because they inferred that the model had tried, but failed, with one method and so they used the other. Overall, for chimpanzees, the end-state, rather than the action itself, appears to be of more importance to them, which Call *et al.* (2005) concluded was further evidence that chimpanzees are more likely to emulate than imitate.

Unlike the chimpanzees in Call *et al.*'s (2005) study, the children performed better in the social (Full Demo and Action Only) than in the nonsocial (End State and baseline) conditions. Additionally, there was no significant difference between the

two social conditions with regards to the level of matching the method showed. Like the chimpanzees, the children were more likely to open the transparent, rather than the opaque tubes. Overall, Call *et al.* concluded that, unlike the chimpanzees, the children are more likely to take advantage of the social information and thus evidenced imitation rather than emulation.

A second way to test the emulative abilities of children is to use a ghost condition, as detailed in *Chapter 1*. To date, there remain just two published studies that have presented children with a ghost condition (Thompson & Russell 2004; Tennie *et al.* 2006).

Thompson & Russell (2004) presented 14- to 26-month-old children with one of two apparatuses with either an adult demonstration or a ghost condition. In the first condition (the 'single-mat' condition) the child had to push a mat away from them, to move a toy towards them. This action was created by a hidden pulley system under the table which moved the toy. Similarly, in the second condition (the 'double-mat' condition), a toy was sat on one mat and to retrieve it, the child had to pull an adjacent mat towards them which, also using a hidden pulley mechanism, caused the mat with the toy on it to move forward within reach of the child.

The adult demonstrations for both conditions resulted in a greater number of retrieval acts than in the baseline. In the single-mat condition, the children replicated the actions in both the adult demonstration and the ghost condition, in fact, they were more successful in the ghost condition. However the same was not true for the double-mat condition. Thompson & Russell (2004) suggested that the ghost condition did not enhance the children's responses for the double-mat task because it did not result in a single, unambiguous, movement (both mats moved simultaneously), as was the case in the single-mat task.

Ghost conditions are sometimes cited as being used to detect emulation learning as highlighted by the title of Thompson & Russell's (2004) article: *The ghost condition: imitation versus emulation in young children's observation learning*. Yet, in the single-mat task, all that the children appeared to learn was the affordances of the task i.e. that the mat could be moved away and the toy moved forward. Thompson & Russell concluded as they stated that the task demonstrated "learning about an object's dynamic affordances" (p. 882) and so care should be taken to distinguish goal-emulation (Whiten & Ham 1992) from affordance learning (Klein & Zentall 2003).

A second study to use a ghost condition with children was that of Tennie *et al.* (2006). Children aged 12-, 18- and 24-months-old were presented with a box with a hinged door that could be opened by either pushing or pulling it to retrieve a reward. The children were shown how to open the box, using one of the two methods, either with a full demonstration by an experimenter, or with a ghost condition in which the door was moved discretely with fishing-line.

An interesting age-difference in the responses of the children tested by Tennie *et al.* (2006) was found. Those aged 24-months-old matched both demonstration forms, those aged 18-months-old only matched the adult demonstration while the 12-month-olds did not match either demonstration. Tennie *et al.* concluded that their results "with 24-mo-old children question the idea that emulation tasks may be too complex for human infants" (p. 1166). However it should be noted that the children tested were able to open the box successfully in the baseline, so Tennie *et al.* concluded that the information from the 'demonstrations' provided was somewhat redundant.

2.5 Conclusions

The literature reviewed in *Chapters 1* and *2* reveals a wealth of work that has investigated the occurrence, and underlying mechanisms, of social learning among both chimpanzees and children. Despite this plethora of work, there remain pockets which could benefit from a greater depth of inquiry. Two main spheres are (i) the transmission of a new behaviour within a social setting tested with diffusion chains and open diffusion paradigms and secondly, (ii) the use of ghost conditions to study potential emulative learning. The experiments presented within this thesis utilise a range of techniques, including diffusion chains, open diffusion experiments and ghost conditions, to research the behaviours of chimpanzees and children. The findings of both species are compared and contrasted with and set within a broader context of the social learning evidenced by other species including monkeys, rats, fish and birds. In addition, the ability of chimpanzees to learn from conspecific models presented as video-footage is also investigated and reported with a view for potential application for future social learning experiments.

Ethical considerations

For all experiments conducted, and reported in this thesis, the following ethical considerations were maintained.

Studies with chimpanzees

During all testing the chimpanzees were not food deprived and had constant access to water. The animals were housed in facilities that have been accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care International and in accordance with current United States Department of Agriculture, Department of Health and Human Services, and National Institutes of Health regulations and standards. All experiments reported herein were approved by the University of Texas Institutional Animal Care and Use Committee. For testing in isolation or dyads, all chimpanzees were separated from their cage-mates without the use of force or negative coercion. No chimpanzee was made to continue with the testing process if they showed signs of distress.

Studies with children

L. M. Hopper, for whom a clean Scottish Police background check had been obtained, conducted all testing. All schools were contacted and informed of the structure of the testing and the apparatus to be used to allow the headteacher to make an informed

decision. Only those children for whom parental consent had been gathered participated in the tests. Additionally, on the day of testing, children were asked if they wished to take part and only did so if they wished to. All children were informed of their right to withdraw at anytime and no child was made to continue with the testing process if they showed signs of distress.

Chapter 3: An Experimental Study of Social Transmission among Chimpanzees in a Group Context⁶

Summary

Multiple regional differences in tool use have been identified among wild chimpanzees but the hypothesis that these represent traditions, transmitted through social learning, is difficult to substantiate without experimentation. To test chimpanzees' capacity to sustain traditions, alternative tool use techniques were seeded via individuals in different captive groups. One technique, 'Lift', spread in the group into which it was introduced but not among those chimpanzees in the second group which was seeded with the alternative technique, 'Poke'. Poke was also not discovered by control animals tested individually. However, Poke emerged spontaneously in the Lift group and became dominant in both groups, regardless of the founder's Lift or Poke technique. Accordingly, this study demonstrated a statistically significant, differential spread of alternative techniques through social

⁶ The contents of this chapter have been published in Hopper *et al.* (2007). Additionally it should be noted that Experiment 3.1 was conducted in collaboration with Antoine Spiteri who also attends the University of St Andrews. Lydia M. Hopper personally ran all the testing (loading the Pan-pipes with food rewards, filming and giving an oral commentary) during which time A Spiteri made additional videotape recordings from the roof of the corral for *his own* analysis. All analysis of the data reported herein (including the coding of the videotapes and statistical analysis) was conducted by L M Hopper alone.

learning, yet no clear separation of traditions, unlike an earlier study with a different population of chimpanzees. This difference may be attributable to prior experience with relevant tools.

3.1 Introduction

Decades of field research on wild chimpanzees have documented numerous regional differences in behaviour which have been attributed to social learning, and thus described as traditions or cultural variations (McGrew 1992, 2004; Boesch & Tomasello 1998; Whiten *et al.* 1999; Boesch 2003; Whiten 2005). A variety of circumstantial evidence has been marshalled to substantiate this cultural interpretation. Alternative genetic or environmental explanations that may account for these regional differences have been rejected because even geographically close communities show the behavioural variations of interest, representing the null hypothesis. In addition, social-learning opportunities have been shown to correlate with predicted differential outcomes, both within (Lonsdorf *et al.* 2004) and between (van Schaik *et al.* 2003) communities.

However, under field conditions it is difficult to exclude the possibility that some undetected environmental or other noncultural factor is responsible for the observed variations, in the clear way that an experimental intervention can demonstrate (Tomasello 1990; Laland & Hoppit 2003; Galef 2004). Logistic and ethical constraints have meant that field experimentation has been limited to the introduction of novel materials (Matsuzawa 1994; Biro *et al.* 2003). Studies using the crucial contrast of experimental (with a model, permitting social learning) and control (no

model) conditions have been limited to captive populations (reviewed in Tomasello & Call 1997; Whiten *et al.* 2004) and these have typically been restricted to one-to-one learning, so leaving unclear the extent to which the social learning documented is sufficient to sustain traditions. Those few studies conducted at the group level have lacked control conditions designed to reject the hypothesis that the spread of new behaviour patterns reflects learning at the individual level (Menzel *et al.* 1972; Tonooka *et al.* 1997; Huffman & Hirata 2004).

Whiten *et al.* (2005) therefore conducted a captive study which combined experimental and control conditions with the powerful two-action method used to investigate imitation (Dawson & Foss 1965; Shettleworth 1998). In this study, a member of one group of chimpanzees was trained to use one of two alternative tool use techniques before reintroduction to her group, while a member of a second group was trained in the alternative technique before reintroduction. Both groups were then compared to members of a third, control group who were exposed to the task with no model present. The latter failed to solve the task, whereas the alternative techniques seeded in the two experimental groups spread differentially, providing the first experimental evidence of alternative traditions diffusing among groups of primates. More recent support for this methodology has been provided with subsequent studies with captive chimpanzees (Bonnie *et al.* 2007; Whiten *et al.* 2007).

To my knowledge, prior to these, this experimental design for studying the transmission of two alternative traditions has been completed before only in a study of rats, that concerned choices between two different diets (Galef & Allen 1995) rather than behavioural techniques. A further study seeding two alternative techniques, not related to tool use, in capuchin monkeys is in progress (Fragaszy *et al.* 2004). These studies add to a small but growing corpus of controlled, experimental studies designed

to investigate the transmission of traditions in chimpanzees (Menzel *et al.* 1972), rats (Laland & Plotkin 1990), guppies (Laland & Williams 1997; Reader & Laland 2000), blackbirds (Curio *et al.* 1978), pigeons, *Columba livia* (Lefebvre 1986) and humans (Mesoudi & Whiten 2004). However, these studies have typically used simpler designs where a single experimental group is compared to a control group, or to the behaviour of the experimental subjects during a baseline condition, permitting only weaker conclusions about what is learned than in the three-group, two-action design of Whiten *et al.* (2005) and the present study.

Given so few studies with primates, one of the primary goals in the present study was to replicate the multiple group approach of Whiten *et al.* (2005) using a different population of chimpanzees. In addition, whereas Whiten *et al.* tested their control subjects through initial solitary exposure followed by exposure in small groups of two to four animals, this study was able to use a population sufficiently numerous to permit a control condition to be run in a whole group of similar size (nine) to that of the experimental group, so complementing the individual control tests of Whiten *et al.* and exploring the possibility that such a potentially supportive social context may facilitate individual exploration and learning.

3.2 Methods

a. Experimental design

Subjects	31 chimpanzees
Apparatus	Pan-pipes (two-action task)
Conditions	2 open group diffusions: Group C 'seeded' with Poke method (n = 10) Group L seeded with Lift method (n = 9) 1 control group (n = 12)
Independent variable	Method seeded (Poke or Lift) with model chimpanzee
Dependent variable	Method employed by observing chimpanzees

b. Initial and amended experimental designs

The experimental design of this experiment was amended in the course of the project because of the responses of the chimpanzees in two of the conditions. The initial design incorporated four populations of chimpanzees, each exposed to a different condition: (1) experimental group L, seeded with an individual performing the Lift technique, described below; (2) experimental group P, similarly seeded with an individual proficient in the alternative Poke technique; (3) control chimpanzees pseudo-group I consisting of 12 control chimpanzees individually exposed to the apparatus but with no trained model; and (4) control group C, exposed to the apparatus as a group, again with no model. The contrast between groups L and P was intended to provide information on the spread of alternative techniques, while

contrasts between these and the two control conditions would further clarify what chimpanzees learned by observation, over and above their spontaneous responses to the task. Condition 3 replicated the individual control testing in Whiten *et al.*'s. (2005) study, but condition 4 was new, included to check whether with time and the support of the whole-group context, chimpanzees might eventually discover one of the techniques spontaneously. From the previous negative control results (Whiten *et al.*) it was predicted they would not.

Unfortunately, unlike the model in group L and those used by Whiten *et al.* (2005), the model in group P was reluctant to perform Poke in the group context, and a second trained model also proved to be poorly motivated. At the same time, one of the techniques (Poke) was spontaneously performed in control group C. Since the method discovered by this chimpanzee (BE) was the very one that had been attempted to be seeded in group P, and this negated further use of group C to collect control data, group C was henceforth treated as the second 'seeded' group, and group P was set aside for the remainder of the present study. Below, data is reported initially from the perspective of C as group control (no model), and then a comparison of groups C and L from the point where each had an initial model performing one of the two different techniques.

c. Subjects and housing

All the chimpanzees were housed at MDACC. Group C comprised of 6 females and 4 males aged 24 - 4 years (mean 14.8 yrs) while Group L comprised of 7 females and 2 males aged 43 – 3 years (mean 13.3 yrs). The 12 control chimpanzees comprised of 3

females and 9 males aged 43 – 14 years (mean 28.5 yrs). Table 3.1 summarises demographic details for all participants.

Experimental groups				Control individuals	
C		L			
Female ID	Male ID	Female ID	Male ID	Female ID	Male ID
MU (24)	AX (19)	MY (40)	PI (43)	GI (43)	PE (42)
AA (20)	PE (17)	BE (40)	HU (14)	LA (27)	SI (37)
TI (19)	MA (12)	MR (39)		RO (20)	ZI (34)
SO (16)	GA (4)	KE (39)			JO (33)
BE (10)		TI (21)			AJ (27)
LE (7)		CE (14)			SK (27)
		ZO (3)			SA (20)
					NI (17)
					CH (14)

Table 3.1 Demographic details of experimental and control subjects. Each ID code is followed by age (years). Group C was housed in corral 7, group L in corral 8 while the control individuals were housed in Primadome buildings 101-107 (Figure 3.1a).

Chimpanzees in groups C and L were studied in their outdoor corrals (diameter 21.3 m) each of which also had adjoining indoor quarters, to which the chimpanzees had continuous access. Chimpanzees in the individual control condition, housed in groups of two to five with outdoor enclosures (Primadomes) either 2.4 x 3.7 m and 2.4 m high or 10.4 m in diameter were tested singly in their inner housing 2.4 x 2.4 m and 1.8 m high (Figure 3.1a).

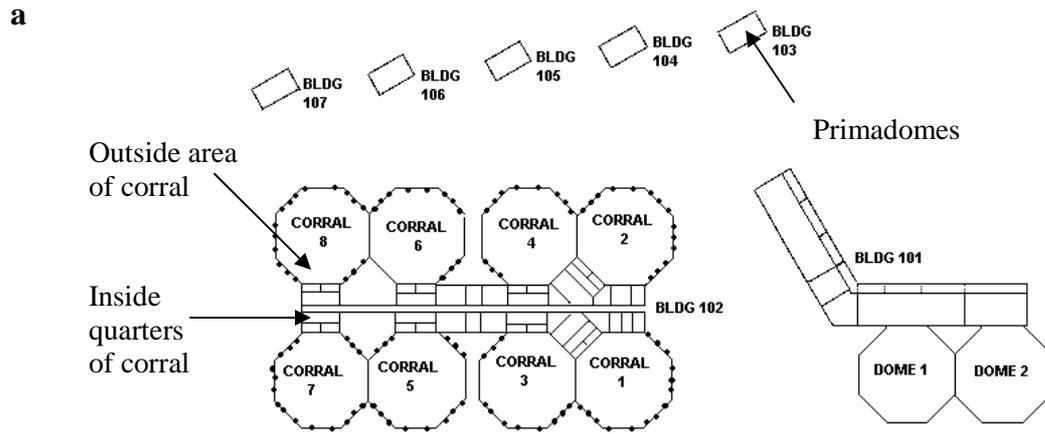


Figure 3.1 The housing for the chimpanzees. **(a)** A plan of the housing at MDACC, where each dot on the corrals represents a barred-window. **(b)** Looking into a corral through the caging, against which the Pan-pipes were placed on the outside.

d. Apparatus and techniques trained

The apparatus was the same ‘Pan-pipes’ used by Whiten *et al.* (2005), a two-action task that consists of two sloping pipes lying one on top of the other, forming a solid unit (Figure 3.2). From the rear, a food reward (a grape) could be rolled by the experimenter into the upper of the two pipes, where it was trapped by a blockage. The

Pan-pipes apparatus was presented outside the chimpanzees' enclosure such that its nearest point to the caging was 20 cm (Figure 3.1b). The chimpanzees were given a polycarbonate rod-tool 450 mm long with 18 mm diameter, affording them alternative ways of freeing the trapped food from the Pan-pipes outside their enclosure.

(i) Lift method

To perform the Lift method a chimpanzee must place the tool under the T-bar and raise it up. This action draws the block up allowing the food reward to drop forward and fall into the lower pipe, from where it can fall out of the front opening of the bottom 'false' pipe and be retrieved by the chimpanzee (Figures 3.2a & c).

(ii) Poke method

To retrieve a reward using the Poke method a chimpanzee must use the tool to push in the small, top, flap over the entrance to the upper pipe, and insert the tool. The chimpanzee can then use the tool to push back the block and consequently the food reward too. The food reward is ultimately pushed to the back of the upper pipe from where it drops down into the bottom pipe. When in the lower pipe, the food reward rolls down and out through the opening as for the Lift method, from where the chimpanzee can retrieve the reward (Figures 3.2b & d).

(iii) Comparison of the two methods

These two techniques were judged to be relatively novel for these chimpanzees. Using a stick to lift things has not been described in wild chimpanzees and had not previously been observed in the MDACC groups. Poking with sticks is common in the wild and is used by chimpanzees at MDACC to obtain fluid from enrichment devices, but poking with sticks as a means to retrieve food by pushing it away was thought to be novel. In addition, the enrichment devices provided to the chimpanzees at MDACC require a stick to be pushed down at a 45-degree angle, whereas the Pan-pipes require the chimpanzee to insert a tool upwards through the mesh, requiring significantly different motor movements.

It was intended that the Poke method was as difficult as Lift by covering the poking-hole with a hinged flap, but the experimental design does not depend on the two techniques being precisely matched in difficulty: the prediction is simply that the relative prevalence of the techniques will be affected by the nature of the first model introduced. Other possible techniques included pushing the blockage backwards by placing the tool end against the T-bar on the outside of the pipes.

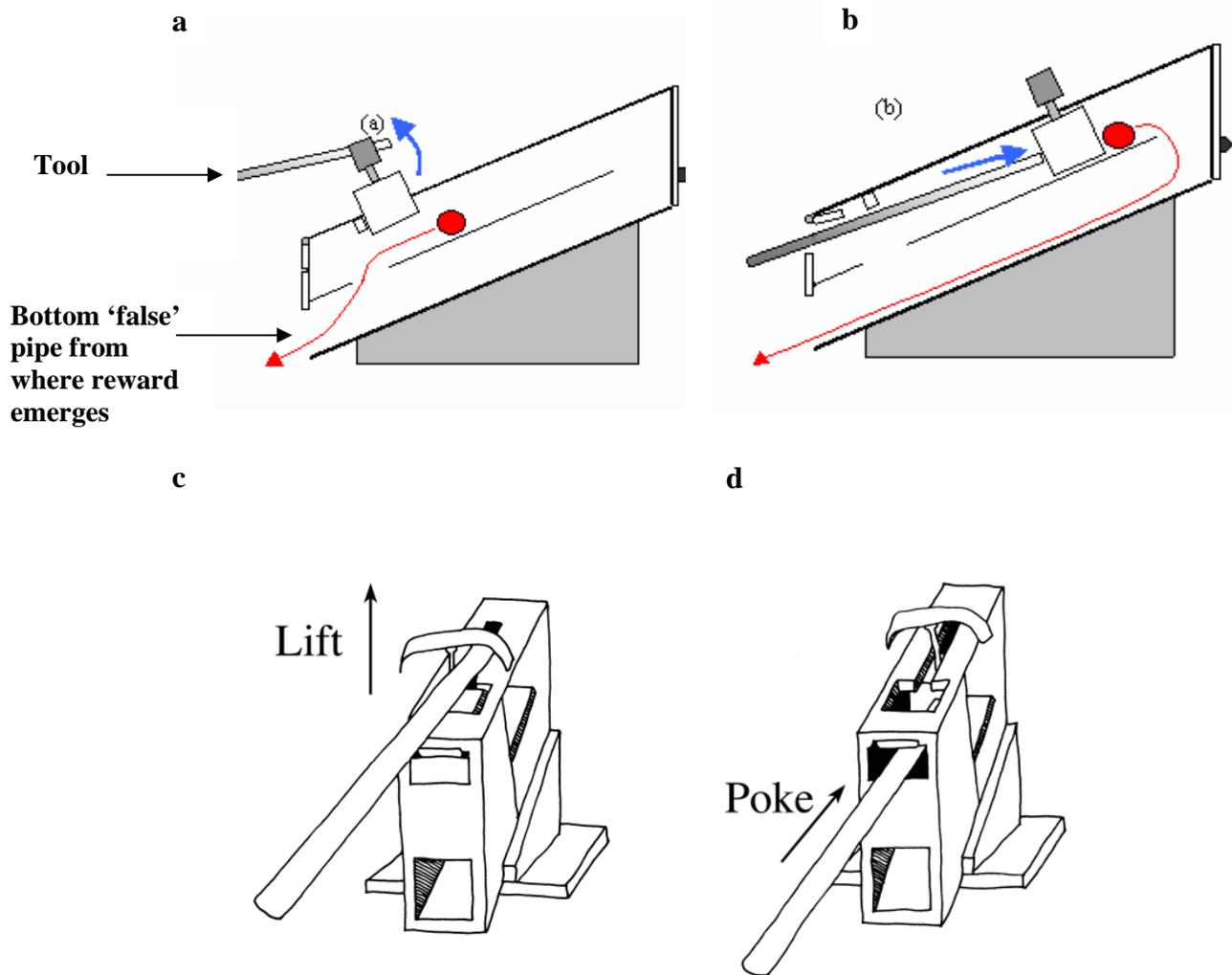


Figure 3.2 Pan-pipes apparatus showing diagrammatic representation of the (a) Lift and (b) Poke methods and the (c) Lift and (d) Poke methods from the perspective of the operating chimpanzee.

e. Procedure

(i) Individual control condition

Each of the 12 chimpanzees in the individual control condition was separated from the others with whom it was housed for testing in their inner housing (Figure 3.1a).

The Pan-pipes apparatus was placed against the mesh in the usual way and the chimpanzee presented with the rod-tool for a 1 hour session, during which time the chimpanzee was able to interact with the apparatus and tool as it chose. The apparatus was baited at the start in view of the chimpanzee. The rule for re-baiting was, as for the group tests, to re-bait as soon as the first food reward was successfully retrieved.

(ii) Model selection and training for experimental open diffusion

For experimental group L, a high-ranking female (MY) was chosen as a model so that she would be unlikely to be displaced from the apparatus and would thus provide ample observation opportunities to other group members. She was trained in the Lift technique by the experimenter (LMH), assisted by E. Thiele (an animal trainer employed by MDACC), through shaping and positive reinforcement, out of sight of the rest of her group (see Figure 3.3). Once she achieved 30 consecutive successes using this technique she was judged a reliable model.



Figure 3.3 LMH training a chimpanzee to use the Lift technique.

(iii) Group L open diffusion testing phase

The observation phase began with the release of the whole group from their inner quarters into the outside enclosure prior to which the Pan-pipes had been placed up against one of the barred windows of the corral (Figure 3.1b). In this observation phase, which occupied 20 min on each of 3 consecutive days, the trained model was allowed to operate the Pan-pipes in front of their group mates, but on the rare occasions that other chimpanzees acquired the tool, the experimenter (LMH) pulled the apparatus out of reach. This procedure was designed to ensure that all chimpanzees had witnessed successful use of the technique before attempting it themselves.

As in Whiten *et al*'s. (2005) study, once all the group members had seen the model operate the apparatus successfully on eight or more occasions, the experiment progressed to an 'open diffusion' phase in which any chimpanzee was allowed to operate the Pan-pipes. This phase ran for 23 h, occupying five test-days spread over a 15-day period during which work with the other groups was also completed. Each session lasted for 3-5 h, to facilitate access of even low-ranking individuals to the task as performers became satiated and released the tool.

(iv) Group C control condition

As for experimental group L, the chimpanzees were released into their outside enclosure against one of the barred-windows of which the Pan-pipes had been placed. The rod-tool was introduced into the corral and the chimpanzees were allowed free-access to the Pan-pipes as in the individual control condition with no trained model for instruction. Once one individual, a female (BE), spontaneously showed success (see below), the procedure became essentially the same as in the open diffusion phase with group L described above, except that no chimpanzee had been trained as a model, but was instead self-selected.

f. Coding

All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). A running commentary was provided by the experimenter (LMH) on the identity of

the chimpanzee operating the Pan-pipes each time, and which chimpanzees were within the 1-m radius and oriented towards the Pan-pipes, indicating they were watching closely what the model was doing. Chimpanzees' actions were coded from videotape using the Action Codes detailed in Table 3.2.

An advantage of the two-action Pan-pipes design is that the critical actions of Poke and Lift were particularly clear and unambiguous because of the very different ways in which the tool and the blockage moved.

Action Code	Action Name	Definition
P*	Poke	Insert tool through flap door into top pipe, pushing blockage completely backwards; food reward released and gained
L*	Lift	Place tool under T-bar to raise T-bar (and blockage); food reward released and gained
ITP*	Insert tool Poke	Insert tool into the top hole, as for P, but not far enough to release food reward
ITL*	Insert tool Lift	Place the tool under the T-bar, as for L, but fail to raise it sufficiently to allow a food reward to be released
BOTTOM*	Insert tool bottom	Insert the tool into the bottom (food exit) hole. No food reward gained
H*	Hit	Make contact between the tool and other part of the Pan-pipes including food chute, sides of the Pan-pipes and table; no food reward gained
TFC†	Touch food chute	Make contact with food chute with either hand, mouth or foot
TT†	Touch tool	Make contact with tool with either hand, mouth or foot
TC†	Touch cable	Make contact with cable with either hand, mouth or foot
PC†	Pull cable	Hold cable or tool with hand and pull the cable/tool away from the Pan-pipes with force

*Codes used in the experimental and control conditions

† Codes used only in the control condition

Table 3.2 Coding categories applied to videotape analysis

3.3 Results

a. Individual controls

None of the individual control chimpanzees discovered how to apply the techniques of Lift or Poke to the Pan-pipes and so none gained a food reward. Two of the chimpanzees (both male) made no contact at all with the Pan-pipes, food chute or tool, but the rest interacted with the task in varied ways, (Figure 3.4). The majority of chimpanzees thus investigated the apparatus, but without discovering a solution. To confirm against the possibility that this outcome was not a result of apprehension occasioned by individual testing, the chimpanzees' contacts with the apparatus were plotted separately for the first and second 30 min of the test session (Figure 3.5). The chimpanzees made a significantly greater number of contacts in the first half of the test session (median = 7, mean = 23) compared to the second half (median = 1, mean = 4.1; $z = 2.78$; $P \leq 0.01$) which suggests that investigation was limited not by apprehension, but rather by having explored the materials sufficiently for attention to the Pan-pipes to wane.

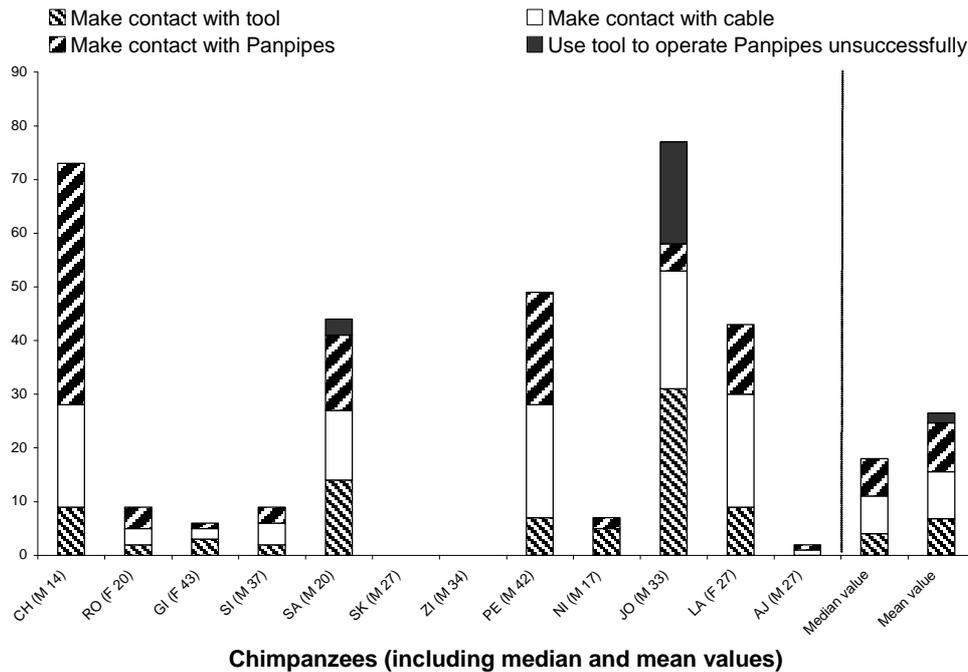


Figure 3.4 Frequency of action types on Pan-pipes by individual control subjects. Median and mean values also given. The number of actions within each coding category (as detailed in Table 3.2) were small and were thus collapsed as follows: Touch tool was termed ‘Make contact with tool’, Touch cable and Pull cable were combined and termed ‘Make contact with cable’, Hit other and Touch food chute were combined and termed ‘Make contact with Pan-pipes’ and the three Insert tool actions were combined and termed ‘Use tool to operate Pan-pipes unsuccessfully’. Each ID code is followed by sex (M, F) and age (years).

b. Control group C

Like the individual controls, members of group C also investigated the apparatus, but differed in that after 20 min, a mid- to high-ranking, 10-year-old female, BE, achieved success through discovering the poke method. BE initially ineffectively inserted the tool into the bottom hole, then explored around the apparatus with the end of the tool, during which she discovered it could be inserted into the critical Poke hole. She continued poking, moved the obstacle back sufficiently and gained a reward, later

going on to repeat this successful approach. Unlike for MY, in group L, the protocol BE was not given protected use of the Pan-pipes ('observation phase') to ensure that the other group members were able to watch her use Poke because she discovered it during the control period. However, it should be noted that although the protocol was to ensure MY had protected access to the Pan-pipes, the experimenter (LMH) never had to intervene as MY was sufficiently dominant to maintain her own sole-use of the apparatus meaning that these two 'demonstration' phases for BE and MY are comparable regarding experimenter control.

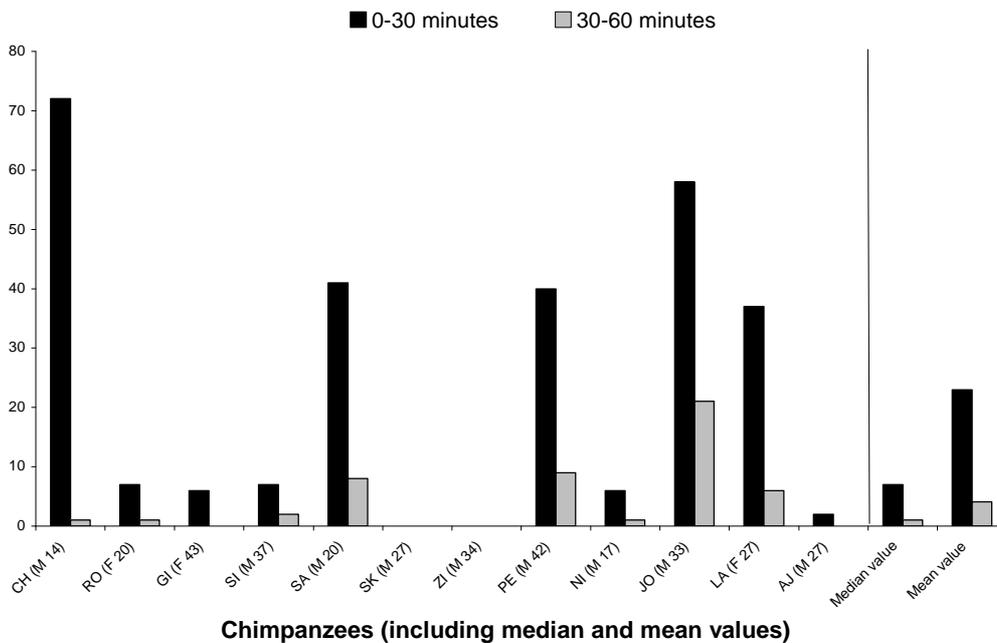


Figure 3.5 Contacts of individual control subjects with Pan-pipes in the first and the second half of the test session. Median and mean values are also given. Each ID code is followed by sex (M, F) and age (years).

It may be suspected that the chimpanzees in the group control situation (group C) would have received less access to the Pan-pipes than would chimpanzees tested

individually for the control/baseline condition and that as a consequence each animal in group C would have had fewer interactions with the apparatus in the time available to them. This was not the case, however for when the number of interactions per chimpanzee were calculated for those tested in a group setting (median = 21.0, IQR = 91.5) and individually (median = 8.5, IQR = 48.5), there was no significant difference (two-tailed Mann Whitney U test: $U = 74.5$ $n_1 = 10$, $n_2 = 12$, $P \geq 0.05$).

Once BE had achieved success, it was not possible to consider the rest of the group as controls, because two chimpanzees (LE and MU, both females) observed BE Poke. It was not logistically feasible to remove BE from the group setting at this point. Instead, the responses of group C were compared with those of group L, in which a model performing Lift had been introduced.

c. Groups L and C compared

In the 23 h of the open diffusion phase, all members of group C were successful on at least one occasion and all predominantly used the Poke technique, as discovered by BE (Figure 3.6a). Three individuals performed Lift on a total of just four occasions. These had the appearance of being accidental insofar as these chimpanzees did not continue to use the Lift method after its initial discovery.

In group L, not including the model MY, five members were successful on at least one occasion, but three never were: a 3-year-old female and the two adult males. Although all members of group L watched large numbers of Lift actions by the original model, the successful individuals all applied the Poke technique predominantly. However, they also used the Lift method, and although this never

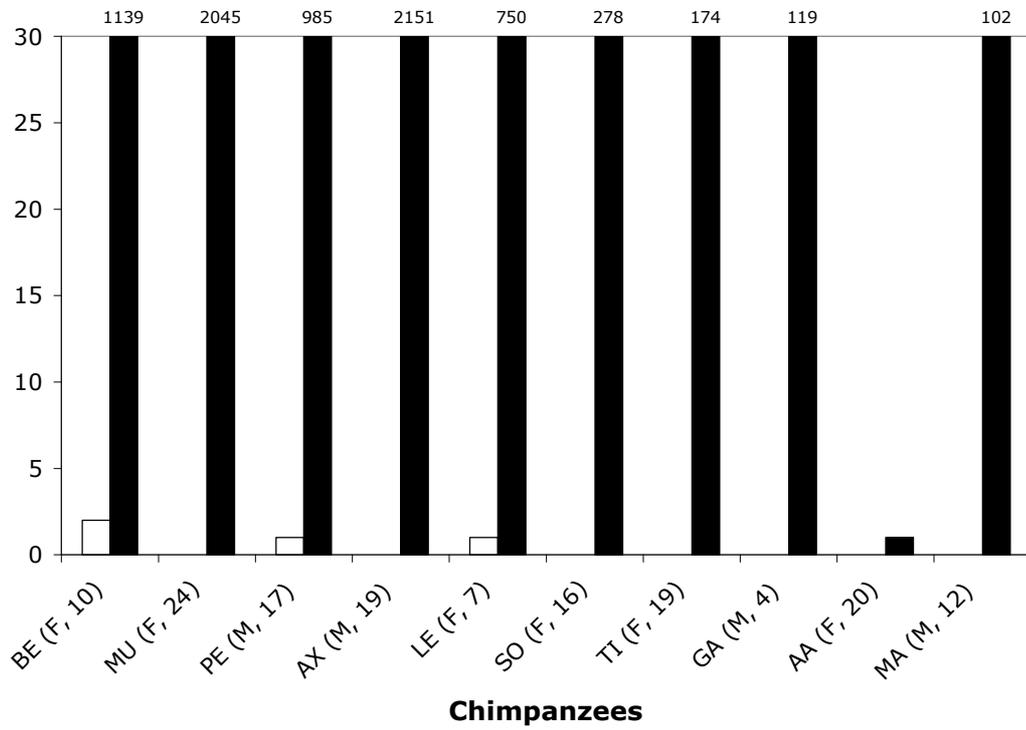
occurred on the scale of Poke, Lift was more common in group L than in group C (Figure 3.6b). To test this difference, following Whiten *et al.* (2005), the percentage Lift for the total number of actions made by all chimpanzees within the 23 h open diffusion phase was calculated. This was calculated thus; % Lift = [total number of Lifts/(total number of Lifts + Pokes)] and the % Lift for group L was 39.9%, while for group C it was 0.1%.

Across the whole experiment, this index when calculated for each individual chimpanzee was significantly higher in group L (median = 2.3%, IQR = 8.5) than in group C (median = 0.0%, IQR = 0.1; two-tailed Mann Whitney *U* test: $U = 60$, $n_1 = 6$, $n_2 = 10$, $P \leq 0.05$). For two of these chimpanzees Lift peaked in the third quarter of the test phase and in another two in the fourth quarter (Table 3.3), confirming that this was not a response that faded with time, despite the accumulation of opportunities for converging on Poke.

Chimpanzee	1	2	3	4
MY (model)	682	580	140	499
CE	1	0	7	3
BE	11	5	1	190
KE	7	1	0	1
TI	0	0	1	0
MR	0	0	0	8

Table 3.3. The total number of Lift actions used by each chimpanzee from group L within each of the four quarters of testing in Experiment 1

a group C



b group L

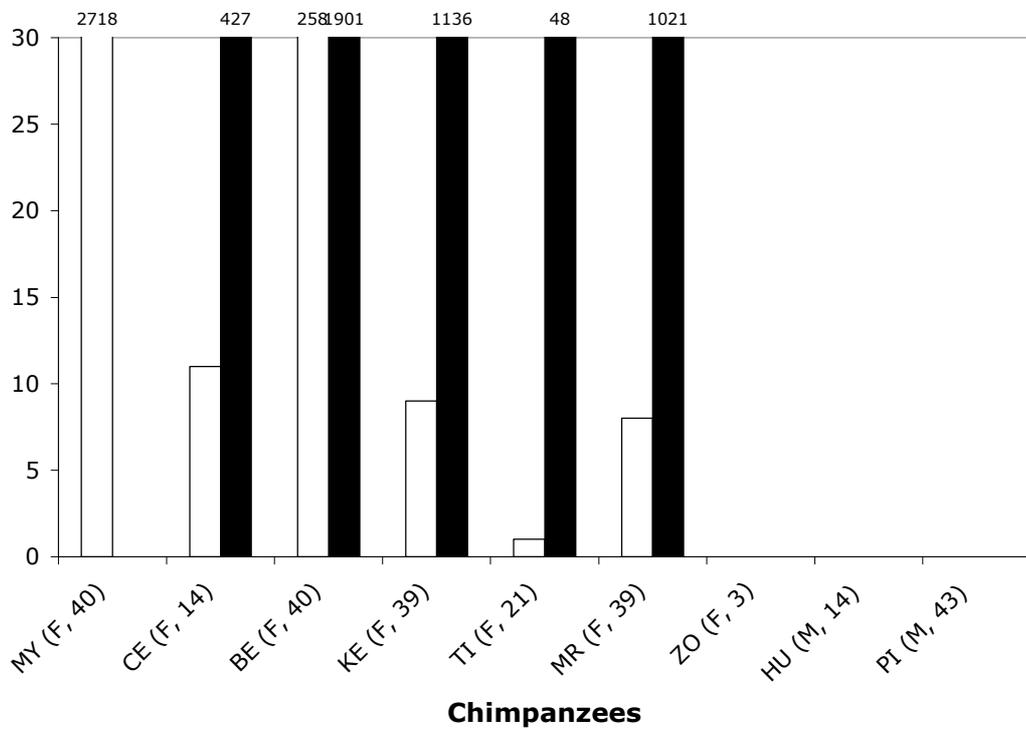


Figure 3.6 (previous page) The actions used by chimpanzees in groups C (**a**) and L (**b**) to operate the Pan-pipes, shown in order of acquisition. Lift and Poke actions by members of both groups are capped at 30 successes to reveal the interactions of those chimpanzees who only made a few responses, with the true values for all of those which exceed 30 interactions provided at the top of each bar. Each ID code is followed by sex (M, F) and age (years).

3.4 Discussion

No clear traditions were maintained between groups C and L at MDACC, insofar as both groups could be characterized as using Poke, even though one group had been seeded with a model who never deviated from using Lift throughout the study. This contrasts with Whiten *et al.*'s (2005) study, which generated a tradition of predominant lifters in one group and pokers in another. However, at a finer level of analysis there was some evidence of traditions, for the statistically significant difference in the proportion of the use of Lift means that group L sustained a different tradition to group C using Lift significantly more.

This bias towards one of the actions (Poke) is reminiscent of that reported by Bugnyar & Huber (1997) in which marmosets showed a preference for one of two techniques of a two-action imitation task ('push' rather than 'pull'). In a later study, Voelkl & Huber (2000) found marmosets preferred one method ('hand opening') over another ('mouth opening'). Such preferences may reflect 'preparedness' (Seligman 1970) whereby animals are naturally predisposed to certain behaviours and responses. This may apply to the bias towards poking observed at both Yerkes (Whiten *et al.* 2005; 'weak bias') and MDACC (this present study; 'strong bias').

A promising hypothesis to explain the difference in this bias between the Bastrop and Yerkes populations arises from the fact that environmental enrichment for chimpanzees at MDACC has regularly (and for many years) included opportunities to dip bamboo sticks into pipes containing a variety of attractive foodstuffs. Yerkes chimpanzees have had similar experience but much more intermittently. Thus, MDACC chimpanzees may be so practiced in poking that even having observed a skilled chimpanzee using the Lift technique on the Pan-pipes, their own work on the apparatus focused more on opportunities for poking.

The second aim of this study was to determine whether the chimpanzees' adoption of the Lift technique depended on social learning. Here, the answer must be yes, for as in the Whiten *et al.* (2005) study, the Lift technique occurred at non trivial levels only in the group seeded with a Lift model, and Lift was performed in that group significantly more often than in the group that had an alternative model. The same social-learning effect was thus evident in both the present study and Whiten *et al.*'s study but generated only weak forms of alternative tradition at MDACC. Additionally none of the chimpanzees tested in the individual control condition discovered Lift.

Whether chimpanzees' adoption of the Poke technique depended on social learning is more difficult to answer definitively, because of the contrast of the achievement of BE in the group context with that of the individual controls. It is clear that for three chimpanzees at least, Poke was adopted without any copying of it from others: these were the first chimpanzees to adopt the Poke technique in group C (which had no model), in group L (which started with a consistent Lift model) and in the Lift-dominated group at Yerkes. However, in favour of the importance of social learning is the fact that individual learning opportunities were insufficient to permit mastery of the task for all 12 individual control subjects tested here and the six

chimpanzees tested individually and in small groups by Whiten *et al.* (2005). Indeed, it remains possible that apart from the single clear case in which BE discovered the Poke method without sight of any model, those that first performed Poke in group L and in the Lift group at Yerkes had learned something important about the task from the models they watched performing Lift. Nevertheless, considering all the results together, we cannot know whether this observation was necessary for these subjects, or if they relied on the same nonsocial processes that allowed BE to succeed.

The contrast between the findings reported here and those of Whiten *et al.* (2005) confirms the importance of pursuing research with large and varied populations, such as at MDACC and/or comparing those to chimpanzees at Yerkes. Historically, behavioural experiments with great apes have been restricted to very small sample sizes. Of the 31 social-learning experiments with apes listed in Whiten *et al.*'s (2004) review covering the last 15 years, 22 had sample sizes in single figures (range for 31 studies, 1 – 20) and each was conducted with a single population of the species concerned. By contrast the present study incorporated 37 chimpanzees and the previous study at Yerkes used 38. Together, these studies of 75 chimpanzees indicate that the probability of particular foraging techniques achieving the status of traditions is affected by the interaction of multiple factors.

At present all of these factors cannot be precisely characterized, but the results are consistent with the hypothesis that traditions arise for techniques that fall between two thresholds in a population's cognitive capacity (Boyd & Richerson 1985). Below the lower threshold, most animals will be able to discover the techniques themselves, whereas above it the task is unlikely to be solved by any animal learning on its own, except for rare innovators. The task must also be below an upper cognitive threshold, such that animals have the capacity to learn the task by observing a model already

expert in it. Above this threshold, it cannot be learned even by observation. Of the two techniques that the Pan-pipes were designed to afford, Lift appears to fall between these thresholds for nearly all chimpanzees studied: among 50 chimpanzees in the two studies who never witnessed an expert model Lift, Lift never became part of their repertoire, whereas it did for 15 of the 20 in the two studies that mastered the task in the groups containing expert Lift models. By contrast, although the Poke technique was above the lower threshold for those tested individually as controls at MDACC, for at least three chimpanzees at the two sites (the first to perform it in groups P and L, and in the Lift group at Yerkes) it was above this lower threshold of individual discovery. It is possible that this was true of other chimpanzees who mastered the task after the first in their group to do so, but we cannot determine this. The implication of these contrasts for the question of traditions among wild chimpanzee is that if in a natural equivalent of our Pan-pipes task, chimpanzees could successfully apply only the Lift technique, the conditions for regional traditions would be met, because a technique this difficult or improbable falls between the two thresholds outlined above. This is plausibly the case for many putative tool use traditions in the wild: in the case of using natural hammers to crack nuts, for example, the behaviour is customary at certain West African sites, but absent at others further east that possess all the raw materials (McGrew *et al.* 1997; Whiten *et al.* 1999).

Whether the success of BE, the one chimpanzee known to solve the Pan-pipes task without observing a model of any kind, was linked to testing in a larger group that may have motivated her in a different fashion to those tested individually or even to those in small aggregations at Yerkes, or whether she brought special individual characteristics to the task and so should count as the necessary ‘rare innovator’ differentiated from the 18 chimpanzees that have so far failed to solve the task, cannot

be known without further experiments. The same is true for the earlier speculation that an important factor in this respect may be the extensive prior experience in poking available at MDACC. The variability in tradition adoption identified here thus suggests a number of lines for further experimental studies building on these results.

It should be noted that although the Pan-pipes is described here as a two-action task (see also Whiten *et al.* 2005; Hopper *et al.* 2007) it differs from the two-action task as typically described (Dawson & Foss 1965; Zentall *et al.* 1996). Unlike these, in which there is only one manipulandum operated in different manners with one outcome, the Pan-pipes exploit one apparatus with two ‘action points’ at different locations with one resultant outcome. A potential criticism therefore of the Pan-pipes could be that the attention of observers would be drawn to these action points, as a result of stimulus enhancement, rather than the particular method used. Yet, when operating the Pan-pipes, a chimpanzee would create different body topographies for each of the two methods and the observing individual would be just as likely to imitate these. Differing body topographies would also have been created by the budgerigars using the original two-action apparatus (Dawson & Foss 1965) insofar as to manipulate it, the budgerigars used either their beak or feet to move a disk. Imitating such different body postures follows in the tradition of both the do-as-I-do studies with chimpanzees (Hayes & Hayes 1952; Cusance *et al.* 1995, although see Byrne & Tanner 2006) and neonatal facial imitation studied both within comparative (Ferrari *et al.* 2006) and developmental psychology (Meltzoff & Moore 1977; Meltzoff 1988*d*).

Overall, the mixed outcomes across the two groups detailed here confirms further the value of using the multiple-group, two-action design despite the potential criticisms as described above. If the study had incorporated only Poke and control

conditions, for example, the role of social learning would have remained indeterminate. It should be noted, however, that the conclusions drawn the study reported here in Chapter 3 are limited because there is only one group per condition. This is somewhat counteracted as these results can be compared to those reported by Whiten *et al.* (2005) with a comparable design tested with the chimpanzees housed at Yerkes. In contrast to the chimpanzees at MDACC the contrast between groups seeded with Lift and Poke models at Yerkes provides statistically significant evidence of social learning, which extended to strong evidence of traditions in the Whiten *et al.* case, but much more marginal evidence of traditions in the present study. The role of the control conditions is to indicate the relative importance of social learning for the two techniques of interest. In the present study, it is the Lift technique for which observational learning is most clearly necessary. Accordingly, in a further experiment (described in *Chapter 4* of this thesis) ‘ghost conditions’ were used to investigate further what information is necessary for observational learning of the Lift technique.

Chapter 4: Chimpanzees Require an Animate Model in Order to Learn a ‘Pan-pipes’ Technique⁷

Summary

Multiple captive traditions among captive chimpanzees have been seeded by Whiten and colleagues, two of which involved the Pan-pipes apparatus. This is a two-action task (Poke and Lift being the two methods) for which Lift has never been discovered through trial-and-error learning. In a first experiment, the basis of the social learning evident in acquisition of the Lift technique shown in *Chapter 3* was investigated using ‘ghost’ conditions in which the task was operated automatically rather than by a chimpanzee. Differential movement of the feeding device either by itself, or with the tool coupled to it, was not sufficient for learning to occur. In a second experiment a series of demonstrations were presented to the chimpanzees to examine which was efficacious. As in the first experiment, the chimpanzees did not learn from the ‘inanimate’ conditions; the baseline and further ghost conditions. In contrast they did learn from the ‘animate’ demonstrations, involving either a human demonstrator, a video of an unfamiliar chimpanzee or a live conspecific.

⁷ Experiment 4.1 of this chapter has been published in Hopper *et al.* (2007)

4.1 Introduction

The results of the open diffusion experiment in *Chapter 3* are in line with those of Whiten *et al.* (2005) and describe the transmission of two variant methods for using the two-action apparatus, the Pan-pipes. Despite this, little or no information is provided from such open diffusion experiments about (i) the underlying mechanism for such social learning, or (ii) what information would be necessary for an observing chimpanzee to allow for such transmission.

To answer the first question, ghost studies can be employed to determine to what extent observing chimpanzees need to learn from a demonstrating chimpanzee who operates an apparatus. Ghost studies are termed as such because the manipulanda appear to move as if guided by an invisible, ghostly agent (Fawcett *et al.* 2002). This approach was pioneered by Heyes *et al.* (1994) with rats which observed a rod move to either the left or right in one of two ways causing a food reward to be released. In the first condition the rats observed a conspecific move the rod whilst in the alternative condition the rod was moved automatically with no demonstrator present. Only those rats that had observed a fellow rat push the rod in a particular direction moved the rod in the same direction as that demonstrated, from which Heyes *et al.* concluded that the rats showed learning by imitation. However, more recently Mitchell *et al.* (1999) determined that the observing rats in a test scenario such as that described by Heyes *et al.* may have been affected by odour cues left on the bar by the demonstrating rats.

Despite the limitations of Heyes *et al.*'s (1994) study, the ghost condition has been used in a small number of other studies. At least two such ghost studies with human

children have provided evidence of emulation learning (Thompson & Russell 2004; Tennie *et al.* 2006). For example Tennie *et al.* arranged for a door that a model had pushed or pulled open to move automatically, and 24-mo-old children's later actions matched the direction of door movement in both modeled and 'ghost' conditions.

Ghost experiments with non-human subjects have produced more mixed results. In two, the task proved inappropriate for demonstrating social learning in the first place (rats, Heyes *et al.* 1994; Mitchell *et al.* 1999; apes, Tennie *et al.* 2006; Hopper *et al.* 2007). Of the remaining five non-human studies, four have generated negative results in the emulation condition (pigeons, Akins *et al.* 2002; starlings, *Sturnus vulgaris*, Fawcett *et al.* 2002; rhesus macaques, Subiaul *et al.* 2004). Only one non-human study reported positive evidence for emulation learning in a ghost condition with pigeons (Klein & Zentall 2003).

These somewhat mixed results beg further investigation to learn whether chimpanzees can operate the Pan-pipes from observing a ghost demonstration. Tomasello and colleagues have concluded that their experiments show chimpanzees are emulators rather than true imitators and if chimpanzees could learn from observing a ghost condition it would suggest that they were emulative learners.

The second point of interest raised by the findings of *Chapter 3* is to determine what forms of demonstration are sufficient for learning from a live agent. Two alternative forms of demonstration that may have potential benefit for chimpanzees are (i) that given by another species of ape – a familiar human; or (ii) that presented only by video footage of a chimpanzee demonstrator.

The use of human demonstrators for chimpanzees has a long tradition in the field of social learning (for example Hayes & Hayes 1952; Nagell *et al.* 1993; Horner &

Whiten 2005; see Whiten *et al.* 2004 for a review). Such a form of demonstration seems appropriate for the chimpanzees housed at MDACC because they have regular contact with humans including the experimenter (LMH) as part of their daily routine. If chimpanzees were found to be capable of learning from a human demonstrator in a complex tool task like the pan-pipes, it could prove to be a beneficial testing tool, because it negates the need to invest time training chimpanzee demonstrators.

Presentation of a chimpanzee operating the Pan-pipes on video could also be a potentially viable form of demonstration, the main benefit of which is the increased reliability of the demonstration provided. A wide range of species have shown ability in recognising, and responding to, images presented on a television screen (for a review see D'earth 1998, also see *Chapter 9*). Chimpanzees should be particularly adept at this as their vision system is comparable to that of humans (Landis 1954), for whom television monitors are designed, and additionally the chimpanzees housed at MDACC are regularly provided with television enrichment and so are used to observing moving images in such a manner. If chimpanzees were shown to learn from video, it would potentially mean that only one chimpanzee would need to be trained and filmed as this video footage could then be shown to multiple groups or individuals. In addition to within-group diffusion, video footage could also facilitate the testing of group-to-group transmission as pioneered by Whiten *et al.* (2007).

Accordingly, reported here are a series of experiments run to examine the mechanisms underlying the transmission of the behaviour documented in *Chapter 3*. In particular, the distinction between whether observers learn information about the model's actions or about the objects that are being moved (Call & Carpenter 2002) was focused upon. To test this, a series of ghost conditions (Fawcett *et al.* 2002) were used. To expand upon the ghost conditions described in Experiment 4.1, a second

experiment was run to provide the chimpanzees with a series of demonstrations of the Pan-pipes to determine further what sources they are able to learn from. The individual ghost conditions from Experiment 4.1 acted as a springboard for this second series of tests.

The tool use task, the Pan-pipes, used in the experimental study of traditions (*Chapter 3*; Whiten *et al.* 2005; Hopper *et al.* 2007) was thought to be potentially instructive for this approach. Since the whole apparatus was on the experimenter's side of the chimpanzees' enclosure, fine fishing line could be used to make parts of it move as if manipulated by an invisible chimpanzee; this made it possible to apply two different levels of ghost condition, in one making the device operate to release food as if moved by an invisible tool, and in the other adding the tool protruding through the bars into the chimpanzee's cage, moved as if by an invisible hand. In neither case was a chimpanzee model present. An investigation of whether witnessing such movements would be sufficient for chimpanzees to learn a tool use technique earlier demonstrated to be a socially transmitted tradition could be investigated.

Experiment 4.1: Ghost conditions with the Pan-pipes

The experiment was designed to determine whether chimpanzees could learn the Lift method for operating the Pan-pipes apparatus by observing the relevant object movements with no demonstrator present, thus the affordances of the task whereby the T-bar and blockage rise releasing the food reward. The Lift method was selected because, when presented with the Pan-pipes individually and in a group setting, no

chimpanzee discovered the Lift method (*Chapter 3*) while one chimpanzee *was* able to discover the Poke method.

4.2 Methods

a. Experimental design

Subjects	18 chimpanzees
Apparatus	Pan-pipes (two-action task)
Conditions	3 individual ghost conditions showing Lift method: Basic ghost (with baseline) Ghost-with-tool (with baseline) Basic ghost (without baseline)
Independent variable	Form of ghost condition
Dependent variable	Ability of chimpanzees to operate Pan-pipes and, if able to solve Pan-pipes, which method was used

b. Subjects and housing

The 12 chimpanzees (group A) were housed at MDACC. The test population comprised of 3 females and 9 males aged 14 - 43 years (mean 28.4 yrs), housed in groups of two to five. Table 4.1 summarises demographic details for all participants. Testing took place in their inner housing, which measured 2.4 x 2.4 m and 1.8 m high (*Chapter 3* Figure 3.1a). These 12 chimpanzees were previously exposed to the Pan-

pipes in the individual control condition described in *Chapter 3*, none of whom had learned to operate the apparatus successfully.

A further six chimpanzees (group B, also housed at MDACC), naïve to the Pan-pipes, were also assigned to a basic ghost condition to check that the prior exposure to the Pan-pipes experienced by the other 12 subjects did not determine their responses through habituation to the task. These six chimpanzees comprised of 3 females and 3 males aged 13 – 18 (mean 15.3 yrs) detailed in Table 4.1.

Group A		Group B	
Female ID	Male ID	Female ID	Male ID
GI (43)	PE (42)	TR (18)	BA (15)
LA (27)	SI (37)	IN (18)	HO (14)
RO (20)	ZI (34)	BE (14)	KE (13)
	JO (33)		
	AJ (27)		
	SK (27)		
	SA (20)		
	NI (17)		
	CH (14)		

Table 4.1 Demographic details of the chimpanzees in groups A and B, where each ID code is followed by age (years).

c. Apparatus

The apparatus used in this study was the Pan-pipes (Whiten *et al.* 2005), for a full description see *Chapter 3*.

d. Procedure

Six chimpanzees from group A and the six chimpanzees in group B were assigned to a basic ghost condition while the remaining six chimpanzees from group A were assigned to a ghost-with-tool condition. In each condition the chimpanzees observed a form of ghost condition showing the Lift method (see *Chapter 3* for a full description).

(i) Basic ghost condition

For the basic ghost condition, a length of fishing line was tied to the top of the T-bar, and looped through the top of the chimpanzee's caging to create an unobtrusive pulley system with which the experimenter (LMH) could covertly raise and lower the T-bar. The Pan-pipes were placed in front of the chimpanzee's cage out of reach, but in sight of the chimpanzees, with the food chute resting on a small bucket. The experimenter used the fishing line to raise the obstacle 225 times, which was the average number of times that chimpanzees in group L (*Chapter 3*) had observed Lift during the observation phase. With each Lift, a grape rolled out and along the food chute into

the bucket. To replicate further the experience of members of group L, on every 20th demonstration the experimenter removed the bucket and placed the food chute through the caging so that the grape fell into the chimpanzee's cage, thus simulating scrounging opportunities that had occurred in the group situation.

When the 'ghost' demonstration had been completed, the fishing line was removed and the apparatus was presented to the chimpanzees for a one-hour free-access period during which the chimpanzees could interact freely with the Pan-pipes.

(ii) Ghost-with-tool condition

The ghost-with-tool procedure was identical to that of the basic ghost condition described above, except that the tool was attached to the T-bar so the tool moved as if lifting the obstacle up.

e. Coding

All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). A running commentary was provided by the experimenter (LMH) and the chimpanzees' actions were coded from videotape (Table 4.2).

Action Code	Action Name	Definition
P	Poke	Insert tool through flap door into top pipe, pushing blockage completely backwards; food reward released and gained
L	Lift	Place tool under T-bar to raise T-bar (and blockage); food reward released and gained
ITP	Insert tool Poke	Insert tool into the top hole, as for P, but not far enough to release food reward
ITL	Insert tool Lift	Place the tool under the T-bar, as for L, but fail to raise it sufficiently to allow a food reward to be released
BOTTOM	Insert tool bottom	Insert the tool into the bottom (food exit) hole. No food reward gained
H	Hit	Make contact between the tool and other part of the Pan-pipes including food chute, sides of the Pan-pipes and table; no food reward gained
TFC	Touch food chute	Make contact with food chute with either hand, mouth or foot
TT	Touch tool	Make contact with tool with either hand, mouth or foot
TC	Touch cable	Make contact with cable with either hand, mouth or foot
PC	Pull cable	Hold cable or tool with hand and pull the cable/tool away from the Pan-pipes with force

Table 4.2 Coding categories applied to videotape analysis, which are consistent with those described in *Chapter 3* Table 3.2.

4.3 Results

Ten observer chimpanzees ate the grapes immediately; one watched all appear but did not eat them, and another gathered them quickly only when their cage-mates were released to join them at the end of the test session. All chimpanzees watched these ‘demonstrations’, eight of them intently throughout.

a. Basic ghost vs. ghost-with-tool

For the chimpanzees in group A (Figures 4.1a, b) there was no significant difference between the number of interactions that they made with the Pan-pipes in the basic ghost condition (median = 1.5, IQR = 14.3) compared to those made in the ghost-with-tool condition (median = 2.0, IQR = 2.8; two-tailed Mann Whitney U test: $U = 23.5$, $n_1 = 6$, $n_2 = 6$, $P \geq 0.05$).

b. Basic ghost: group A vs. group B

No significant difference was found between the number of actions chimpanzees performed on the Pan-pipes in the basic ghost condition in group A (median = 1.5, IQR = 14.3) and the number performed by naïve subjects in group B, Figure 4.1c, (median = 2.0, IQR = 7.3; two-tailed Mann Whitney U test: $U = 16.0$, $n_1 = 6$, $n_2 = 6$, $P \geq 0.05$).

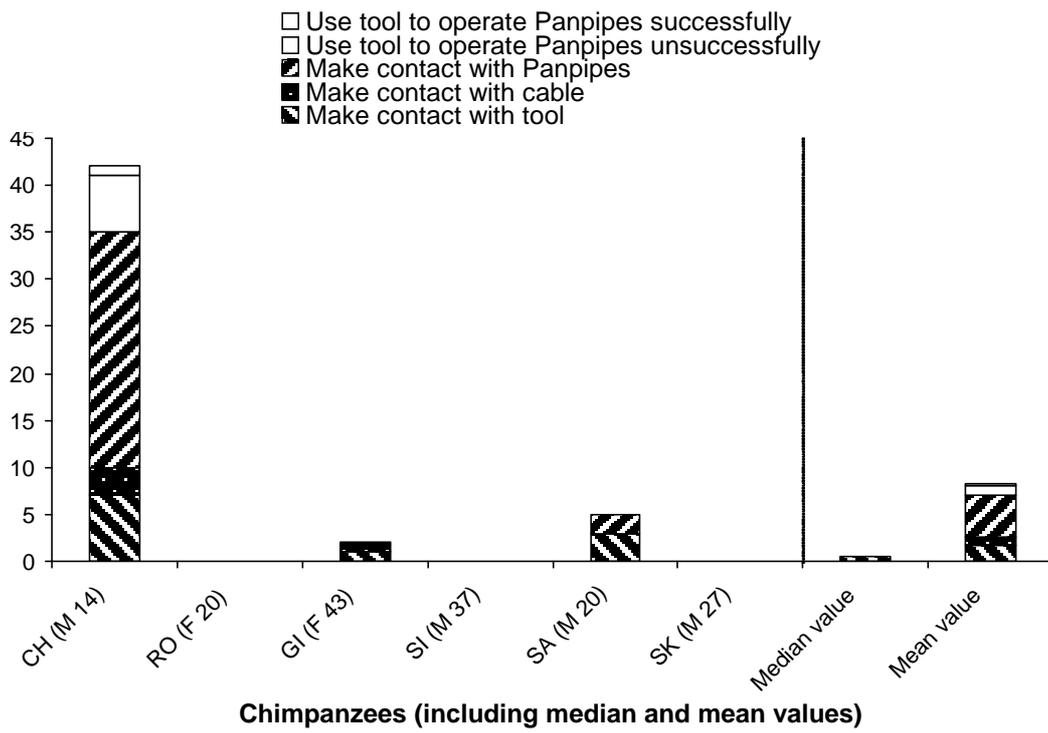
c. Ghost conditions vs. Individual control condition

Across all ghost conditions, only one of the 18 chimpanzees, CH, successfully operated the Pan-pipes on a single occasion but this was through the Poke, not the Lift method, and was never repeated. As there was no significant difference between neither the number of interactions made between chimpanzees in groups A and B and nor the number made between the two ghost condition forms they were consolidated.

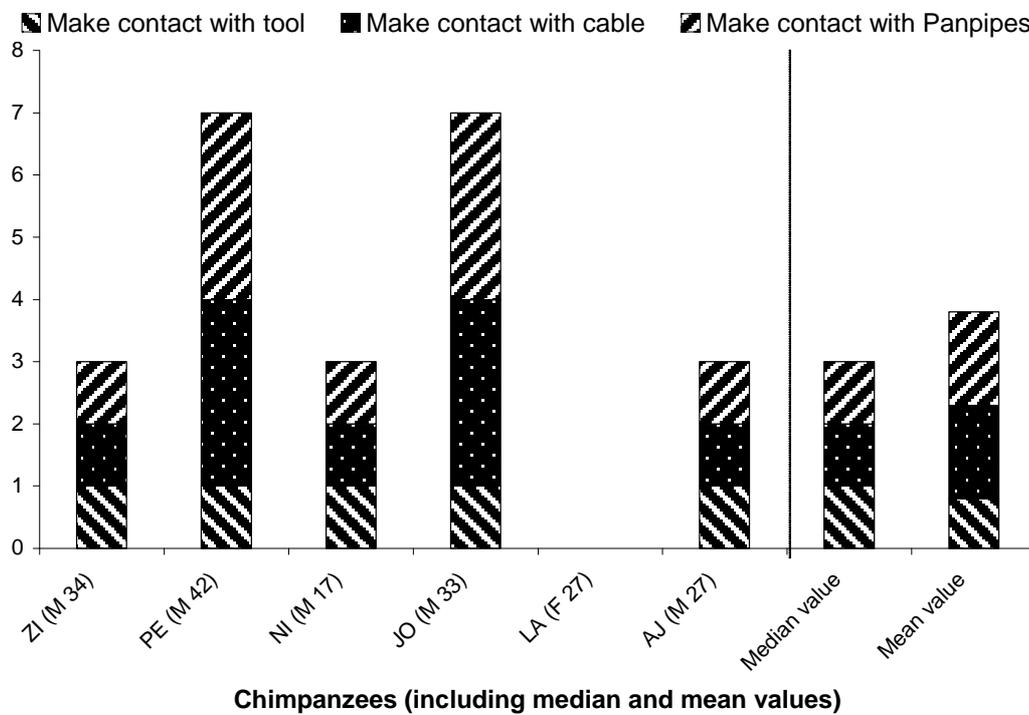
The actions applied during the ghost conditions were no more effective than in the earlier individual control condition (*Chapter 3*). Although these chimpanzees had watched numerous grapes fall from the Pan-pipes and (with the exception of one subject) gained and eaten all 11 items they received, they showed no increase in actions likely to gain food.

To the contrary, the number of interactions with the apparatus in the ghost conditions (median = 2.0, IQR = 4.5) was less than during the earlier individual control condition in those chimpanzees that experienced both (median = 8.5, IQR = 44.5; two-tailed Mann Whitney U test: $U = 104.0$, $n_1 = 12$, $n_2 = 12$, $P \leq 0.05$).

a basic ghost (group A)



b ghost-with-tool (group A)



c basic ghost with no prior baseline (group B)

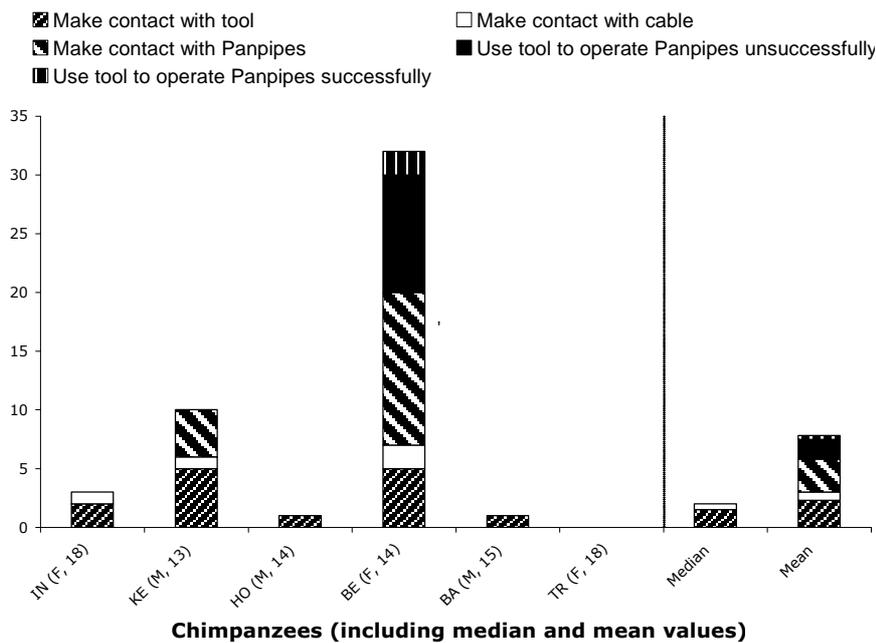


Figure 4.1. (Including that on previous page) Frequency of action types on Pan-pipes by individual subjects in (a) the basic ghost condition (group A), (b) the ghost-with-tool condition (group A) and (c) the ghost condition with no prior baseline (group B). The number of actions within each coding category (as detailed in Table 2) were small and were thus collapsed as follows: Touch tool was termed ‘Make contact with tool’, Touch cable and Pull cable were combined and termed ‘Make contact with cable’, Hit other and Touch food chute were combined and named ‘Make contact with Pan-pipes’. The three Insert tool actions were combined and termed ‘Use tool to operate Pan-pipes unsuccessfully’ and Poke and Lift were grouped together and defined as ‘Use tool to operate Pan-pipes successfully’. Median and mean values are also given. Each ID code is followed by sex (M, F) and age (years).

4.4 Discussion of Experiment 4.1

The results of Experiment 4.1 indicate that the Lift technique, which the diffusion experiments described in *Chapter 3* highlighted as the one most clearly dependent on social learning, is not easily acquired merely by watching movements of the tool and apparatus. Instead, it appears important that a model is involved in making these

movements happen, a result that suggests imitation may be a possible term to describe the mode of social-learning, so long as this is interpreted broadly enough to acknowledge that what the model makes the tool do may well be an important element copied by the learner, however response facilitation can not be ruled out. Although these results are promising, in future testing, a ghost-with-tool condition without a baseline should also be run

The chimpanzees' inability to learn the Pan-pipes from observing these ghost conditions follows the previous findings of studies using comparable methods, detailed previously (Akins *et al.* 2002; Fawcett *et al.* 2002; Subiaul *et al.* 2004). However such a result would suggest that the chimpanzees did *not* show emulative learning contradicting Tomasello and colleagues' previous suggestions that chimpanzees are emulators. Furthermore, the chimpanzees actually showed reduced responsiveness during the ghost response period than during the baseline which may suggest the chimpanzees were inhibited by the ghost condition. Throughout testing, it should be noted, that the chimpanzees showed no signs of distress and always sat near the Pan-pipes observing, so neophobia does not seem to explain this pattern. One possible explanation could be that the chimpanzees learnt that food was 'automatically' dispensed from the Pan-pipes during the ghost condition and so in the response period they 'assumed' that grapes would still be delivered to them and so made no efforts to retrieve them themselves.

Caution should be maintained however when drawing comparisons between the responses of chimpanzees in the open diffusion experiment (*Chapter 3*; Hopper *et al.* 2007) and those in the ghost conditions reported here. The chimpanzees only had access to the Pan-pipes for a one-hour period whilst those in group condition reported in *Chapter 3*, had up to 23 hours exposure to the Pan-pipes. Therefore, for a true

comparison between the two conditions to be drawn the chimpanzees in the ghost conditions should be provided with a total of 23 hour access period (preferably yoked to the comparison group) and secondly the chimpanzees should all be tested in a group setting. The chimpanzees in this experiment, unlike those in *Chapter 3*, were tested in isolation and, being gregarious animals by nature, testing in isolation may have inhibited their responses. Experiment 4.2 was designed in part to address this by conducting comparable ghost conditions but with chimpanzees in their groups, rather than individually.

Experiment 4.2: Animate and inanimate conditions with the Pan-pipes

The results detailed in Experiment 4.1, and *Chapter 3*, show no chimpanzee was able to learn Lift from either trial-and-error individual learning or after a ghost demonstration of that method. In addition to expanding upon the experimental design of Experiment 4.1, the procedure of this experiment was designed to provide chimpanzees, in a group setting, with increasing, and varied, forms of information about how to operate the Pan-pipes with the Lift method, to determine which is useful to them.

4.5 Methods

a. Experimental design

Subjects	29 chimpanzees
Apparatus	Pan-pipes (two-action task)
Conditions	4 group Lift demonstrations preceded by a baseline: <ol style="list-style-type: none">1. Ghost condition2. Human demonstration3. Video chimpanzee demonstration4. Conspecific demonstration
Independent variable	Form of demonstration
Dependent variable	Ability of chimpanzees to operate Pan-pipes using Lift

b. Subjects and housing

The 19 chimpanzees were housed at MDACC. The test population comprised of 8 females and 11 males aged 43 - 10 years (mean 26.7 yrs) housed in four groups, with three to six individuals in each group. Demographic details for these chimpanzees are listed in Table 4.3. The chimpanzees were tested in the outside area of their cage ('Primadome®') for four of the experimental conditions while for the Video condition (see Procedure) the chimpanzees were tested in one quarter of their inside housing. The outdoor dome measured 10.4 m in diameter and 8.5 m high while the indoor testing area measured 2.4 x 2.4 m and 1.8 m high respectively (*Chapter 3 Figure 3.1a*).

Q1	Q2	Q3	Q4
GI (F, 43)	GP (M, 36)	AD (M, 30)	BA (F, 37)
PY (F, 42)	SN (M, 21)	SK (M, 28)	PS (F, 37)
MY (F, 21)	MC (M, 13)	AX (M, 27)	VA (F, 36)
BR (F, 10)		AM (M, 19)	RO (F, 21)
NI (M, 17)		KM (M, 16)	SI (M, 37)
CH (M, 17)			

Table 4.3 Demographic details for the chimpanzees in each of the four experimental groups, each ID code is followed by sex (M, F) and age (years). The chimpanzees were housed in buildings 104-107 (*Chapter 3* Figure 3.1a).

c. Apparatus

(i) Pan-pipes

The apparatus used in this study was again the Pan-pipes (Whiten *et al.* 2005), for a full description see *Chapter 3*. For this study, the Poke method was prevented, by screwing shut the flap at the front of the Pan-pipes into which the rod-tool could be inserted.

(ii) Video-footage filming

The female model for the Lift method in Group L, as described in *Chapter 3*, was used for the model on the video-footage. This female was housed separately from all test subjects in the experiment described here (corral 8, *Chapter 3*, Figure 3.1a) and

was isolated in the indoor quarters of her caging for filming. She was presented with the Pan-pipes and whilst operating them using Lift she was filmed on a Sony miniDV digital handycam (CDR-TRV27). The handycam could be connected directly to a colour television to allow playback of the footage.

Footage was captured from two angles; above and from the side. However due to the constraints of the indoor caging no footage could be taken from behind the chimpanzee as would be seen by observing cage mates in a live chimpanzee model scenario. A still taken from this video forage is shown in Figure 4.2.



Figure 4.2 Still from the footage of MY demonstrating the Lift method with the Pan-pipes that was used as the video demonstration stimulus.

d. Procedure

Figure 4.3 provides the experimental protocol for the presentation of each form of demonstration. Each demonstration, as detailed in Figure 4.3, was followed by a one-

hour free-access period with the Pan-pipes in order to provide the chimpanzees with adequate time to interact with the apparatus.

In each of the ghost demonstrations provided in Experiment 4.1 the observing chimpanzees were given access to the grape reward on every twentieth demonstration to simulate scrounging in an open diffusion scenario. However in Experiment 4.2 this was not continued because one of the demonstration forms provided was video footage of the Pan-pipes on a television screen and it would not have been possible to dispense the grape reward from this format of demonstration. Therefore, to maintain consistency across all demonstration forms, no food rewards were provided, yet in all conditions the observing chimpanzees could see the grape fall from the food chute for every demonstration.

Each of these demonstration and test sessions occurred on different days over a period of one month. If any chimpanzee operated the Pan-pipes during the one-hour free-access period, the chimpanzee received no further demonstrations and entered an open-diffusion phase of the kind described in *Chapter 3*, which lasted for 20 hours or until all the chimpanzees in that group were proficient at using the Pan-pipes.

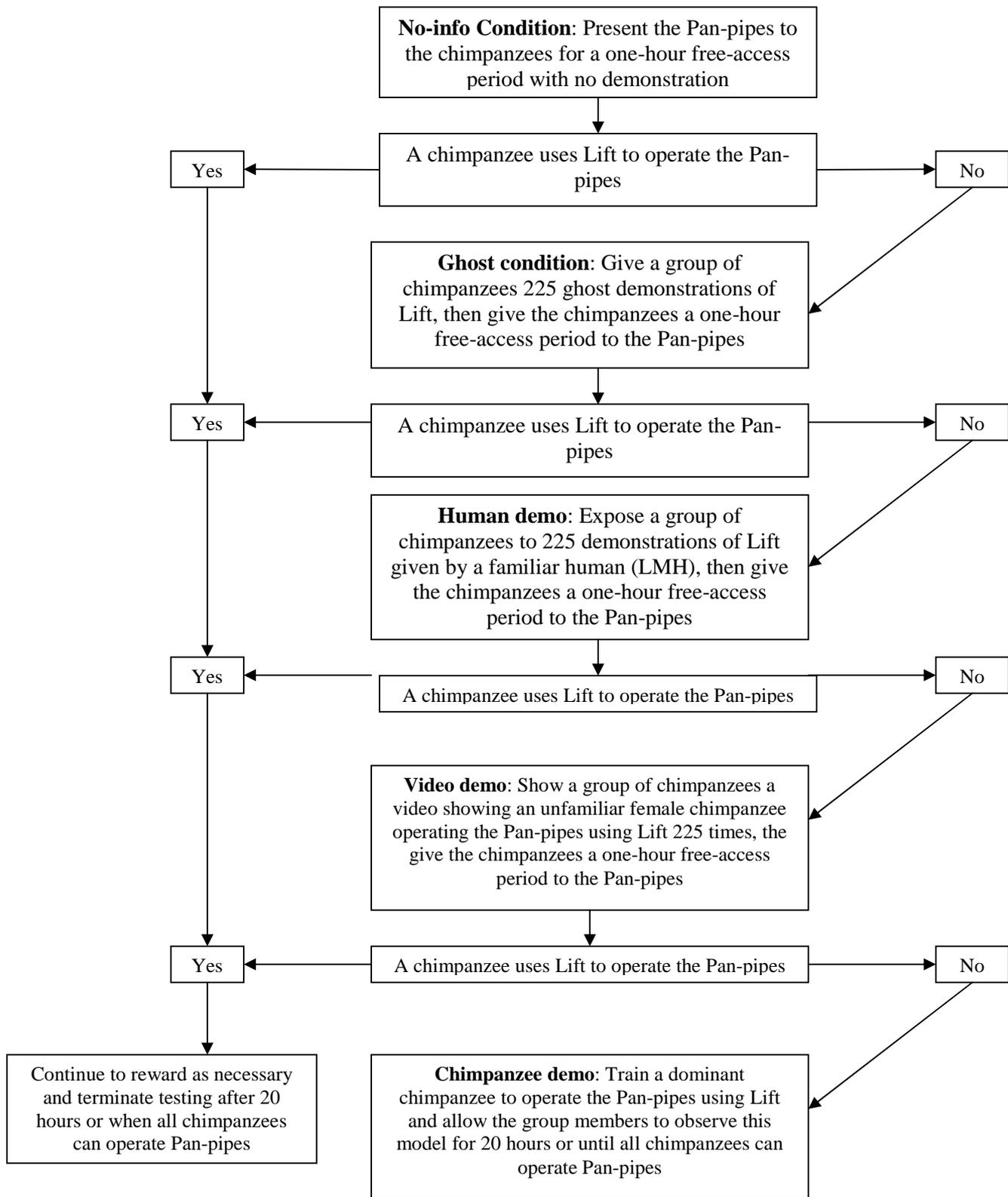


Figure 4.3 Protocol for the series of conditions presented to chimpanzees in Experiment 4.2

(i) No-info condition

Initially, each group was presented with the Pan-pipes set against the caging of their outside enclosure with no demonstration. Each group was given one hour in which to interact freely with the Pan-pipes, prior to which a grape was loaded into the Pan-pipes whilst the chimpanzees watched. As no chimpanzee solved the Pan-pipes during the No-info condition the study proceeded to the demonstration phase.

(ii) Ghost condition

The Pan-pipes were placed in front of the outside caging, in view, but out of reach of the chimpanzees. A pulley was set up alongside and reaching over the Pan-pipes (see Figure 4.4) through which a length of fishing-line tied to the T-bar could be looped. This allowed the experimenter to raise and lower the t-bar discretely by pulling on the free end of the fishing-line.

Following the rationale described in Experiment 4.1, 225 ghost demonstrations of Lift were provided to the chimpanzees in a group. For each Lift, a grape was loaded into the Pan-pipes and when the T-bar was raised the grape would fall into a bucket placed in front of the Pan-pipes.

After the demonstrations, the Pan-pipes were pushed against the caging so that the chimpanzees in their group could interact with them for one hour.

(iii) Human demo

Pan-pipes were presented to the chimpanzees in their outside quarters in a similar manner to that during the Ghost condition. However instead of 225 ghost demonstrations, the demonstrations were provided by a familiar human (LMH). The experimenter sat to one side of the Pan-pipes on the outside of the cage, and used the rod-tool to raise and lower the T-bar 225 times.

(iv) Video demo

A television (a Zenith full-colour television with an 45 cm screen) was placed in front of the chimpanzees' indoor caging on a trolley with the screen 80 cm above the ground level for chimpanzees. The Pan-pipes were placed alongside the television, out of reach of the chimpanzees, so that they could see the apparatus whilst watching the video-footage. The video-footage showed an unfamiliar female chimpanzee operating the Pan-pipes using the Lift method 225 times filmed as described above.

After the presentation of the video-footage the television screen was moved away and the Pan-pipes were pushed against the caging so that the chimpanzees were able to interact with them for one hour.



Figure 4.4 The pulley system allowing for ghost demonstrations to be provided outside the Primadomes. **(a)** An overview of the pulley system and **(b)** a close-up of the Pan-pipes with the T-bar raised by fishing line and showing a chimpanzee (GP (M, 36)) observing.

(v) Chimpanzee demo

A dominant chimpanzee was selected to be the model. This chimpanzee was isolated and trained by the experimenter (LMH) through the use of positive reinforcement training and shaping techniques to operate the Pan-pipes using Lift. Once the chimpanzee was proficient in using Lift (30 consecutive successful operations) they were re-introduced to their group and their group members were able to observe the model operate the Pan-pipes.

e. Coding

All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). A running commentary was provided by the experimenter (LMH) and the chimpanzees' actions were coded from this videotape. A chimpanzee was coded as 'successful' if they could retrieve a grape from the Pan-pipes through the Lift method.

4.6 Results

a. Learning Lift

(i) Inanimate conditions

No chimpanzee from the four experimental groups learnt how to operate the Pan-pipes in either the No-info condition or the Ghost condition (Table 4.4).

(ii) Animate demonstrations

One chimpanzee (KM) from Q3 learnt Lift after seeing the Human demo so this group entered the open diffusion phase, at the end of which three of the five chimpanzees were able to operate the Pan-pipes, representing 16% of the total test population. Presentation of the Human demo to the four groups evidently was not enough to seed Lift at a significant level across the four groups (two-tailed McNemar test: 0/19 vs. 3/19, $P \geq 0.05$).

The remaining three groups were presented with the Video demo and members of two of the three groups learnt how to operate the Pan-pipes; BR from Q1 and VA from Q4. In Q1 MY, and in Q4 BA, also avidly watched the television screen presented to them. However because BR and VA were the first to operate the Pan-pipes in each of the two groups it is not possible to determine whether MY and BA

actually learnt from watching the video or whether it was from watching BR and VA respectively (Table 4.4). Both these groups entered an open diffusion phase, at the end of which all of Q1 and 4/5 members of Q4 could operate the Pan-pipes. Including those chimpanzees in Q3 who had learnt the Pan-pipes, 68% of the chimpanzees were able to operate the Pan-pipes, significantly greater than the number able to operate the Pan-pipes prior to this stage (two-tailed McNemar test: 3/19 vs. 13/19, $P \leq 0.05$).

Comparably, the number of chimpanzees from Q1 and Q4 able to operate the Pan-pipes after having seen the Video demo compared to before they had seen it was significant (two-tailed McNemar test: 0/11 vs. 10/11, $P \leq 0.01$).

Finally, a member of Q2 (SN), the only group unable to operate the Pan-pipes, was trained to operate them and act as a model for his group members. At the end of the 20-hour open diffusion phase 2/3 chimpanzees were able to operate the Pan-pipes. Therefore, in total, 79% of all chimpanzees tested were able to operate the Pan-pipes using the Lift method following animate demonstrations, whilst none had in the inanimate conditions.

b. Overall success

After having seen one of the three forms of animate demonstrations 15 of the 19 chimpanzees tested were able to operate the Pan-pipes using Lift (two-tailed McNemar test: 0/19 vs. 15/19, $P \leq 0.01$).

	Condition					
	No-info	Ghost	Human	Video	Chimpanzee	Open diffusion
Q1 solve Lift		-		1 (2)*		6/6
Q2 solve Lift			-		1	2/3
Q3 solve Lift	-		1			3/5
Q4 solve Lift		-		1 (2)*		4/5

*After the Video demo two chimpanzees from both Q1 and Q4 actively watched the video and operated the Pan-pipes. However as it is impossible to determine whether one learnt from observing the other it is only certain that one chimpanzee from each group learnt from observing the video.

Table 4.4. The chimpanzees that were able to operate the Pan-pipes, using Lift, after seeing each particular demonstration and the total number from each group which subsequently learnt in the open diffusion phase.

4.7 Discussion of Experiment 4.2

No chimpanzee was able to solve the Pan-pipes in the baseline conditions through trial-and-error learning and, as in Experiment 4.1, the chimpanzees were unable to solve the Pan-pipes using Lift when provided with a ghost condition, despite remaining with their cage-mates. These two unsuccessful conditions both represented inanimate presentations of the Pan-pipes. When the chimpanzees were presented with the latter animate demonstrations they were more likely to be able to operate the Pan-pipes and to do so using the demonstrated Lift method; indeed, 15/19 did so.

Across the groups tested, the chimpanzees showed evidence of an ability to learn from a human demonstrator, a video of an unfamiliar chimpanzee operating the Pan-pipes and a live conspecific model. That the chimpanzees were able to learn from a familiar cage-mate is not unprecedented as chimpanzees in *Chapter 3* and in previous experiments (Whiten *et al.* 2005) have also been shown to learn new tasks from

observing conspecifics. However replication of this finding in this experiment adds further weight to these previously reported results. That the chimpanzees were able to learn from a human demonstrator also reflects previous findings (for example Horner & Whiten 2005), however that only one chimpanzee learned from a human confirms the recommendation that providing chimpanzees with conspecifics as demonstrators has more worth for them.

Two, possibly four, chimpanzees were able to learn the Pan-pipes after having viewed video footage of an unfamiliar conspecific operating the Pan-pipes using Lift. This finding raises many potential possibilities, especially for future social learning experiments. Further work needs to be conducted to ascertain the reliability of this finding, but if chimpanzees were found to be able to understand, and recreate, actions they observe on a television screen then this would greatly facilitate social learning testing, as described in the Introduction to this chapter. To answer these questions, a further experiment involving the use of a video demonstration with chimpanzees at MDACC was conducted and *Chapter 9* provides details of this.

In conclusion, the results of this second experiment indicate that chimpanzees require an animate model from which to learn rather than an inanimate demonstration such as given in a ghost condition. Further to this, it appears that a suitable model need not necessarily be a live conspecific present with the chimpanzees but that also, pending future experiments (*Chapter 9*), video footage of a fellow chimpanzee may also suffice. However, no firm conclusions can be made purely from these results as. Caution needs to be maintained because although 15/19 chimpanzees learnt how to operate the Pan-pipes after exposure to an animate demonstration, not one of the forms presented was sufficient for all chimpanzees to learn from. Despite these positive findings, order effects of the demonstration presentation cannot be ruled out.

The chimpanzees may have only learnt how to operate the Pan-pipes as exposure to the task increased over time rather than a crucial difference between animate and inanimate models. This failing should be fully considered when planning future experiments.

4.8 General discussion

In combination, these two experiments suggest that chimpanzees are unable to learn how to operate the Pan-pipes from having observed a ghost condition, whether they are tested in isolation or in a group. This contrasts with the results found from the ‘animate’ conditions of Experiment 4.2, along with those described in *Chapter 3*, in which chimpanzees were able to learn from conspecifics, both live and presented on video, and human demonstrators.

The ghost condition is often referred to as a ‘ghost control’ i.e. a control condition for the main focus of such studies, which are concerned with whether there is evidence for imitation (Fawcett *et al.* 2002; Klein & Zentall 2003). The logic applied is that if the explanation for an individual’s observational learning is a focus on the environmental results of what the model does, often called ‘emulation’ (Wood 1989; Tomasello 1990) or ‘affordance learning’ (Klein & Zentall 2003), the individual will learn in the ghost control condition. If an observer does not learn in the ghost condition, then the conclusion is that the observational learning already documented should properly be classed as imitation.

Terming such conditions as only a ghost ‘control’ undermines its interest as it is of equal interest whether the learning is of an emulative character (learning in the

ghost condition) or not. This said, following the logic above, the overwhelmingly negative results of the ghost conditions used in both experiments lead to the conclusion that those chimpanzees who used the Lift technique significantly, both in the study described in *Chapter 3* and in that of Whiten *et al.* (2005), were influenced crucially by the model's actions, and not simply by the movements of the apparatus, as would have been expected if stimulus enhancement or emulation were sufficient. This could be argued to amount to saying that imitation was involved.

Such a conclusion would not imply that when a naïve chimpanzee watches an expert conduct a Lift, it pays no attention to what the tool does. To the contrary, this was what chimpanzees appeared to be looking at, although it is difficult by observation alone to be sure. However, this does not preclude an ascription of imitation, for in tool use the tool becomes an extension to the model's effectors and what is done with the tool is the action imitated. Whether chimpanzees' attention is on the limb movements of the model, the movements of the tool, the movements of the obstacle and food and/or on dynamic relations between these, the present results show it is important that a chimpanzee is seen to be responsible for these means and hence, terms such as imitation or copying (Miklosi 1999) become apt. In other words, what appears to be copied is how a model *does* all these things, or how the model *makes them happen*. Of the other ghost condition studies noted above, the results of Fawcett *et al.* (2002) with starlings were also in accord with imitation, whereas the study of Klein & Zentall (2003) offered evidence supporting the existence of emulation (in their terms, 'affordance learning') as pigeons did learn an appropriate action by watching movements of the apparatus alone.

At first sight, the conclusions presented here are the opposite of those from a recent experiment by Call *et al.* (2005), in which chimpanzees learned one of two

ways to open foraging devices from observing the outcome alone; in this case, the devices already opened in one of the two ways. Unlike children, chimpanzees did not copy the actions of a model they had seen try to open the devices in either of two ways. Thus, the results were interpreted as showing emulation in chimpanzees, rather than imitation.

These studies are not necessarily in conflict. First, the manipulation in Call *et al.*'s (2005) study was sufficiently simple that the task was completed by a majority of individuals in the baseline control condition as fast as those who watched a model, whereas the Pan-pipes apparatus has not been mastered by 18 such controls in two studies and is thus clearly more challenging. It therefore seems very likely that chimpanzees can learn sufficiently well about relatively simple tasks by individual inferential learning, but may use imitative copying where they cannot achieve an unguided solution. Second, in one observation condition of Call *et al.*'s study, the device was glued so it would not open: observer chimpanzees later actively avoided the unsuccessful efforts that the model applied to this part of the task. This suggests that they actively attended to what the model *did* (as we suggest was important in our own study), but then actively avoided copying this unfruitful activity. In the experimental context, this was an adaptive response. Thus rather than being in conflict, the study presented here and Call *et al.*'s together offer a new and mutually consistent picture of the ways in which social and asocial learning are strategically applied by chimpanzees to tasks that differ in ease of learning (Laland 2004; Whiten *et al.* 2004).

Chapter 5: Children Learn from a Human

Demonstration and also from a Ghost Condition

Summary

In recent years much information has been gathered about *whether* children show social learning from both adults and their peers, but *how* such learning occurs is still an open debate. The first experiment detailed here follows from a previous two with chimpanzees, which employed a ghost demonstration of the Pan-pipes task. When each of the two methods (Lift and Poke) for operating the Pan-pipes were demonstrated to the children by an adult human model a high number of children responded and all used the particular method shown. However when the children were shown the two methods through a ghost condition, whereby the pertinent parts of the apparatus were moved discretely with fishing-line by the experimenter, fewer children responded and only one of the children tested used the same method as that demonstrated. A fifth group of children acted as controls and were presented with the Pan-pipes with no formal demonstration. Significantly fewer children were able to operate the apparatus after a ghost condition than full demonstration by a human, suggesting the importance of social learning through imitation rather than emulation. A second experiment extended on the human demonstrations of the first experiment by investigating how the use of the Pan-pipes spreads among children along a diffusion chain. When a chain was seeded with a child taught to use Lift, there was no corruption of this method shown by the consecutive nineteen children, with none

discovering alternative methods. The results are discussed with a view to the wider perspective of human culture.

5.1 Introduction

There has long been an interest in the social learning processes shown by children and infants (Piaget 1962) and many of these early investigations concluded that children are primarily imitators (see Meltzoff & Moore 1977; Zentall & Galef 1988; Bornstein & Bruner 1989; Meltzoff & Prinz 2002; Want & Harris 2002). Want & Harris concluded from a comprehensive review that human children develop from using mimicry, to the ability to imitate and emulate the results of the action ('goal emulation') and then finally to emulate in the sense of learning about using the affordances of the objects. Indeed, Want & Harris stated that children between the ages of 18-months to 4-years-old are characterised by their use of imitation, which is in accordance with the findings of Horner & Whiten (2005).

In response to Want & Harris (2002), Bauer & Kleinknecht (2002) were critical of their conclusion. Bauer & Kleinknecht cited Bauer's (1992) finding that 20-month old children simultaneously used imitation *and* emulation suggesting that this linear development of social learning forms was restrictive in its simplistic outline. More recently, other studies have suggested that children are capable of using both imitation and emulation depending on the circumstances or difficulty of the task (Gergely *et al.* 2002; Biro *et al.* in press).

Carpenter & Call (2002), also in response to the review of Want & Harris (2002), offered a new approach for describing the behaviour of children in response to

observing a demonstration, through detailing the sources of information to which children paid attention, namely actions, results and goals. These three ‘elements’ could then be applied to the conventionally used terms of mimicry, emulation, goal emulation and imitation. Ultimately, Carpenter & Call believed that considering children merely with reference to their documented imitating and mimicking abilities was limited, and a child’s ability to engage in emulation of results and/or goals should also be noted when trying to dissect and describe their behaviour and learning processes.

These findings and proposed theories for describing social learning among children therefore still require further investigation. One method previously employed to untangle what children pay attention to when observing a demonstration is that of the ghost method detailed previously in *Chapter 4*. To date, two studies have been published which have used the ghost method with children, to determine whether they are capable of emulative learning (Thompson & Russell 2004; Tennie *et al.* 2006). These studies were designed to ascertain whether the children were capable of replicating an action on an apparatus after seeing only the pertinent parts of the device move (made to happen by remote control), thus revealing its ‘affordances’ (Klein & Zentall 2003). The studies of both Thompson & Russell and Tennie *et al.* found evidence that children were able to learn from, and replicate, object movements displayed only in a ghost ‘demonstration’.

Thompson & Russell (2004) used the ghost method to compare emulation and imitation in the observational learning of young children whilst also considering the role of mimicking and stimulus enhancement. To recap and extend upon the description in *Chapter 2*, the study involved the use of two conditions, the single-mat and double-mat, in which the children had to retrieve a toy, based on a methodology

of Frye (1991). In the single-mat condition, a toy was placed on a mat on a table in front of the child. The child had to push the mat away from themselves, which, as the result of a hidden mechanism, caused the toy to move forwards, towards the child. In the double-mat condition, two mats were on the table, with a toy on one of them. To gain the toy in this context the child had to pull the mat *without* the toy on it, towards them, which also caused the mat with the toy on it to move forwards.

These two methods were demonstrated either by an adult human, or through a ghost demonstration via the use of a hidden mechanism which made the mats move automatically. As may be expected, Thompson & Russell (2004) reported that, for both conditions, providing a human demonstration resulted in more successful retrievals of the toy than during a baseline in which no demonstration was provided. Secondly, and perhaps more surprisingly, the ghost demonstration of the single-mat task also resulted in more retrievals of the toy not only compared to baseline, but also compared to the human demonstration, although the same was not true for the double-mat task. Thompson & Russell concluded that the ghost demonstration was not successful for the double-mat task because this test “did not present a single, unambiguous, movement...(and did) not show a unique contingency between pulling the empty mat and the toy coming within reach” unlike the single-mat task (p. 886).

Tennie *et al.* (2006; detailed in *Chapter 2*) presented 12-, 18- and 24-month-old children with a box based on the design of Bugnyar & Huber (1997). It had an opaque door on hinges which could either be pulled out toward the operator, or pushed inward, to retrieve the reward inside. The children were provided with a demonstration of either method by an adult human, or by a ghost demonstration in which the door was moved discretely by the experimenter using fishing line. It was found that, unlike the non-human ape species studied with the same paradigm,

children aged 18-months-old and those aged 24-months-old matched the human demonstration, while 12-month-old children did not. However, only those children aged 24-months-old matched the ghost demonstration.

Thus both Tennie *et al.* (2006) and Thompson & Russell (2004) have demonstrated that young children are able to learn from these ghost demonstrations. However, the results of Tennie *et al.* suggest that only older children, aged 24-months-old, are able to do so. This is in contrast to Thompson & Russell. They tested two groups of children; those aged 14- to 20-months-old and those aged over 20- to 26-months-old. No age effect was found across conditions, so analysis was conducted on all the children's data collapsed. The children used in the present study will constitute an older age category with the children twice the age of those successful in Tennie *et al.*'s study (mean age was 49-months-old) with the outcome predicted by these earlier studies that they should learn from a ghost demonstration.

The apparatus employed by Thompson and Russell (2004) was of a counterintuitive nature. Although it provided some positive support for the use of ghost conditions with young children, it does not reflect everyday scenarios with which children may be faced. Additionally, neither that study, nor that of Tennie *et al.* (2006) employed a task in which a tool was required to achieve the final goal. One of the main lessons drawn by Want and Harris (2002) from their review was the lack of information gathered about how children learn to use tools. The aim of the present study is to address this omission whilst also addressing the deeper-level question of whether children are capable of emulative as well as imitative learning in such situations. The apparatus selected for such analysis is the same Pan-pipes that has been used with chimpanzees (Whiten *et al.* 2005; Hopper *et al.* 2007) both in open diffusion experiments (*Chapter 3*), individual learning tests and ghost conditions

(*Chapter 4*). This will allow for comparisons to be drawn about the learning strategies of the two species.

One limitation of these previously described studies is that they have focused only on dyadic learning scenarios and often with an (unfamiliar) adult as the demonstrator. However many common day-to-day learning experiences of children revolve around their interactions with other children; either siblings or peers at nursery. Such horizontal transmission was tested by Hanna & Meltzoff (1993), who showed that peers represent reliable models for fellow children. More recently, this paradigm has been extended by comparative psychologists employing a method of 'serial reproduction' born from the early work of Bartlett (1932, Bangerter 2000; Kashima 2000; Mesoudi & Whiten 2004). This paradigm, termed here, and by other comparative psychologists, as a 'diffusion chain', is analogous to the parlor game 'Chinese Whispers' as described in *Chapter 1*. Such a method has high ecological validity, relating more readily to the processes involved in real-life situations whereby information spreads throughout a community.

It is only within the last few years that this diffusion chain method has been applied to the study of social learning among children, as its use was pioneered by Curio *et al.* (1978) investigating mobbing behaviour of blackbirds. Curio *et al.*, as with more recent experiments following this method, wished to determine whether, and how rapidly, information would degrade when transmitted between subjects in such a chain. This early study determined that the information did not diminish across the chain of six birds.

Such a diffusion chain has also been used when investigating social learning among chimpanzees by Horner *et al.* (2006), who wished to determine how learning spread in a previously tested open diffusion paradigm (Whiten *et al.* 2005), and also

to simulate intergenerational transmission observed in the wild. Unlike the earlier work of Curio *et al.* (1978), Horner *et al.* seeded two chains, each with one of the two methods used to operate a two-action task. A third control group of chimpanzees was also presented with the apparatus and provided with no information. The two methods spread along the diffusion chains with high fidelity, which must be attributed to social learning. This conclusion is reinforced by the failure of all control chimpanzees to operate the task.

Recently, diffusion chains have been used when studying human children (Horner *et al.* 2006; Flynn & Whiten in press; Whiten *et al.* under review) and adults (Mesoudi & Whiten 2004). Mesoudi & Whiten concluded that the results of such a transmission process illustrated “the value of the transmission chain method over standard single generation memory experiments, and confirms that the effect is genuinely 'cultural' ” (p. 18).

The second experiment presented here will allow for an extension of previous social learning studies of tool-using tasks by children through the use of a diffusion chain paradigm. Additionally, such a method allows one to identify if, and when, corruption occurs in this learning process. Further, the children will also be presented with the same tool-use task in a diffusion chain experimental design, to determine whether the observational learning employed by children to learn new tasks is robust enough for the transmission of such a skill between multiple children, as might occur in real life, or whether it is open to corruption.

Experiment 5.1: Observational learning among children

5.2 Method

a. Experimental design

Subjects	48 children
Apparatus	Pan-pipes (two-action task)
Conditions	2 dyadic child demonstrations: 1. Lift (n = 10) 2. Poke (n = 10) 2 individual ghost conditions: 1. Lift (n = 10) 2. Poke (n = 10) No-information control (n = 8)
Independent variable	1. Method demonstrated 2. Form of demonstration
Dependent variable	Ability of observing children to use Pan-pipes Method used by children

b. Participants

Forty-eight children (20 females and 28 males) with an age range 3 yrs 3 mo – 4 yrs 10 mo (mean age = 4 yrs 1 mo) were recruited from three nursery schools in Fife, Scotland. Table 5.1 provides full demographic details for the participants. Children were tested in rooms familiar to them at their nursery school.

c. Apparatus

The two-action Pan-pipes apparatus (Whiten *et al.* 2005) was used in this study (for a detailed description see *Chapter 3* Figure 3.2). When the chimpanzees were tested the Pan-pipes were set on the outside of the chimpanzees' caging and so could only be accessed through the use of the rod-tool, and not directly by touch. To replicate this as closely as possible with the children, the Pan-pipes were set within a clear acrylic box (Figure 5.1a) so that the children could not touch the Pan-pipes directly. Fifteen access-holes arranged in a grid on the front panel of this box (Figure 5.1b) allowed for the rod-tool to be inserted through and operate the Pan-pipes, thus simulating the chimpanzees' caging.

Demonstration Lift	Demonstration Poke	Ghost condition Lift	Ghost condition Poke	Control
HD (F, 4yr 9mo)	LD (F, 4yr 8mo)	BS (F, 4yr 2mo)	LT (F, 4yr 10mo)	LB (F, 3yr 9mo)
EC (F, 4yr 5mo)	CB (F, 4yr 6mo)	EM (F, 4yr 0mo)	KT (F, 4yr 5mo)	JC (M, 4yr 10mo)
DB (F, 4yr 3mo)	NR (F, 4yr 3mo)	SH (F, 3yr 7mo)	TT (F, 4yr 5mo)	JA (M, 4yr 6mo)
SM (F, 3yr 6mo)	KC (F, 4yr 2mo)	SG (F, 3yr 3mo)	RC (F, 4yr 0 mo)	FI (M, 4yr 6mo)
JP (M, 4yr 3mo)	NH (F, 3yr 9mo)	AF (M, 4yr 4mo)	IM (F, 3yr 9mo)	HW (M, 4yr 3mo)
AB (M, 4yr 3mo)	DH (F, 3yr 5mo)	PP (M, 4yr 4mo)	JC (M, 4yr 10mo)	DC (M, 3yr 8mo)
MM (M, 4yr 0mo)	KC (M, 4yr 8mo)	OG (M, 4yr 3mo)	TD (M, 4yr 8mo)	VI (M, 3yr 6mo)
MS (M, 3yr 11mo)	EF (M, 4yr 4mo)	BL (M, 4yr 3mo)	RO (M, 4yr 8mo)	RR (M, 3yr 6mo)
RW (M, 3yr 9mo)	SG (M, 4yr 3mo)	MP (M, 3yr 11mo)	RC (M, 4yr 0mo)	
OG (M, 3yr 8mo)	JR (M, 4yr 2mo)	CS (M, 3yr 9mo)	JS (M, 3yr 6mo)	

Table 5.1. Demographics of the children tested in each experimental condition and the control. Each ID code is followed by sex and age (years and months).

d. Procedure

Forty children were randomly assigned to one of four experimental conditions, detailed below with ten children per condition. A further eight acted as controls. For all conditions, the reward used was a small plastic egg-shaped capsule containing a sticker.

(i) Demonstration 'Lift'

The child was asked to sit in a chair in front of the Pan-pipes and was told by the experimenter (LMH) "I am going to have a go, and then you can have a go". Then the experimenter inserted one end of the rod-tool through hole B2 at the front of the clear box (Figure 5.1b). This allowed the experiment to use the Lift method (see the Methods in *Chapter 3*). After the reward emerged, it was shown to the child but not given to them. Once the experimenter had done Lift 15 times the rod-tool was lain on the table in front of the Pan-pipes. The experimenter then told the child that it was their turn by saying "Now you can have a go, you can touch anything on the table".

a



b

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

Figure 5.1. The plastic box encasing the Pan-pipes used when testing children. (a) The Pan-pipes in the box viewed from the front, showing the rod-tool inserted through hole B2 and (b) the grid of access-holes, showing the codes used for each hole. The hole through which the rod-tool was inserted to demonstrate Lift, being the most efficacious for this, was B2 while hole D2 was used for demonstrating the Poke method.

(ii) Demonstration 'Poke'

The procedure as for 'Demonstration Lift' was conducted but instead of doing Lift, the experimenter (LMH) did Poke, all other factors remained the same.

(iii) Ghost condition 'Lift'

Prior to the child entering the testing room, a length of fishing line was tied to the top of the T-bar. Once the child entered the room they were asked to sit in a chair in front of the Pan-pipes. The experimenter (LMH) stood behind the Pan-pipes and discretely raised and lowered the T-bar using the length of fishing line. As the T-bar was raised, it released the reward from the Pan-pipes. Each time, the experimenter showed the child the reward but did not let them keep it. Throughout the demonstration the rod-tool was lain on the table in front of the Pan-pipes in full view of the child. Once this action had been completed 15 times, the fishing line was removed from the T-bar. The child was then told: "Now you can have a go, you can touch anything on the table".

(iv) Ghost condition 'Poke'

The procedure for 'Ghost condition Lift' was followed, as above, but instead of raising and lowering the T-bar, the experimenter (LMH) stood behind the Pan-pipes and discretely pulled back the fishing line which in turn caused the T-bar to move back. As the T-bar was moved back, it also forced the reward back, releasing it.

(v) Free-access test period

After each of these conditions, the children were given a free-access test period during which they could interact with the Pan-pipes and rod-tool freely. This lasted for 5 minutes or until the child had completed 15 successful operations of the Pan-pipes (regardless of the method used). An interaction was deemed successful when the child used the rod-tool to retrieve the reward from the Pan-pipes. The children were allowed to keep all the stickers that they were able to obtain. If after one minute the child had not acted on the Pan-pipes or rod-tool they were given the prompt “You can do anything you want, you cannot break it”. However if after a further four minutes the child had still not been able to get the reward from the Pan-pipes, they were classed as ‘unable to solve the task’.

(vi) Control

In the Control, the child was asked to sit in front of the Pan-pipes on a chair as in the four experimental conditions. The rod-tool was placed on the table in front of the Pan-pipes in full view of the child. The child was then told: “You can do anything you want, you can touch anything on the table, you cannot break it”. If after one minute the child had not got the reward from the Pan-pipes the same verbal prompt was repeated. The Control lasted for five minutes or until the child had completed 15 successful interactions with the Pan-pipes, using either method.

e. Coding

All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). To complement the video footage, a running commentary on the actions of the child operating the Pan-pipes was provided by the experimenter (LMH). The children's actions were coded from the videotape (Table 5.2) using codes adapted from those used for the chimpanzees (*Chapters 3* Table 3.2).

Action Code	Action Name	Definition
P	Poke	Insert rod-tool through flap door into top pipe, pushing blockage completely backwards; reward released and gained
L	Lift	Place rod-tool under T-bar to raise T-bar (and blockage); reward released and gained
PSlide	Push-slide	Push T-bar (and blockage) completely backwards using rod-tool; reward released and gained
ITP	Insert tool Poke	Insert rod-tool into the top hole, as for P, but not far enough to release reward
ITL	Insert tool Lift	Place the rod-tool under the T-bar, as for L, but fail to raise it sufficiently to allow a reward to be released
BOTTOM	Insert tool bottom	Insert the rod-tool into the bottom (food exit) hole. No reward gained
H	Hit	Make contact between the rod-tool and other part of the Pan-pipes including food chute, sides of the Pan-pipes and table; no reward gained
TFC	Touch food chute	Make contact with food chute with either hand or rod-tool
TT	Touch tool	Make contact with tool with either hand, mouth or foot

Table 5.2 Coding categories applied to videotape analysis

5.3 Results

Although the rule was set to end the free-access period and Control condition when the child had made 15 successful responses, or after 5 minutes if the child had made no interaction with the apparatus, some children, even if able to successfully operate the Pan-pipes, were unwilling to use it the requisite 15 times. To prevent undue stress to such children they were not made to continue if they did not want to, hence some children's responses are under 15 (Figure 5.2).

a. Overall success

Of the 48 children tested in all four experimental conditions and the Control, 29 were able to successfully operate the Pan-pipes and retrieve a reward using either Lift, Poke or the Push-slide method. Of those children who were unsuccessful in the Demonstration conditions, all interacted in some way with the Pan-pipes, mostly either doing 'Insert tool Lift' or 'Insert tool Poke' (Figure 5.2a, b). In the Ghost conditions, only three of the eleven children unable to solve the task made no action on it. The remaining unsuccessful children either did 'Insert tool Lift' or 'Insert tool Poke' (Figure 5.2c, d) but the majority did 'Insert tool Bottom'. In the Control, only one of the five children unable to operate the Pan-pipes performed no action on it and those that did so, mainly did 'Insert tool Bottom'.

(i) Success in the Demonstration conditions compared to the Control

Nine of the ten children tested in the Demonstration Lift condition acted on the Pan-pipes and they did so successfully and unanimously using Lift. Likewise, eight of the ten children tested in the Demonstration Poke condition acted on the Pan-pipes, all using Poke (Figure 5.2a, b). In contrast, only three of the eight children in the Control group operated the Pan-pipes successfully with one of them using Lift, and the remaining two using Poke (Figure 5.2e). Regardless of method used, significantly more children in the Demonstration Lift group were successful, than in the Control (Fisher's Exact test: $P \leq 0.05$). In contrast, there was no significant difference between the number of children who made successful responses in the Demonstration Poke condition compared to those in the Control (Fisher's Exact test: $P \geq 0.05$). Overall, there was a significantly higher proportion children able to operate the Pan-pipes in both the demonstration conditions combined (17 children) compared to the Control (Fisher's Exact test: $P \leq 0.05$).

(ii) Success in the Ghost conditions compared to the Demonstration conditions

Seven children in the Ghost condition Lift made one or more successful operations on the Pan-pipes (see Figure 5.2c). Regardless of method used, there was no significant difference in the number of children who successfully operated the Pan-pipes in the Ghost condition Lift compared to Demonstration Lift (Fisher's Exact test: $P \geq 0.05$). In contrast, only two children in the Ghost condition Poke made one or more successful actions on the Pan-pipes (see Figure 5.2d), which was significantly fewer

than the number of successful children in the Demonstration Poke group (Fisher's Exact test: $P \leq 0.05$). When the two Ghost conditions are collapsed, it is found that significantly more children were successful in the demonstration conditions compared to the ghost conditions (Fisher's Exact test: $P \leq 0.05$). It should further be noted that the children failed to comment on, or show overt interest, in the fishing line used in the ghost conditions to move the block.

(iii) Success in the Ghost conditions compared to the Control

The number of children who were successful in the Ghost condition Lift was no greater than in the Control (Fisher's Exact test: $P \geq 0.05$). Nor was there a significant difference in the number of successful children in the Ghost condition Poke compared to the Control (Fisher's Exact test: $P \geq 0.05$). When collapsed, the children in the ghost conditions show no significantly greater level of success than those in the Control (Fisher's Exact test: $P \geq 0.05$).

b. Level of matching

(i) The Demonstration conditions compared

As each child in the Demonstration groups responded with either Lift or Poke responses, but never both, each child could be classed as a 'lifter' or 'poker'. In the

Demonstration Lift condition there were significantly more lifters than pokers (binomial test: $P \leq 0.01$) and in the Demonstration Poke condition there were significantly more pokers than lifters (binomial test: $P \leq 0.01$).

(ii) The Demonstration conditions compared to the Control

Significantly more children in the Demonstration Lift group used Lift than did children in the Control (Fisher's Exact test: $P \leq 0.01$). Similarly, significantly more children in the Demonstration Poke group used Poke compared to those in the Control (Fisher's Exact test: $P \leq 0.05$).

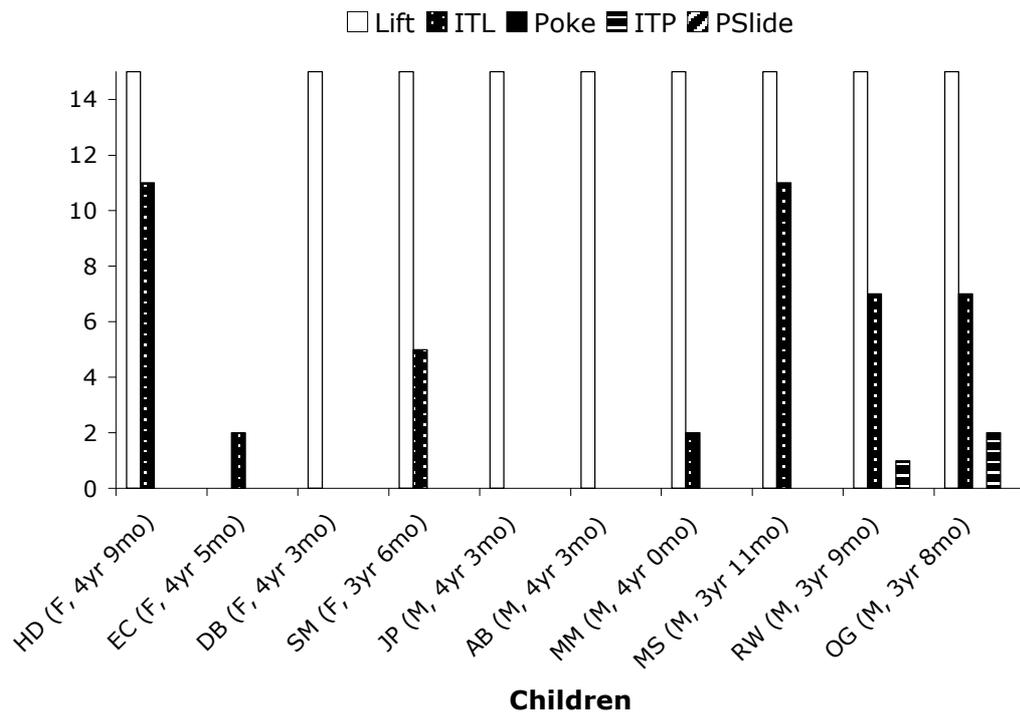
(iii) The Ghost and Demonstration conditions compared

Only one of the seven children who made a successful operation with the Pan-pipes in the Ghost Lift condition used Lift. Significantly more children used Lift in the Demonstration Lift group than in the Ghost condition Lift (Fisher's Exact test: $P \leq 0.001$). None of the successful children in the Ghost condition Poke used Poke, they both used Push-Slide. Of these successful children, significantly more used Poke in the Demonstration Poke group than in the Ghost Condition Poke (Fisher's Exact test: $P \leq 0.05$). When considered as a whole, there was significantly more matching in the demonstration conditions compared to the ghost conditions (Fisher's Exact test: $P \leq 0.05$).

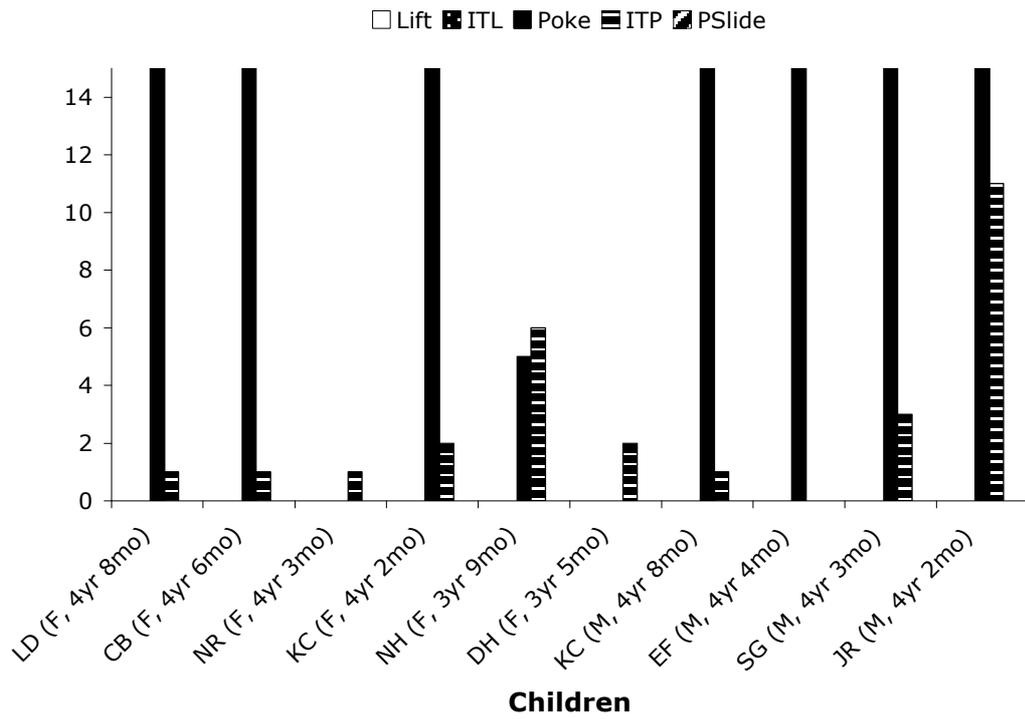
(iv) *The Ghost conditions compared to the Control*

There was no significant difference in the proportion of children who used Lift in the Ghost condition Lift compared to the Control (Fisher's Exact test: $P \geq 0.05$) and nor was there a significant difference in the proportion of children who used Poke between the Ghost condition Poke and the Control (Fisher's Exact test: $P \geq 0.05$).

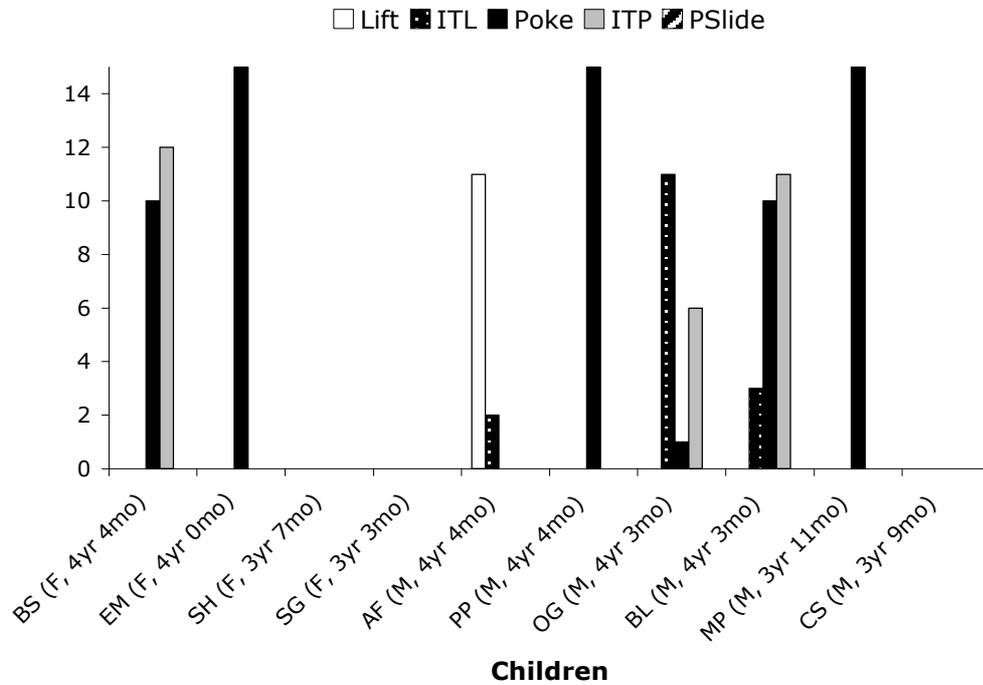
a Lift



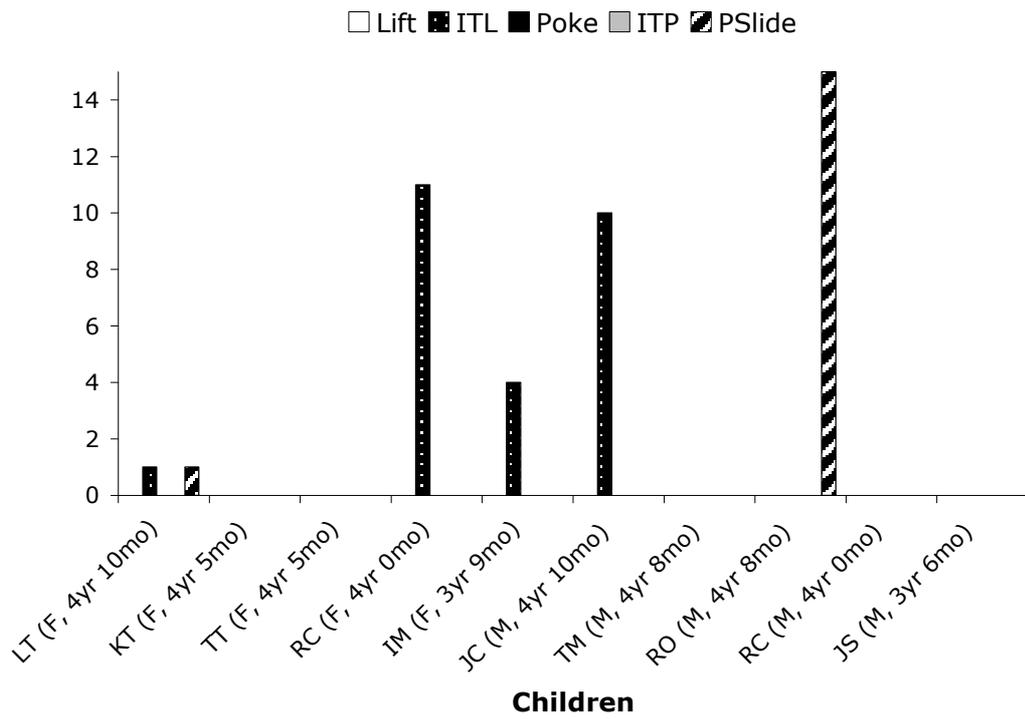
b Poke



C Ghost Lift



d Ghost Poke



e Control

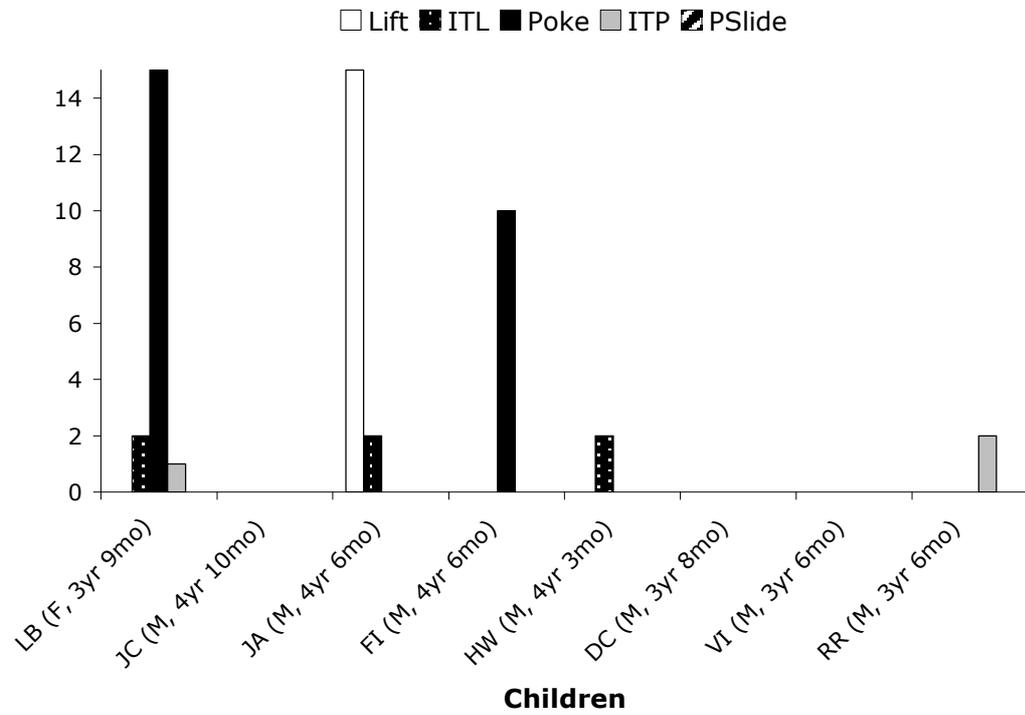


Figure 5.2 (Including the previous two pages) The number of responses made by the children in each of the four experimental conditions and the control. The responses shown are for (a) Demonstration Lift, (b) Demonstration Poke, (c) Ghost condition Lift, (d) Ghost condition Poke and (e) Control. Each child ID code (Table 5.1) is followed by sex and age (years and months). For clarity, the categories of responses made by the children are a reduced selection from those listed in Table 5.2.

5.4 Discussion of Experiment 5.1

When the children were presented with a full demonstration, by an adult, of either Lift or Poke, 17 of the 20 children (85%) successfully operated the Pan-pipes during the free-access period. Not only did a high proportion of children retrieve the reward in the Demonstration Lift and Poke conditions, but all the children that responded used the same method as that which they saw demonstrated.

Overall, there were more children able to retrieve the reward from the Pan-pipes, regardless of method used, after having seen an adult demonstration compared to those in the Ghost conditions. However, there was no significant difference between the number of children able to successfully operate the Pan-pipes, regardless of the method that they used, between Ghost condition Lift and the Demonstration Lift conditions.

The high fidelity of matching to the adult demonstrations contrasts with the responses shown by children in the two Ghost conditions. One child used Lift in the Ghost condition Lift, but none of the children used Poke in the Ghost condition Poke. Such a finding reflects the conclusion of Bellagamba & Tomasello (1999) who, after presenting young infants with either the end-states of a task or showing a model's intentions, concluded that infants "have a stronger tendency to imitate human

intentional actions (imitative learning) than to reproduce interesting changes of states in objects in the absence of human behavior (emulation learning)” (p. 281).

However, the stark contrast between the two forms of demonstration seems at odds with the study of Tennie *et al.* (2006) who found that 24-month-old (but not 12- or 18-month-old) children matched a ghost demonstration of a two-action task. Such a finding suggests that older children show emulative learning, unlike younger ones, which parallels the conclusions of Want & Harris (2002). However the children tested in the study presented here were 49-months-old on average, so the age of children does not appear to provide an explanation of the differences in responses of the children tested here and by Tennie *et al.*.

The reasoning provided by Thompson & Russell (2004) for their positive ghost condition responses in 14- to 26-month-olds, however, may provide an insight into the findings of the present study. Thompson & Russell concluded that the reason the ghost condition was effective for the single-mat task was because the action was ‘counterintuitive’, whereas the double-mat task, for which a ghost demonstration was insufficient, did not result in a single, unambiguous, movement (both mats moved simultaneously). The Pan-pipes, when shown with a ghost demonstration, may have also proved confusing or insufficiently informative for the observing child. For example, when Poke was done, the child observed the T-bar moving backwards, but there is more than one way that this can be achieved, as shown by the two children who reproduced this movement through employing the Push-slide method (Table 5.2), rather than Poke. Such a conclusion is consistent with that of Call *et al.* (2005) who stated that young children were likely to use information about someone’s actions rather than the results of a task. This experiment suggests that the demonstration provided by another person was more salient to the children than

seeing purely the movement of the apparatus, in that not only did more children respond in the Demonstration conditions compared to the Ghost conditions, they also were more likely to match what they had seen.

The findings of this current study raise more questions to be answered, namely about the amount, and form, of information provided to the child in the ghost condition. Further experiments could help clarify the findings presented here. One such experiment would be to conduct a further ghost condition with the Pan-pipes, but including the tool in the presentation. Secondly, just the 'end-states' of the Pan-pipes could be shown to the children (Bellagamba & Tomasello 1999). Thirdly, a more radical step would be to create a new apparatus, the mechanism of which would be simpler and more transparent for use with ghost conditions.

The two successful children in the Ghost Poke condition retrieved the reward from the Pan-pipes through the use of the Push-slide method rather than Poke. These children had not seen how the tool could be inserted into the front of the Pan-pipes to push the blockage backwards to release the reward. For the chimpanzees (*Chapter 4*), including a tool in the ghost conditions had no effect on the chimpanzees' ability to operate the Pan-pipes. However the reaction of chimpanzees cannot be used as a basis for ascertaining how children would react and so a future experiment, which included a tool in the ghost condition, would be instructive to run.

The second proposed extension that could be conducted would be to show only the end-states of the Pan-pipes, both for the Lift and Poke methods. For Lift, the T-bar could be suspended in the final 'raised' position, while for Poke, the T-bar could be placed at the far end of the upper pipe as if fully pushed back by the tool. Such end-state work has previously been pursued with younger children by Bellagamba & Tomasello (1999) whose conclusions were noted above. Such an additional condition

to this experiment would potentially elucidate what information the children can learn from.

A final possible extension would be to provide further ghost conditions to children but employing simpler apparatus with more explicit movements, perhaps without the use of a tool, as done previously with children by Thompson & Russell (2004) and Tennie *et al.* (2006). To pursue this, a replication of Klein & Zentall (2003) was conducted with children of a similar age to those tested in this study (see *Chapter 7*). This employs a simple bidirectional task more comparable to that of Tennie *et al.* The ghost conditions provided in this present study of the Pan-pipes did not incorporate the rod-tool. Additionally, because of the presence of the plastic box which encased the Pan-pipes (Figure 5.1), it would have been a practical difficulty to have included the rod-tool in the ghost demonstrations. It seems however, especially for the Ghost condition Poke, that the information provided was insufficient for the children to solve the task and this is a further reason why a ghost condition should be conducted of a simple, non-tool-use task (*Chapter 7*).

Emulation: working definitions

These proposed extensions all serve one end; to pinpoint what form of information the children can learn from by their responses. The ghost conditions conducted here, and also described further in *Chapters 6* and *7*, aim to determine whether children are capable of emulation learning. Emulation has been used to describe a wide variety of behavioural responses (Byrne 2002a), which may cause confusion. To delineate these,

and to provide clearer working definitions of emulation, a number of subcategories are proposed here.

(i) Level 1: 'Goal' or 'end-state' emulation

Tomasello (1990) introduced a concept of emulation, based on that originally described by Wood (1989) who stated that an individual achieves the same goal as a model, but through their own means. Tomasello was clear to note that the observer did not attempt to reproduce the specific behaviour of the individual that they watched and wrote:

“A focus on the demonstrator's goal may lead the observer to be attracted to, and seek to attain, the goal...The observer may attempt to “emulate” the demonstrator's behavior, that is, to reproduce the completed goal by whatever means it may devise” (p. 284)

In their proposed social learning distinctions, Whiten & Ham (1992) thus termed emulation as the more specific ‘goal emulation’, reflecting Tomasello’s (1990) definition of emulation. More recently, Whiten *et al.* (2004) reformulated goal-emulation to consider ‘end-state emulation’ as encompassing the reproduction of either observable results *or* inferred goals (see Gattis 2002 for a comment on results *vs.* goals). Whiten *et al.* noted that although the specific behaviour was not matched in end-state emulation a form of *copying* was still involved (copying of the end-state).

They therefore classed end-state emulation, object movement reenactment (OMR) and imitation all as forms of ‘copying’.

‘Level 1 emulation’ therefore encompasses all these proposed definitions (Wood 1989; Tomasello 1990; Whiten *et al.* 2004) and represents the most basic form of emulation. In Level 1 emulation the end-state of the target behaviour is replicated, but not necessarily through the same means as that used by the model.

(i) Level 2: ‘Global’ emulation

Byrne (2002a) recognized four potential meanings for the term emulation, the first of these being ‘goal emulation’ (discussed in Level 1 emulation). The remaining three connotations are; that an individual (i) learns about the physical properties of objects, (ii) learns the relationships among objects and (iii) gains an understanding of the cause-and-effect relationships and changes of state of objects.

These definitions of emulation are considered here as ‘Level 2 emulation’. The properties of emulation detailed by Byrne (2002a) all refer to the learnt affordances of the object from the observation of another interacting with it, and so can be related to affordance learning (*Chapter 1*).

The rationale underlying Level 2 emulation could be considered in parallel with that of various ghost conditions (Thompson & Russell 2004; Tennie *et al.* 2006; Hopper *et al.* 2007). In a ghost condition the affordances and movements of an apparatus are displayed to an observer to ascertain whether they can achieve the same result by reproducing the movements of the apparatus.

(iii) Level 3: 'Specific' emulation

The final proposed sub-level of emulation, 'Level 3 emulation', refers to a more specific reproduction of environmental changes that do not involve the physical movements of a live model. This definition has similarities with Whiten *et al.*'s (2004) definition of OMR, which they described as "copying what the object does" (p. 39). However their definition of OMR implies the presence of a live model, which is not required in this definition of Level 3 emulation.

The ghost condition conducted by Klein & Zentall (2003) provides a perfect example of Level 3 emulation. In the experiment pigeons were presented with a screen-door that could be slid simply to either the left or right to reveal a food reward. Klein & Zentall presented the pigeons with one of four conditions, two of which are of interest here (see *Chapters 6* and *7* for a more detailed description). The first condition of note was a demonstration of either push-left or push-right by a conspecific (demonstration condition), while in the second, the observing pigeon saw the door move to either the left or right as it was pulled discretely by the experimenter using fishing-line (ghost condition).

Klein & Zentall (2003) were interested in whether the pigeons would push the door in the same direction as that which they had seen in the experimental conditions. The pigeons matched in the demonstration condition which Klein & Zentall concluded was evidence of imitation. In the ghost condition, the observers also matched. Klein & Zentall concluded that the pigeons were capable of 'affordance learning'. Under the proposed terminology, the matching responses by the pigeons in the ghost condition represent Level 3 emulation as not only did the pigeons learn that the- door *slid*, but they also reproduced the specific *direction* in which it had.

Suppose the pigeons in the ghost condition had slid the door significantly more than pigeons in a control group but had not necessarily used the same direction as that seen in the experimental condition. Using the proposed terminology, such a response would represent Level 2 emulation because the pigeons had clearly learnt something about the door from the ‘demonstration’ (that it *slid*), but not necessarily that it slid in a specific direction. This is distinct from Level 1 emulation because the pigeons had not used a novel behavioural strategy to gain the food reward behind the door that had been revealed to them.

To distinguish these three levels a new apparatus could be designed and this will be discussed in more depth in *Chapter 10*. The apparatus, as above, could be used if, as well as sliding to either the left or right, the door could also be hinged at the top so that it could be raised to gain the food reward. In addition to the conditions, and possible results described above, if the observers, having seen a model slide the door to the left, *raised* the door to gain the reward, then this would be suggestive of Level 1 emulation.

The children’s responses to the Ghost condition Lift and Poke with the Pan-pipes can also be classified with these proposed definitions. Although neither group showed significantly greater success than the controls, and thus no significant levels of emulation, their responses are still worth discussing here to demonstrate how they would be interpreted using the proposed terminology.

In the Ghost condition Lift, six of the seven successful children used Poke to gain the reward, as they used their own method to achieve the same goal, this could be termed Level 1 emulation. In contrast, the responses of the children in the Ghost

condition Poke are more difficult to interpret. Neither of the two successful children in this condition used Poke, they both used Push-slide. However, although this is a different method, one should not be hasty in also terming this Level 1 emulation. In both Poke and Push-slide the T-bar moves up the top pipe, away from the child, releasing the reward. As no tool was provided in the demonstration, the children would have been unable discriminate options Poke versus Push-slide, but they still learnt about the affordances of the block and T-bar, namely that it could move backwards up the pipe. Under the proposed definitions, the responses of the children in the Ghost condition Poke should therefore be classed as Level 2 emulation.

Experiment 5.2: The Pan-pipes Diffusion Chain

The children in Experiment 5.1 were typically able to match the demonstration of the Pan-pipes having observed a live adult human model but did not match what they saw in a comparable ghost condition. This second experiment was run in order to determine whether this high fidelity of matching to a live demonstrator would be maintained, over time, along a diffusion chain.

5.5 Methods

a. Experimental design

Subjects	20 children
Apparatus	Pan-pipes (two-action task)
Conditions	Diffusion chain seeded with Lift (n = 20)
Independent variable	Method seeded (Lift)
Dependent variable	Method selected by subsequent children to use the Pan-pipes

b. Participants

20 children (14 females and 6 males) with an age range 3 yrs 6 mo – 4 yrs 10 mo (mean age = 3 yrs 7 mo) were recruited from a nursery school in Fife, Scotland. Table 5.3 provides full demographic details for the participants. Children were tested in a room familiar to them at their nursery school.

c. Apparatus

The apparatus used was the two-action Pan-pipes as described for Experiment 5.1 of this chapter, encased in the same clear acrylic box. The reward, a sticker in a small plastic capsule, was also the same as that used in Experiment 5.1.

Place in chain	Child ID
A	JN (F, 4yr 9mo)
B	CB (M, 4yr 8mo)
C	CM (F, 4yr 3mo)
D	EP (F, 3yr 6mo)
E	CT (M, 3yr 11mo)
F	LT (F, 3yr 6mo)
G	DB (F, 3yr 7mo)
H	HL (F, 4yr 3mo)
I	KD (F, 4yr 0mo)
J	GK (M, 4yr 2mo)
↓	K* (F, 3yr 7mo)
L	IS (F, 4yr 9mo)
M	CM (F, 4yr 3mo)
N	AS (F, 4yr 5mo)
O	CP (F, 3yr 11mo)
P	RH (M, 4yr 10mo)
Q	NT (F, 3yr 7 mo)
R	JT (M, 4yr 10mo)
S	SC (F, 3yr 8mo)
T	NI (M, 3yr 10mo)

* Child K (ND) was the only child who, although they operated the Pan-pipes successfully using Lift in their response period, was unwilling to act as a demonstrator to the next child in the diffusion chain (see 5.6 Results) and so child J acted as the demonstrator for child L.

Table 5.3. Demographics of the children tested in the diffusion chain. Each ID code is followed by sex and age (years and months). The children are listed in the order in which they participated in the diffusion chain.

d. Procedure

The experimental procedure employed in this experiment followed the diffusion chain design as described previously in the Introduction in which a child (A) proficient in using the Pan-pipes operate the Pan-pipes using Lift in the presence of a second child (B). Subsequently, child A was removed from the room and child B was then given the opportunity to use the Pan-pipes. When child B was able to operate the Pan-pipes they became the model as a third child (C) was brought into the room and allowed to watch child B. This same procedure was repeated, with child C becoming a model for

child D, and so on and so forth until all 20 children in the chain have observed a demonstration and had a go at operating the Pan-pipes.

For the diffusion chain that was conducted, Lift was selected as the method with which the chain would be seeded. This was because only one of the eight children in the Control group of the previous experiment (Experiment 5.1) discovered Lift by individual learning, so it was deemed the least likely that children would discover it by chance in the diffusion chain and that observational learning would be a more likely explanation if transmission were to be observed.

(i) Model (Child A) training

Each child (Table 5.3) was tested in a room familiar to them at their nursery school and asked to sit in a chair placed in front of a table on which the Pan-pipes were sat. The experimenter (LMH) then showed child A how to retrieve the reward from the Pan-pipes through the use of the Lift method, by inserting one end of the rod-tool through hole B2 at the front of the clear box (Figure 5.1). The experimenter then placed the rod-tool under the T-bar and raised it to release the reward (see *Chapter 3* for a more detailed description) in full view of the child. The reward was shown to the child and then placed back in the Pan-pipes. These demonstrations were repeated five times.

The child was then asked “Would you like a go?”. If the child agreed they were presented with the tool and the Pan-pipes re-baited with the reward. If the child was able to operate the Pan-pipes adeptly using Lift they were considered a suitable model to seed the diffusion chain. For every successful operation the child was allowed to

keep the sticker. If, however, the child was unable or unwilling to operate the Pan-pipes they were given a further five demonstrations as described. After these extra five demonstrations the child was again asked “Would you like a go?” and if they agreed they were allowed to use the Pan-pipes as previously. If the child was able to operate the Pan-pipes they then became the model for the chain, but if not, the child was thanked for taking part and another child was selected to seed the chain.

Once a child was trained to use the Pan-pipes using Lift they were deemed to be the model and the diffusion chain begun.

(ii) The diffusion chain

For each dyadic interaction there was an initial ‘demonstration period’. A second child (B) was brought into the testing room and asked to sit on a chair next to child A’s. The experimenter then told child B that “[appropriate child’s name here] is going to have fifteen goes at this new game and then you can have a go, OK?”. Child A was then given the rod-tool and told that they could have a go. Child A was allowed to operate the Pan-pipes 15 times using the Lift method, gaining a reward for each, all in full view of child B. At the end of this session the experimenter re-baited the Pan-pipes and placed the tool on the table then child A was removed from the room and returned to their classroom.

After this demonstration period, there was then a ‘response period’ during which the observing child was allowed to operate the Pan-pipes. The experimenter told child B “Now it’s your turn, you can have a go if you would like”. The child was allowed to have five uses of the Pan-pipes and was deemed proficient if they were able to

retrieve the reward on all five occasions, regardless of what method they used to do so.

If the observing child was deemed proficient, they became the demonstrator and entered the next demonstration period. At this point a third child (C) was brought into the room and child B operated the Pan-pipes 15 times in front of them as described above for child A and B. This continued until all 20 children had acted as ‘observer’ in a demonstration period and operated the Pan-pipes during a response period.

If, after one minute, the observing child (child B in this instance) had not interacted with the tool or Pan-pipes, the demonstrating child (child A here) was brought back into the room and allowed to operate the Pan-pipes a further five times and a second response period provided to the observing child (B). However if the observing child (B) was still unable or unwilling to operate the Pan-pipes then they were ‘skipped’ and the demonstrating child (A) was brought back to operate the Pan-pipes in front of a second child (C) and the chain would continue.

e. Coding

All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). To complement the video footage a running commentary was provided by the experimenter (LMH) on the actions of the child operating the Pan-pipes during both the demonstration and response periods. The children’s actions were coded from the videotape using codes adapted from those used for the chimpanzees (Table 5.2).

5.6 Results

Nineteen of the 20 children in the chain were able to operate the Pan-pipes having seen the demonstrating child operating the Pan-pipes using Lift 15 times during the demonstration period for their dyad. One child (Q) did not want to touch either the rod-tool or Pan-pipes during the first response period and so child P was brought back into the testing room to give a further five demonstrations. After this second demonstration period, child Q used the Lift method happily in her second response period. Secondly, another child (K), although able to operate the Pan-pipes using Lift in her response period, was unwilling to act as a model and operate the Pan-pipes in the presence of child L. Therefore child J became the model for child L.

Child K was unwilling to demonstrate the Pan-pipes but was still able to operate them during her response period. All analysis will be conducted on the method used by the children to operate the Pan-pipes during their response periods, rather than during their demonstration periods.

During the response periods, all 20 children used the same Lift method to operate the Pan-pipes with which the diffusion chain was seeded. In Experiment 5.1 only one of the eight children in the Control condition (who were provided with no information about the Pan-pipes) used the Lift method. Therefore, significantly more children used the lift method in the diffusion chain than in the Control (Fisher's Exact test: $P \leq 0.01$).

5.7 Discussion of Experiment 5.2

The findings reported suggest that children copy from their peers and that such high fidelity of matching was maintained so that the Lift method was transmitted down a series of 20 children. All the 20 children tested were able to operate the Pan-pipes after observing a fellow child demonstrate the Lift method, and all children used the same Lift method as that used by the child preceding them in the diffusion chain. This finding is important because although a few previous studies have shown transmission of a behaviour along a number of individuals tested in a diffusion chain (Curio *et al.* 1978; Mesoudi & Whiten 2004; Horner *et al.* 2006; Flynn & Whiten in press; Whiten *et al.* under review), none have shown such transmission across more than ten individuals, as this present study does. Diffusion chains have often been used to assess whether information degrades over multiple ‘generations’; perhaps surprisingly these previous studies, as well as the present one, suggest that this is not the case, even when, as with the current experiment, there were 20 children with 19 child-to-child transmissions. These impressive results should be regarded with care, however, as there was only a single experimental condition and the responses of the children were compared to those in a control condition of a former experiment. The former of these complaints is particularly detrimental as not only was only one of the two methods (Lift) tested, only one chain per condition was run too. Ideally, multiple chains of children should have been seeded with one of both methods and a further control group given access to the Pan-pipes.

Diffusion chain experiments are useful in helping to determine the longevity of a behaviour and also to look at the transmission process with more detail than can be learnt from merely conducting an open diffusion experiment (*Chapter 3*). In addition,

they allow for the study of inter-generational learning by simulating such dyadic interactions, without the time constraints which would result from observing such transmission across multiple human generations. However the limitation of the present design is that it can only provide information on horizontal transmission among peers. An extension to the presented study could therefore be to test individuals from extended families comprising of three or more extant generations (e.g. grandmother to mother to daughter). As human culture is assumed to be indebted to such transmission through imitation such paradigms are required to determine how such culture is sustained across many generations (Whiten *et al.* under review).

5.8 General discussion

The children tested in a series of experiments were able to learn how to retrieve the reward from the two-action Pan-pipes task after observing either an adult or fellow child model. Not only were these children able to operate the task but those that did, used the same method as that used by the model with 100% fidelity. The children tested in the first experiment (Experiment 5.1) were tested in dyads, while those in the second experiment (Experiment 5.2) maintained the use of the Lift method along a chain of 20 children, which involved 19 child-to-child transmissions, or ‘cultural generations’ (Flynn & Whiten in press).

In contrast to those children who observed a human model (whether adult or child), those tested in the ghost conditions (Experiment 5.1) were less likely to be able to operate the task than those who had observed an adult model. Additionally, there was no significant difference in the number of children able to operate the task in the

ghost conditions compared to those in the control. The one exception to this was the Ghost condition Lift, when there was no significant difference in the number of children able to operate the task compared to those in the Demonstration Lift. Overall, however, this finding is in contrast to the conclusion drawn by Want & Harris (2002) that older children favour the use of emulative, rather than imitative, learning, but is consistent with the conclusions of much research that children are primarily imitators, learning from the actions of a conspecific (Call *et al.* 2005; Nielson 2006; Whiten *et al.* 2006; Williamson & Markman 2006).

The reduced learning from the ghost conditions in Experiment 5.1, as discussed previously, could be attributed to the paucity of the information provided in the condition, and hence why a ghost-with-tool condition was suggested (see also *Chapter 4*). Indeed, as Bauer & Kleinknecht (2002) stated “...age alone does not determine whether children will evidence emulation. Rather, children can emulate novel causal sequences well before the age of 4, just so long as the task demands are manageable. In short, it appears that the learning strategy a young child is capable of using varies as a function of task demands, not age” (p. 19). It could be, therefore, that children of the age tested are quite capable of emulative learning, and responding to ghost demonstrations (Thompson & Russell 2004; Tennie *et al.* 2006) if tested with a more straightforward task. Indeed, this has been tested and the findings of this study are discussed in *Chapter 7*.

The children in the ghost conditions in Experiment 5.1 did show reduced learning compared to those in the demonstration conditions; however they were much more successful than the chimpanzees whose data are reported in *Chapter 4*. None of the 12 chimpanzees presented with a comparable ghost condition were able to operate the Pan-pipes and nor were the additional six in the ghost-with-tool condition. This

suggests that the children gleaned far more from the ghost conditions about the affordances of the task, than did the chimpanzees. This may seem contrary to the general conclusion that chimpanzees are more likely to emulate than children (Tomasello *et al.* 1987; Nagell *et al.* 1993; Horner & Whiten 2005). Following the framework for emulation terminology proposed in the discussion to Experiment 5.1 the children in the ghost conditions, although not significantly, showed behaviour suggestive of Level 1 and 2 emulation while the chimpanzees showed neither. However, as stated, the failure of both the chimpanzees and children may have been due to the complexity and validity of the task, rather than an inability of either species to show emulation learning.

The rich and complex nature of human culture results from cumulative transmission of information down generations (Boyd & Richerson 1996; Mesoudi *et al.* 2006; see also Kashima 2000). Castro & Toro (2004) stated further that this ‘cumulative inheritance system’ allows for the transmission of information and behaviours which could have positive, neutral or negative value to the species. Although the diffusion study described here does not test for a ratcheting effect of information which has ultimately allowed for the development of culture and traditions (Boesch & Tomasello 1998, but see Henrich & Boyd 2007; Henrich *et al.* 2007) such properties of transmission could only be feasible if the basic unit of information was maintained and passed on with high fidelity, as shown by the results of Experiment 5.2. The diffusion chain method described here could be developed and extended upon in future through the use of an apparatus which could have different methods for solving it which represent different levels of efficiency. The first child in the chain could be taught the most inefficient of the available methods and the chain could be run as described to determine whether children further along in

the chain would continue to use the original inefficient method or whether a corruption or development of the method would occur, leading to children further down the chain employing a new, and more efficient, method.

Similar diffusion chains to that run here with children, have been conducted with chimpanzees and other nonhuman animals. Horner *et al.* (2006) conducted a diffusion chain with chimpanzees using a two-action task, with each chain seeded with a model proficient in one of the two methods. For each chain five chimpanzee-to-chimpanzee transmission events occurred and across all, the fidelity of replication was 100%, reminiscent of the findings for children presented here (see also Horner *et al.* 2006; Flynn & Whiten in press; Whiten *et al.* under review).

In conclusion, the results of these two experiments show that children copy both from their peers and from an unfamiliar adult, although the proportion of children who copied from a fellow child was greater. The children copied a conspecific in a dyadic interaction and this fidelity of matching was maintained along a series of transmission events, which reflects findings of comparable studies conducted with chimpanzees. Additionally, for the Pan-pipes apparatus, provision of a ghost condition of either of the Lift or Poke method, was usually insufficient for the children to then operate the apparatus, let alone with the same method as demonstrated. However, compared to chimpanzees tested previously, the children responded with a greater degree of success and new terminology to discuss the various forms of emulation learning were introduced. The value and efficacy of ghost conditions for children and chimpanzees will be discussed further in *Chapters 6* and *7*.

Chapter 6: Observational Learning in Chimpanzees: The Use of Ghost Conditions Refined⁸

Summary

Emulation has been distinguished from imitation as a form of observational learning because it focuses not on a model's actions but on the action's environmental results. Whether a species emulates, imitates, or displays only simpler observational learning is expected to have profound implications for its capacity for cultural transmission. Chimpanzees' observational learning has been suggested to be primarily emulative, but this is an inference based upon low fidelity copying in experiments comparing chimpanzees with humans, rather than direct testing⁹. Here, emulation learning by chimpanzees was directly tested for using a ghost condition in which a sliding door obscuring a reward was moved to left or right with no agent visible, a context associated with the only published evidence of this type for emulation learning, in pigeons. The chimpanzees matched the observed direction of the 'ghost' door movement on their first test trial. This is the first of such evidence for emulation in a non-human primate. The chimpanzees continued to match with high fidelity when viewing a conspecific model operate the door. It was concluded that chimpanzees can, and will, display emulation learning when the task is as simple as the present one, which contrasts with a failure to do so in a more complex manipulative task tested earlier. However even with this simple task, emulation alone created only fleeting

⁸ The experiment reported in this chapter is also reported in Hopper *et al.* (in press).

⁹ But see Call *et al.* (2005) and Tennie *et al.* (2006).

fidelity compared to the opportunity to copy a conspecific, when considerable conformity was displayed.

6.1 Introduction

An influential distinction in recent analyses of social learning has been between imitation (copying another's actions), and emulation (Wood 1989), a term promoted by Tomasello (1990) to label learning about the environmental results of another's actions. Tomasello and colleagues have concluded their experiments show chimpanzees are emulators rather than true imitators (Nagel *et al.* 1993; Tomasello 1999; Call *et al.* 2005). This has implications for the evolution of culture, for by its nature, emulation is less likely than imitation to provide high fidelity behavioural transmission (Tomasello 1999).

However, emulation has been inferred in these studies largely on the basis that the observer (i) learns more than can be explained by mere stimulus enhancement, in which an observer's attention is simply drawn to relevant stimuli, yet (ii) fails to show evidence of detailed imitative matching of the model's action. Here, emulation is not directly tested for; rather, it is a default explanation, simply appealed to when imitative fidelity was low, which led Byrne (2002*a*) to entitle his response to Want & Harris (2002) *Emulation in Apes: Verdict 'Not Proven'*.

More recently, Call *et al.* (2005) *did* find evidence for emulation learning in chimpanzees, as detailed previously. Briefly, the chimpanzees were shown a tube, which could open in one of two ways to reveal a reward, in one of four conditions. The conditions were (i) a full demonstration, (ii) only the action, (iii) only the end-

state or (iv) a no information baseline. Call *et al.* found that the chimpanzees, unlike children, were more like to replicate the results after having observed the end-state condition than the action-only condition, from which they concluded that the chimpanzees had shown emulation learning.

Another direct test for emulation *per se*, that might allow a potential learner to watch the events normally caused by the model but with no model visible, is a ghost condition (Fawcett *et al.* 2002). Ghost experiments were introduced in *Chapter 4* where the mixed results for studies with both humans and non-humans were detailed (Heyes *et al.* 1994; Akins *et al.*, 2002; Fawcett *et al.* 2002; Subiaul *et al.* 2004; Tennie *et al.* 2006; Hopper *et al.* 2007).

The only non-human study, testing for emulation learning¹⁰, to provide positive evidence for emulation learning in a ghost condition is that of Klein & Zentall (2003), who studied pigeons. Pigeons were tested in one of four experimental conditions designed to delineate imitation, affordance learning and a mere presence effect. A bidirectional method, in the tradition of Heyes *et al.* (1994), was employed in which a screen door could slide to either the left or right to reveal a food reward. In the first of the four conditions (Push) a conspecific model moved the door to either the left or right. The second condition (No Push) also had a conspecific present, but one which was inactive, as the slide door was moved discretely by the experimenter using a length of fishing line. Similar to the No Push condition, was the No Demo condition, in which the door was moved in the same manner, but no conspecific was present. The final condition (Vision Blocked) replicated the Push condition but the conspecific moved the door whilst behind a screen such that they were occluded from the

¹⁰ An earlier study had shown that rats were capable of matching the movements of an automatically operated joystick have been reported also but in this study the author was using it as an experimental tool (to reduce the number of models to be trained) rather than as a test for emulation or affordance leaning (Denny *et al.* 1988).

observing pigeon. This was conducted to act as control for olfactory and gustatory cues, which had been identified by Mitchell *et al.* (1999) as a drawback of the original study of Heyes *et al.* (2004).

It was found that the pigeons matched the direction in which the model slid the door in the Push condition. Additionally, Klein & Zentall (2003) found 74% matching to the direction pushed in the No Demo condition, significantly above chance, and thus concluded that emulation ('affordance') learning had occurred.

This literature is thus somewhat paradoxical. The earlier conclusion that chimpanzees are emulators rather than imitators is contested by the negative results of the ghost experiment of Hopper *et al.* (2007; *Chapter 4*) while conversely, positive evidence for emulation in such a test has been offered for pigeons (Klein & Zentall 2003). Accordingly, a replication of Klein & Zentall's study with chimpanzees was conducted. An additional replication with children was also conducted following the same experimental protocol (*Chapter 7*). The negative results of Hopper *et al.* would predict that chimpanzees would not learn in a ghost condition. However, the tool-use task used by Hopper *et al.* was sufficiently challenging that none of 18 individuals performed it when tested without benefit of observing a model (Whiten *et al.* 2005; Hopper *et al.*). Klein & Zentall's apparently task, which does not require the use of a tool, might be predicted to be learnable via emulation, as with pigeons, and its simplicity for chimpanzees could be checked and confirmed with a no-model control.

6.2 Method

a. Experimental design

Subjects	40 chimpanzees
Apparatus	Slide-box (bidirectional task)
Conditions	3 forms of demonstration of door-push (Left or Right): <ol style="list-style-type: none">1. Push-demo (dyadic conspecific demo, n = 8)2. Enhanced-ghost (individual ghost with conspecific present, n = 8)3. Ghost (individual ghost, n = 8) No-info control (n = 8)
Independent variable	Form of demonstration
Dependent variable	Ability of chimpanzees to operate Slide-box and direction in which they pushed the door

b. Subjects and housing

Chimpanzee participants were 25 females and 15 males aged 11 – 44 yrs (mean 30.5 yrs), eight of which acted as ‘demonstrators’ and 32 as ‘observers’; see Procedure below and all were housed at MDACC, Table 6.1 provides more detailed demographic information. Chimpanzees were tested in one half of their inside-cage, measuring 2.4m x 2.4m x 1.8m. At other times they lived in social groups with access to outside corrals (21.3m diameter, *Chapter 3* Figure 3.1a).

c. Apparatus

The 'Slide-box', (Figure 6.1) was designed to allow replication of the methodology described by Klein & Zentall (2003). From the top panel of an opaque, acrylic cube measuring 32 cm on each side, a reward-chute led to a 4 cm diameter hole in the centre of the front panel. On the front panel was an 8 cm x 8 cm opaque acrylic door that could slide to the left or right with equal ease. When in the centre, the door hid the reward-chute hole.

d. Amendments to the experimental protocol of Klein & Zentall (2003)

As in the methodology described by Klein & Zentall (2003), there were three experimental conditions and one control condition. Klein & Zentall termed the three conditions 'Push', 'No Push' and 'No Demo' which have been re-named here, for clarity, as 'Push-demo', 'Enhanced-ghost' (the term of Fawcett *et al.* 2002) and 'Ghost' respectively.

Additionally, Klein & Zentall (2003) tested their pigeons in adjacent cages, while it was deemed more appropriate to test the chimpanzees with no physical barrier between them. Not only was it thought that this would enhance the social interaction between the dyad of chimpanzees being tested, but also, because of the physical design of the indoor caging, the chimpanzees, if tested in the same cage, would be afforded a clearer sight of the apparatus.

e. Model selection and training

Demonstrator chimpanzees were selected to be of higher rank than their observers so they could complete the task without being displaced. The demonstrator chimpanzees in the Push-demo condition was trained by the experimenter (LMH) with the use of shaping and positive reinforcement techniques to push the door on the front of the Slide-box to either the left or the right and retrieve the awaiting food reward (a grape). Once a chimpanzee was able to do this successfully on 30 successive occasions they were deemed proficient and were introduced to their observer for testing. 'Pseudo-demonstrator' chimpanzees in the Enhanced-ghost condition was trained by the same experimenter, also through the use of shaping and positive reinforcement techniques, to sit in front of the Slide-box whilst the experimenter moved the door using fishing-line and to retrieve the food reward when it was revealed but not to touch the door whilst it was moved.

	Demonstration	Demonstrator ID	Observer ID
a	Push door Left	HG (F, 40)	UR (F, 42)
	Push door Left	HG (F, 40)	KN (F, 44)
	Push door Left	JS (F, 13)	JY (F, 38)
	Push door Left	JS (F, 13)	BT (F, 32)
	Push door Right	KM (M, 15)	AR (M, 20)
	Push door Right	KM (M, 15)	AX (M, 28)
	Push door Right	GI (F, 44)	MY (F, 22)
	Push door Right	GI (F, 44)	PY (F, 43)
b	Push door Left	MY (F, 41)	MR (F, 40)
	Push door Left	MY (F, 41)	KY (F, 40)
	Push door Left	JN (F, 35)	GE (F, 38)
	Push door Left	JN (F, 35)	NI (F, 23)
	Push door Right	PR (F, 38)	BR (F, 34)
	Push door Right	PR (F, 38)	VE (F, 37)
	Push door Right	AB (F, 41)	SA (F, 34)
	Push door Right	AB (F, 41)	DO (M, 23)
c	Push door Left		CH (M, 15)
	Push door Left		BE (F, 13)
	Push door Left		PE (F, 39)
	Push door Left		MA (M, 36)
	Push door Right		BR (F, 11)
	Push door Right		NI (M, 18)
	Push door Right		MO (M, 34)
d			SA (M, 21)
			GI (M, 35)
			MC (M, 18)
			SI (M, 38)
			RO (F, 21)
			TI (F, 22)
			PI (M, 44)
		CE (F, 15)	

Table 6.1 Demographic details of the chimpanzees in the following conditions: **(a)** Push-demo, **(b)** Enhanced-ghost; **(c)** Ghost and **(d)** No-info condition.

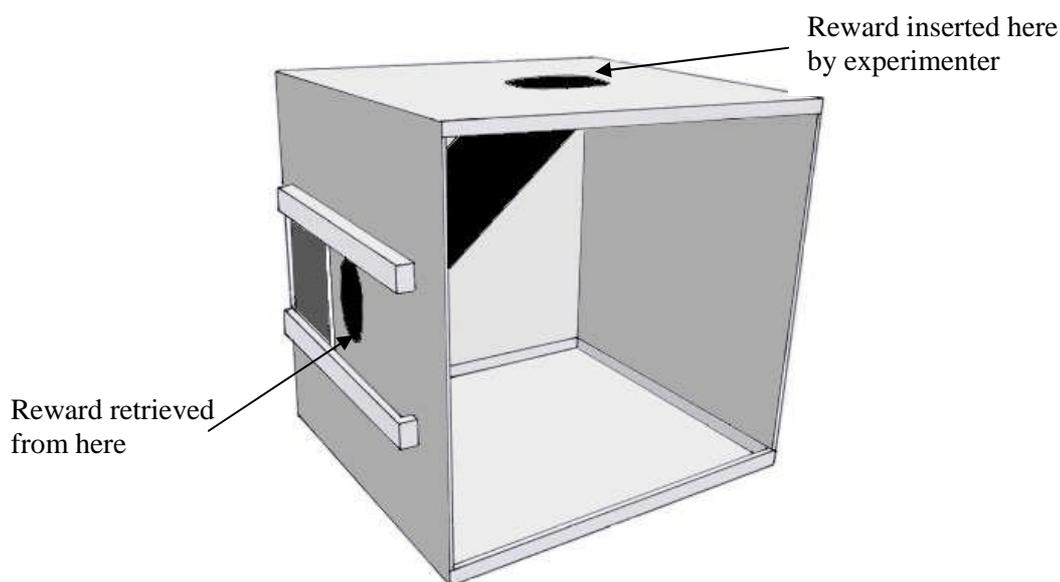


Figure 6.1 A cut-away of the Slide-box revealing the reward dispensing tube inside. Here the door is slid to the left, revealing the hole from which the reward can be retrieved.

f. Procedure

Chimpanzees were tested in one of four conditions in their inside caging whilst all other group members were isolated in the outdoor area of their caging so that they could not disturb those animals being tested. The four conditions were conducted as detailed below. For each of the three experimental conditions the observer saw the door move either to the left or right and after each door movement the experimenter turned the Slide-box away from the chimpanzee to re-set the door back to the central 'start' position, out of the sight of the observer.

For each experimental condition, four subjects observed the door moved to the right and four saw it moved to the left. For each Push-demo and Enhanced-ghost condition, two conspecific demonstrators were 'push-right' models and two were

'push-left' models. This was in accordance with Klein & Zentall's (2003) method, controlling for individual demonstrator effects.

(i) Push-demo

A trained conspecific demonstrated sliding the door in one direction 58 times (the same number as in the pigeon study of Klein & Zentall 2003), obtaining the revealed food reward each time.

(ii) Enhanced-ghost

For this condition and the next, fishing line was tied to attachment points on each side of the door and was fed to the back of the Slide-box. From here the experimenter (LMH) could pull the line to slide the door to either left or right, her actions being occluded from the chimpanzee's view by the Slide-box, although the top part of her body remained visible. In this way the door was moved in one direction 58 times. The pseudo-demonstrator chimpanzee, trained to sit in front of the apparatus, retrieved the rewards for each door-slide, whilst the observer chimpanzees watched.

(iii) Ghost

An observer chimpanzee, alone in the cage, observed the door being moved as in the Enhanced-ghost condition. For each demonstrated slide the food reward dropped into a pipe that led into a bucket outside the cage, so that as in the other conditions, the observer was not rewarded.

Directly after each condition, the observer chimpanzee was given free access to the baited Slide-box for 20 mins, by itself. Subjects recovered a grape for each door slide regardless of the direction in which they moved it.

(iv) No-Info Condition

In this, no information was provided and the subject was free to act on the apparatus for 20 mins.

g. Coding

All test and response sessions were recorded with a Sony miniDV digital handycam (DCR-HC35E). In addition to the film footage of each test session, the experimenter (LMH) kept a written log of each of the chimpanzee's interactions with the Slide-box, noting in which direction they moved the door. The proportion of door slides that matched the direction demonstrated was calculated.

6.3 Results

a. Overall number of responses

In the 20-minute, free-access period, 23 of the 24 chimpanzees tested in the three experimental conditions made one or more responses. In contrast, only 3 of the 8 chimpanzees in the No-info condition responded. Table 6.2 provides an overview of the average number of actions of those chimpanzees that responded successfully in each of the four conditions.

		Push-demo	Enhanced-ghost	Ghost	No-info condition
a		47.8	54.5	69.9	19.8
b		47.8	62.3	69.9	52.7
		Push-demo	Enhanced-ghost	Ghost	No-info condition
a		47.8	54.5	69.9	19.8
b		47.8	62.3	69.9	52.7
a		47.8	54.5	69.9	19.8
b		47.8	62.3	69.9	52.7
		Push-demo	Enhanced-ghost	Ghost	No-info condition
a		47.8	54.5	69.9	19.8
b		47.8	62.3	69.9	52.7

Table 6.2 The mean number of actions (**a**) across all chimpanzees tested and (**b**) by chimpanzees that responded successfully in the three 20-minute experimental and no-info conditions.

b. First responses

Results are summarised in Table 6.3. The binomial P values shown are those for differences this extreme or more so, rather than exact P values. In the Push-demo condition chimpanzee observers matched the direction demonstrated (DD) (binomial test: $P \leq 0.05$). In contrast, for the remaining conditions the chimpanzees did not show significant matching with their first responses.

Condition	1 st response match demo	1 st response match demo Enhanced-ghost & Ghost	Total match demo responses compared to chance
Push-demo	7/8 (P = 0.035)		8/8 (P = 0.01)
Enhanced-ghost	6/7 (P = 0.063)	12/15 (P = 0.018)	4/7 (P = 0.27)
Ghost	6/8 (P = 0.145)		3/7 (P = 0.77)

Table 6.3 Matching to direction witnessed in first responses by chimpanzees (showing binomial test results).

However, since there was no significant difference between results for the Enhanced-ghost and Ghost conditions, and both are forms of ghost condition (in both, the door was operated remotely and not by a conspecific model) the data on first responses were collapsed across these two conditions. When these were combined, the chimpanzees significantly matched the DD (binomial test: $P \leq 0.05$; Table 6.3). Thus, there was evidence of matching for chimpanzees in their first trial, whether watching a model or a ghost condition.

c. Total responses compared to chance

The total responses of each subject were found to be distributed in a bimodal manner (all either less than 0.05, or more than 0.70). Accordingly results were analysed by classing each chimpanzee as ‘matching’ if their responses had a mean proportion of

matching ≥ 0.50 and 'non-matching' if ≤ 0.50 . More chimpanzees in the Push-demo condition matched the DD than chance (binomial test: $P \leq 0.01$; Table 6.3).

Conversely, the chimpanzees did not show greater matching than chance in the Enhanced-ghost condition or Ghost condition.

d. Comparisons between conditions

The overall proportions of matching responses by the chimpanzees in all three conditions are shown in Figure 6.2. *Chapter 7* provides, and discusses, the results of the replication of Klein & Zentall's (2003) methodology conducted with children. In the Results and Discussion the results of both the children, and those of the chimpanzees reported here, will be compared both with one another and to the pigeons tested by Klein & Zentall.

Chimpanzees showed a significantly greater proportion of matching to the DD in the Push-demo condition (median 1.00) than in the Ghost condition (median 0.04: two-tailed Mann-Whitney U test: $U = 11.0$ $N_1 = 8$, $N_2 = 8$, $P \leq 0.05$). The chimpanzees, however, did not show greater matching in the Push-demo condition compared to the Enhanced-ghost condition. There was no significant difference in the level of matching between the Enhanced-ghost and Ghost conditions.

e. Pattern of responses

In summary, high levels of matching in first responses by chimpanzees were followed by failure to match closely in later trials, for all but the Push-demo condition. The

fluctuations implied are charted in Figure 6.3. The most noticeable contrast is between chimpanzees in the Push-demo condition, who matched consistently, and those in the Ghost condition, four of whom matched on their first response but then went on to explore alternative responses.

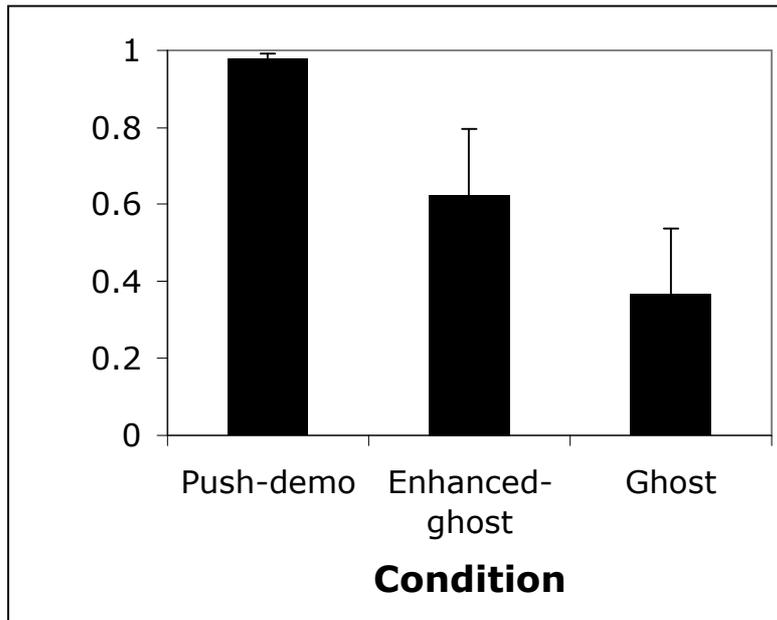


Figure 6.2 Overall matching responses. Mean proportion of responses made by chimpanzees which matched the direction of the door movement demonstrated in the 20-minute free-access period. Means and standard errors are shown to facilitate direct comparison with results for the pigeons tested by Klein & Zentall (2003) which will be discussed further in *Chapter 7*.

f. Responses in No Info condition

Only three of eight chimpanzees moved the slide door (two to the left, one to the right) and retrieved grapes, whereas all of the chimpanzees tested in the experimental conditions did so, regardless of matching the DD (Fisher Exact test: $P \leq 0.05$).

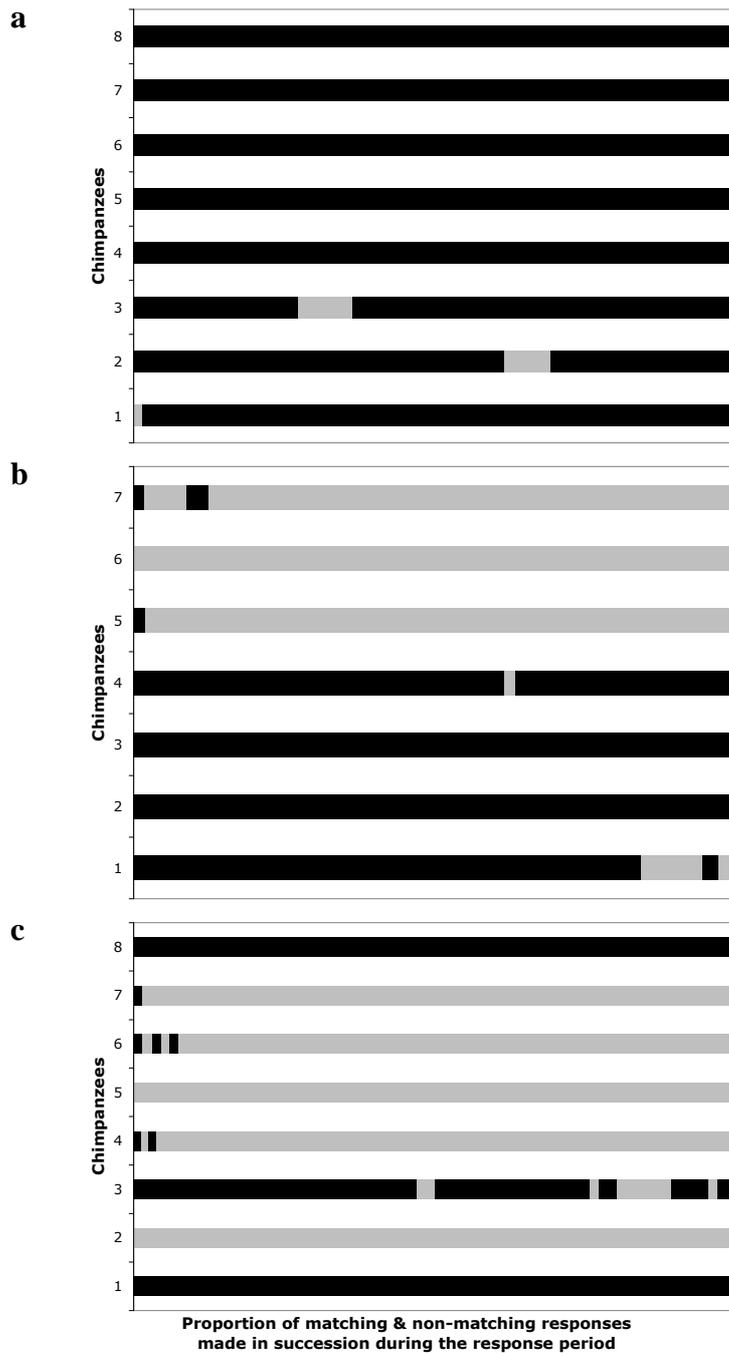


Figure 6.3. Fluctuations in matching. Matching and non-matching pushes made during the free-access period by chimpanzees in the three experimental conditions: (a) Push-demo; (b) Enhanced-ghost and (c) Ghost. Black = % matching responses; grey = % responses in the direction opposite to those demonstrated (n = 58 for chimpanzees).

6.4 Discussion

In the critical ghost conditions (Enhanced-ghost and Ghost), these results provide evidence of emulation in the first responses of chimpanzees. This is the first direct evidence for emulation learning in a non-human primate, in the relatively extreme conditions of a ghost experiment. Such positive results contrast with previous negative ones from ghost condition studies with non-human primates (Subiaul *et al.* 2004; Hopper *et al.* 2007; *Chapter 4*). One possible explanation may be that in the earlier study (*Chapter 4*) which employed a complex tool-use technique that chimpanzees never discovered in two previously-conducted no-model control conditions (Whiten *et al.* 2005; Hopper *et al.*; *Chapter 3*), whereas in the present study three of eight control subjects completed the task. Although motorically simple, the task employed by Subiaul *et al.* was also a complex one involving four steps. A tentative conclusion could be that chimpanzees may be capable of emulation learning in tasks that are relatively simple on their cognitive demands, but not in more complex tasks, where observers instead need to witness the performance of a model. Precisely what factors are critical in determining such a difference thus becomes an important question for future research.

Following a non-social learning approach, it could be suggested that the observers merely learned a reinforced association between the direction of door push and food, similar to ‘action-outcome contingency learning’ (Heyes 1993) and that, in time, the responses of the subjects would even out to a bimodal split with Push-right for half their responses and Push-left with the other half. This clear pattern was not seen, however, and so this conclusion cannot be drawn but this could be due to the short length of the response time.

That the chimpanzees failed to continue to match in the two ghost conditions highlights a difference from the pigeons tested by Klein & Zentall (2003), who showed significant matching in the Ghost condition. Chimpanzees thus appeared innovative, exploring alternative moves after their first response in the ghost conditions, as illustrated in Figure 6.3. This tendency presents a striking contrast with the remarkable median 100% (mean 99%) match that continued in the chimpanzees' Push-demo condition, indicating a strong tendency to conform to the consistent actions of a conspecific.

The pigeons of the Klein & Zentall (2003) study differed from the chimpanzees in that, by contrast with the significant matching shown in the Ghost condition, they showed none in the Enhanced-ghost condition. Klein & Zentall offered no explanation for this. One may speculate that the pigeons were either distracted by the non-acting pigeon, or copied its passivity when tested, but it is not apparent why such biases should affect only pigeons.

Klein & Zentall (2003) interpreted their finding that matching was significantly greater in the Push-demo than in the Enhanced-ghost condition, as implying imitation. This conclusion is questionable. The significant matching recorded in the Ghost condition showed that pigeons could learn from watching the screen move alone (i.e. emulate): accordingly, this might account for their success in the Push-demo condition. A significantly higher degree of matching in this condition would be required to infer imitative effects over and above those expected through emulation. Therefore, from this interpretation, emulation was demonstrated, but not imitation. By contrast, the chimpanzees tested in this present study did show a greater tendency, overall, to match in the Push-demo condition compared to either of the ghost

conditions. Whether this implies imitation was at work depends on how imitation is defined as response facilitation could also be used to explain these findings.

The fact that emulation was sufficient to explain chimpanzees' first matching responses means that it cannot be determined whether or not imitation was also occurring in the Push-demo condition, in the sense of learning specifically from a model's *actions* on the door. However, the striking tendency of chimpanzees to continue to match in the Push-demo condition can be described as imitation in the broader sense of a motivation to match an action that a conspecific consistently continues to perform.

In *Chapter 4*, a new framework for describing emulation was proposed, in which there were three sub-levels of what was learnt. To recap, Level 1 emulation can be equated to end-state or goal emulation (Wood 1989; Tomasello 1990; Whiten & Ham 1992; Whiten *et al.* 2004) in which the result of an act is reproduced through a novel behavioural strategy. In the second, Level 2 emulation, the affordances of the target object are learnt by the observer from watching another individual interacting with it. Finally, in Level 3 emulation these same affordances are learnt and the observer replicated the exact movements of the device. The first responses of the chimpanzees in the two ghost conditions could therefore be classed as Level 3 emulation; however because they failed to continue to match, the overall responses of the chimpanzees could instead be termed Level 2 emulation.

The results presented here may have implications for the cultural transmission of behaviour patterns. However, the ghost condition results suggest that emulation, in the sense of learning from the environmental results of actions alone, may be employed by chimpanzees only for relatively simple events and then only fleetingly. By contrast, when a conspecific model was witnessed, a strong degree of conformity

emerged – a quality that could clearly affect fidelity of transmission. This is not to suggest that a tradition of, say, ‘left-pushing’ would be likely to be sustained by chimpanzees in a task as simple as the Klein & Zentall (2003) paradigm examined here, but in the context of the more complex techniques that have been seen as candidate traditions in wild apes (Whiten & van Schaik 2007) and modeled in captive diffusion experiments (Whiten *et al.* 2007), such a tendency could play an influential role.

Chapter 7: Observational Learning Tested with Ghost Conditions: Children and Chimpanzees Compared¹¹

Summary

In the study of observational learning, two previously published studies have provided positive evidence that children are able to learn from ghost conditions. However, more recent unpublished work conducted by this author has contradicted this. It was proposed that children were unable to match because the task was a complex, tool-use apparatus. In the present study, children were presented with a simpler, bidirectional task in ghost conditions and a full-demonstration condition by a fellow child. The children matched the observed action observed in the ghost demonstration on their first test trial and continued to do so in later trials in certain conditions. This finding suggests emulative matching by the children. Additionally, the children matched with 100% fidelity after having viewed a fellow child operate the door. The apparatus used in this study was designed to replicate one used in a previously-published study which reported evidence of affordance learning by pigeons (Klein & Zentall 2003). Findings for pigeons, children and chimpanzees (*Chapter 6*) are compared and contrasted.

¹¹ The experiment reported in this chapter is also reported in Hopper *et al.* (in press).

7.1 Introduction

There has been much debate over the forms of social learning employed by children (Want & Harris 2002) as well as for other species (Zentall 2006). It has generally been concluded that children imitate with high fidelity (Nagell *et al.* 1993; Call & Tomasello 1995; Tomasello 1999; Call *et al.* 2005) while it was also for children that the term emulation was first applied (Wood 1989). More recently, at least two studies with human children have provided evidence of emulation learning (Thompson & Russell 2004; Tennie *et al.* 2006). Thompson & Russell and Tennie *et al.* employed a ‘ghost’ condition. A ghost condition, as introduced in previous chapters, is one in which an observer sees the pertinent parts of an apparatus move without the direct interaction of a demonstrator. Such ghost conditions are employed to determine whether an individual is able to learn how to operate a task from seeing its affordances, separate from the actions of a demonstrator.

Both Thompson & Russell (2004) and Tennie *et al.* (2006) showed that children were able to learn from ghost demonstrations, as detailed more fully in *Chapter 5*. However these positive responses were not without exception. Thompson & Russell reported that the children only responded to the ghost condition when the task presented resulted in a single, unambiguous, movement but for such a task, the children were more likely to match the ghost condition than a demonstration provided by a human adult. The task employed by Tennie *et al.* also had a clear result yet only children over 24-months-old were able to learn from a ghost condition. This is in contrast to the children tested by Thompson & Russell who were as young as 14-months-old. Ultimately, however, Tennie *et al.* concluded that their “...results with

24-mo-old children question the idea that emulation tasks may be too complex for human infants” (p. 1166).

In accordance with Thompson & Russell’s (2004) conclusion, when children were presented with a more complex, tool-use, task (the Pan-pipes) they only copied the demonstrated method after having observed a fellow human but they did not after a ghost display (*Chapter 5*). It was decided to test children in a ghost condition with a more straightforward, bidirectional task, to determine whether the previous failure of children tested with the Pan-pipes was due to the complexity of the task or a general deficiency in emulation learning.

Following the rationale presented in *Chapter 6*, an apparatus (the Slide-box) was designed to allow for a replication of the methodology of Klein & Zentall (2003). Klein & Zentall used a bidirectional device for testing pigeons in which a screen door could be pushed either to the left or right to reveal a food reward. Klein & Zentall provided both full demonstrations by a conspecific and two forms of a ghost condition. One of these ghost conditions was the ‘no demo’, which was a basic ghost condition (Fawcett *et al.* 2002), in which a subject observed the door on the front of the apparatus moved discretely by the experimenter using fishing-line. The second ghost condition was the ‘no push’, which can be equated to the ‘enhanced ghost’ condition as described by Fawcett *et al.*, in which the door was moved discretely by the experimenter as described while a passive conspecific sat in front of the device and retrieved the food rewards, all of which was observed by the test subject.

The Slide-box, previously used to test the responses of chimpanzees to both ghost and conspecific demonstrations (*Chapter 6*; Hopper *et al.* submitted), was employed here with children. Not only would the use of this apparatus allow for comparisons to be made between the responses of the children and the chimpanzees but the

experimental protocol was consistent with that of Klein & Zentall (2003) so that comparisons with their pigeon results could also be drawn.

7.2 Methods

a. Experimental design

Subjects	40 children
Apparatus	Slide-box (bidirectional task)
Conditions	3 forms of demonstration of door-push (Left or Right): <ol style="list-style-type: none">1. Push-demo (dyadic conspecific demo, n = 8)2. Enhanced-ghost (individual ghost with conspecific present, n = 8)3. Ghost (individual ghost, n = 8) No-info control (n = 8)
Independent variable	Form of demonstration
Dependent variable	Ability of children to operate Slide-box and direction in which they pushed the door

b. Participants and testing environment

Child participants were 18 females and 22 males aged 3 yrs 2 mo – 4 yrs 10 mo (mean 4 yrs 2 mo). Eight acted as ‘demonstrators’ and 32 as ‘observers’; see Procedure. Table 7.1 provides more detailed demographic information. Children were tested in rooms familiar to them at their Scottish nursery schools.

	Demonstration	Demonstrator ID	Observer ID
a	Push door Left	RR (M, 3yr 6mo)	MM (M, 4yr 0mo)
	Push door Left	RR (M, 3yr 6mo)	EF (M, 4yr 2mo)
	Push door Left	SM (F, 3yr 6mo)	JR (M, 4yr 2mo)
	Push door Left	SM (F, 3yr 6mo)	KD (F, 3yr 9mo)
	Push door Right	TD (M, 4yr 8mo)	JC (M, 4yr 10mo)
	Push door Right	TD (M, 4yr 8mo)	MS (M, 3yr 11mo)
	Push door Right	RO (M, 4yr 8mo)	LT (F, 4yr 10mo)
	Push door Right	RO (M, 4yr 8mo)	TT (F, 4yr 5mo)
b	Push door Left	CW (M, 4yr 2mo)	DH (F, 3yr 5mo)
	Push door Left	CW (M, 4yr 2mo)	AW (M, 3yr 2mo)
	Push door Left	LB (F, 3yr 9mo)	JA (M, 4yr 6mo)
	Push door Left	LB (F, 3yr 9mo)	PB (F, 3yr 8mo)
	Push door Right	HM (F, 4yr 9mo)	EY (F, 4yr 7mo)
	Push door Right	HM (F, 4yr 9mo)	PP (M, 4yr 4mo)
	Push door Right	LD (F, 4yr 8mo)	CB (F, 4yr 6mo)
	Push door Right	LD (F, 4yr 8mo)	KC (M, 4yr 8mo)
c	Push door Left		RC (F, 4yr 0mo)
	Push door Left		CJ (F, 3yr 6mo)
	Push door Left		JC (M, 3yr 8mo)
	Push door Left		TF (F, 4yr 3mo)
	Push door Right		MH (M, 3yr 10mo)
	Push door Right		DB (F, 3yr 9mo)
	Push door Right		LA (F, 4yr 3mo)
d			DC (M, 3yr 8mo)
			JF (M, 4yr 8mo)
			EO (F, 4yr 5mo)
			JP (M, 4yr 3mo)
			EJ (F, 3yr 6mo)
			RW (M, 4yr 2mo)
			BL (M, 4yr 3mo)
		GF (M, 4yr 0mo)	

Table 7.1 Demographic details of the children in the following conditions: (a) Push-demo, (b) Enhanced-ghost; (c) Ghost and (d) No-info condition.

c. Apparatus

The 'Slide-box' apparatus was used, which had been designed to allow replication of the methodology described by Klein & Zentall (2003). For a full description see *Chapter 6* (Figure 6.1).

d. Amendments to the experimental protocol of Klein & Zentall (2003)

The terminology for the three conditions were renamed from the original three used by Klein & Zentall (2003) to 'Push-demo', 'Enhanced-ghost' and 'Ghost' as justified in *Chapter 6*. Additionally, Klein & Zentall tested their pigeons in adjacent cages, but it would have been inappropriate to test children in such confined circumstances.

Therefore, when the children were tested in a dyad they were tested in the same room, with each child provided with their own chair to sit on. Testing the children in one room was also comparable to the method used with the chimpanzees tested previously in a single cage (*Chapter 6*).

e. Model selection and training

The children selected to be models were those described as 'confident' by their nursery teachers. The demonstrators in the Push-demo condition were shown how to retrieve the reward (a sticker in a plastic capsule) by pushing the door to either the left or to the right. The task was presented to the children as a game and as a consequence

all children were very happy and willing to interact with the apparatus and retrieve the reward. All the children selected to be the models were able to slide the door with ease and were deemed proficient once they had shown they could do it ten times in succession. The children selected as 'pseudo-demonstrators' for the Enhanced-ghost condition, were shown by the experimenter (LMH) to retrieve the reward only once the door had been moved discretely by the experimenter using fishing-line.

Importantly, the children in this condition were asked not to touch the door itself. As for the Push-demo condition, all children selected to be pseudo-demonstrators were happy and able to do so.

Children selected as demonstrators for both conditions were also asked to remain quiet throughout the demonstration period and not to tell the observing child what they were doing or why they were doing it. Again, this request was presented to the children as a game with the request "Let's see how quiet you can be when X comes in to watch? Remember, we're going to try to not say a word!". All the children seemed excited by this challenge but were quiet throughout. If any demonstrating child began to describe or explain the task to the observing child the experimenter (LMH) again reminded them to be quiet. This was done to maintain comparability between this experiment and those conducted with the chimpanzees (and pigeons) where models could not speak, or explain, to the observers.

f. Procedure

The children were tested in one of four conditions in a familiar room in their nursery, separate from their classroom to avoid possible distractions by their peers. The four conditions were conducted as detailed below.

As for the chimpanzees (*Chapter 6*), for each experimental condition four children observed the door moved to the right and four saw it moved to the left. For each Push-demo and Enhanced-ghost condition, two child demonstrators were ‘push-right’ models and two were ‘push-left’ models. This was in accordance with Klein & Zentall’s (2003) method, controlling for individual demonstrator effects. As for the chimpanzees, after each door movement, the door was re-set to the central position by the experimenter, out of the sight of the children.

The children were tested in the four conditions that were described by Klein & Zentall (2003) and conducted in a manner that allowed for comparison between the two studies. The conditions, as detailed below, vary very little from those in which the chimpanzees (*Chapter 6*) were tested and, aside from being tested in classrooms not cages, there were only three minor differences: (i) the reward was a sticker in a plastic capsule, (ii) based on pilot studies, the children’s level of interest in the task was maintained by reducing the number of demonstrations given in each condition to 15 and (iii) for the same reason the test phase was run only up to the first 15 responses.

(i) Push-demo

A child selected as a demonstrator slid the door in one direction 58 times (the same number as in the pigeon study of Klein & Zentall 2003), obtaining the revealed reward each time.

(ii) Enhanced-ghost

For this condition and the next, fishing line was tied to attachment points on each side of the door and was fed to the back of the Slide-box. From here the experimenter (LMH) could pull the line to slide the door to either left or right, her actions being occluded from the child's view by the Slide-box, although the top part of the experimenter's body remained visible. In this way the door was moved in one direction 58 times. One of the children selected as pseudo-demonstrators retrieved the rewards for each door-slide without touching the door, whilst the observer child watched.

(iii) Ghost

An observer child observed the door being moved as in the Enhanced-ghost condition. For each demonstrated slide the reward was collected by the experimenter (LMH) and not given to the observing child. This was done because in the previous two

conditions, the observing child did not receive the reward and all conditions were designed to be as comparable as possible.

After each set of observation periods the observing child observed the experimenter (LMH) bait the Slide-box with the reward and was then given free access to the Slide-box for 20 mins. Children recovered the reward for each door slide regardless of the direction in which they moved it and for as many times as they could throughout the 20 min period.

(iv) No-Info Condition

In this, no information was provided and the child was free to act on the apparatus for 20 mins.

g. Coding

All test and response sessions were recorded with a Sony miniDV digital handycam (DCR-HC35E). In addition to the video-recording, the experimenter (LMH) wrote down the direction of each door slide made by the observer children. The proportion of door slides that matched the direction demonstrated was calculated for further analyses.

7.3 Results

a. First responses

Results are summarised in Table 7.2. The binomial P values shown are those for differences this extreme or more so, rather than exact P values. The observing children in the Push-demo and Enhanced-ghost condition matched the direction demonstrated (DD; binomial test: $P \leq 0.01$ and $P \leq 0.05$ respectively). However, in the Ghost condition the children matching to the DD was not significantly different from chance.

There was no significant difference between child results for the two ghost conditions (Enhanced-ghost and Ghost) so, also as for the chimpanzee data, the first responses were collapsed across these two conditions. When combined, the children significantly matched the DD (binomial test: $P \leq 0.05$: Table 7.2). Thus, there was evidence of matching for the children in their first trial, whether watching a fellow child or a ghost condition.

Condition	1 st response match demo	1 st response match demo Enhanced-ghost & Ghost	Total match demo responses compared to chance
Push-demo	7/7 (P = 0.01)	13/16 (P = 0.01)	7/7 (P = 0.01)
Enhanced-ghost	7/8 (P = 0.04)		8/8 (P = 0.01)
Ghost	6/8 (P = 0.15)		6/8 (P = 0.11)

Table 7.2 Matching to direction witnessed in first responses by children (showing binomial test results).

b. Total responses compared to chance

The total responses of each child were classed as ‘matching’ following the same criteria as that devised for the chimpanzee data (see *Chapter 6*). More children in Push-demo and Enhanced-ghost matched the DD than chance (binomial test: $P \leq 0.01$ for both, Table 7.2). However, this was not the case in the Ghost condition. However, it might be that the nonsignificance might be a result of the low power of the analysis, both for this analysis and elsewhere due to the small sample size.

c. Comparisons between conditions

Figure 7.2 provides the overall proportions of matching responses by the children in all three conditions. Additionally, Figure 7.2 shows the responses of the chimpanzees tested previously (*Chapter 6*) and the pigeons tested by Klein & Zentall (2003) for comparison with the child results reported here. Parametric results are given in Figure 7.2 to allow for comparison with the published pigeon results¹², but non-parametric statistics were applied to the child data.

A significant, although small, difference was found for the level of matching to the DD by children, between the Push-demo condition (median = 1.00) and the Ghost condition (0.90: two-tailed Mann-Whitney U test: $U = 10.5$ $N_1 = 7$, $N_2 = 8$, $P \leq 0.05$). The children also showed significantly greater matching in the Push-demo condition compared to the Enhanced-ghost condition (0.97: two-tailed Mann-Whitney U test: U

¹² Exact data points and standard error of the means for the pigeon data were kindly provided by the authors (T. Zentall, personal communication, June 2007)

= 14.0 $N_1 = 7$, $N_2 = 8$, $P \leq 0.05$). Finally, no significant difference in level of matching between the Enhanced-ghost and Ghost condition, was shown by the children.

d. Pattern of responses

To allow for more detailed comparisons between the responses of the children with those of the chimpanzees tested previously (*Chapter 6*) graphs were plotted to show the responses of each child over time similar to those created for the chimpanzees' responses. Figure 7.3 shows the fluctuations over time in the responses by the children, additionally, for comparison, the chimpanzee data is re-presented here from *Chapter 6*.

e. Responses in No Info condition

Six of eight children acted successfully in the control condition, not significantly different to the full response rate in the experimental conditions. Three moved the door to the left and three to the right.

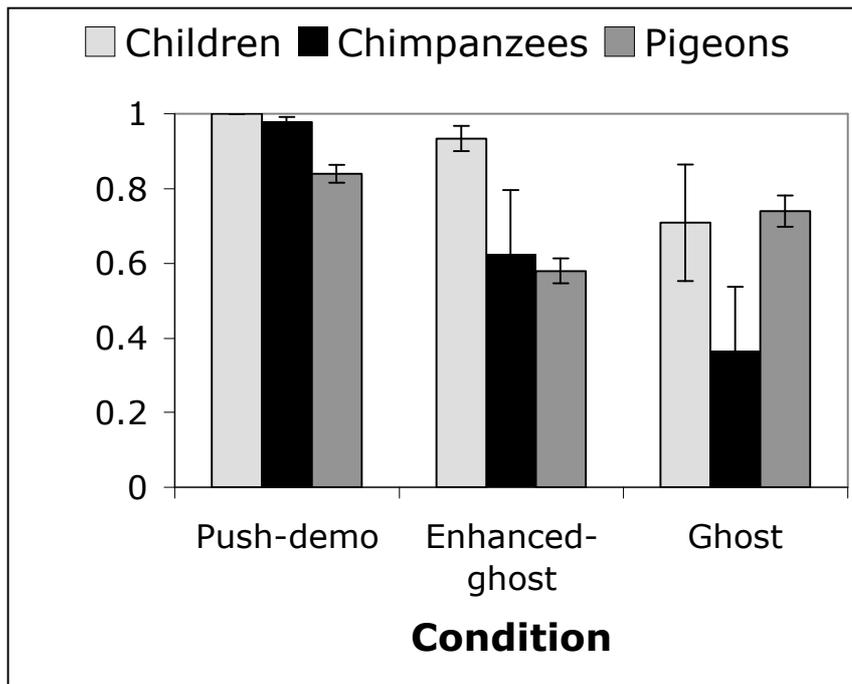


Figure 7.2 Overall matching responses. Mean proportion of responses made by children and chimpanzees which matched the direction of the door movement demonstrated in the 20-min free-access period. Means and standard errors are shown to facilitate direct comparison with results for the pigeons tested by Klein & Zentall (2003), the data for which are also shown.



Figure 7.3 Fluctuations in matching. Matching and non-matching pushes made during the free-access period by children and chimpanzees in three conditions: **(a)** children, Push-demo condition; **(b)** children, Enhanced-ghost; **(c)** children, Ghost; **(d)** chimpanzees, Push-demo; **(e)** chimpanzees, Enhanced-ghost; **(f)** chimpanzees, Ghost. Black = % matching responses; grey = % responses in the direction opposite to those demonstrated (n = 58 for chimpanzees, n = 15 for children)

7.4 Discussion

The child results presented here, along with those given in *Chapter 6* and by Klein & Zentall (2003), allow for a fairly direct comparison between chimpanzees, children and pigeons. Interestingly, all three species behaved similarly in some respects, yet each differed from the others in at least one respect. Of course, testing conditions will never be identical for such different species: for example, the pigeons are operating the device with their beak, the primates with their hands; and the children are acting in the context of an experiment run by a conspecific making verbal requests of them. Nevertheless, moving a door is easy for all three species, making this a reasonable comparative test of emulation.

The children, like the chimpanzees, showed matching with their first responses in both the Push-demo and ghost conditions, the latter of which is indicative of emulative learning. The initial copying in the ghost conditions by the children supports previous experiments with children (Thompson & Russell 2004; Tennie *et al.* 2006). However, these findings are in contrast with those reported in *Chapter 5*. Ghost conditions using the Pan-pipes were shown to children, but the children were better able to copy the actions of conspecifics rather than the ghost conditions. This is comparable with the findings of Call *et al.* (2005) who concluded that the children, unlike the chimpanzees also tested, were more likely to pay attention to the actions involved in a task than the end-state.

It was proposed that the negative results reported for children in *Chapter 5* who were provided with a ghost ‘demonstration’ may have been due to the complex nature of the Pan-pipes task. It was suggested that providing children with a ghost

demonstration of a more simplistic kind, which did not involve the use of a tool, like those employed previously by Tennie *et al.* (2006), may produce positive results. The findings reported here appear to support this.

Regarding the chimpanzees, as discussed in *Chapter 6*, the positive results after having observed a ghost condition of the Slide-box, are in contrast to the negative responses reported by Subiaul *et al.* (2004) and Hopper *et al.* (2007). However they are in accordance with previous findings suggesting chimpanzees are capable of emulative learning (for example Call *et al.* 2005).

Children differed from the other two species in showing a strong tendency to continue matching the door movement in the Enhanced-ghost condition, even when the 'model' did not actually make the door slide. There appears to be no previous work in the developmental psychology literature that helps explain this. Children might be more familiar than the other species with actions that can create effects remotely, as in flicking a light switch: however, in the Enhanced-ghost condition there was no action at all. For the present, it should be noted that the children in this study were sufficiently sensitive to social cues that the mere presence of another child, even though passive, was sufficient to elicit matching to the ghost event witnessed. To replicate the demonstration given in the Enhanced-ghost condition, children do not imitate in the most stringent definition of this term but rather emulate. To truly imitate the demonstration would be impossible for them as the fishing-line is not available to them to move the door, yet the observing children still moved the door in the direction demonstrated, by using their hands. This finding of a use of emulation when imitation is impossible complement findings that children are likely to imitate in preference to emulation even when it is not the most logical method to apply to the task (Horner & Whiten 2005).

When the ghost conditions were combined, the children matched the direction of the door movement with their first response. This emulation shown by the children can be classified using the proposed sub-categories of emulation described in *Chapter 5* (also in *Chapter 6*). Following this, the children's first responses could be termed as Level 3 emulation, as the chimpanzees (*Chapter 6*). However, it was only in the Enhanced-ghost condition that the children showed continued matching and so, overall, also like the chimpanzees, the responses of the children should more appropriately be classed as Level 2 emulation. However, unlike the chimpanzees, a number of children were also successful in the No-Info Condition, and so the conclusion of Level 2 emulation for their overall responses is not possible.

Children have been shown to use emulative learning before (Huang *et al.* 2002; Nielsen 2006; Tennie *et al.* 2006) and the results of the experiments reported in this chapter support those. Interestingly, Nielsen found that 18-month-old children would switch between their use of imitation and emulation depending on the responsiveness of the adult model. When the model was aloof the children were less likely to match the adult's actions (emulate) but when the model interacted with the child they would copy the actions (imitate). Children aged 14-months-old showed less of a distinction between the two conditions and were more likely to imitate in both. The findings reported by Nielson represent an interesting social approach to imitation/emulation by children which could represent an interesting extension to this current study. A second extension, as proposed in *Chapter 5*, could be to show children and chimpanzees the end-state of the task to determine whether children would replicate this.

The series of tests reported in *Chapters 6* and *7* add to a range of previously-published work which have shown emulation in children (Huang *et al.* 2002; Thompson & Russell 2004), apes (Tomasello *et al.* 1987; Toth *et al.* 1993; Call *et al.*

2005; Horner & Whiten 2005) and birds (Huber *et al.* 2001; Klein & Zentall 2003). In conclusion, both children and chimpanzees evidenced emulative learning, yet this matching only persisted in the responses of the children. Additionally, after having observed a conspecific demonstrator, both the children and chimpanzees showed a very high level of matching, which continued throughout the free-access response period (Figure 7.3). These, and other species differences outlined above, lay foundations for future comparative work that may further explain underlying causes

Chapter 8: Slide box open diffusion

Summary

Variant material-traditions have been documented between communities of wild chimpanzees and it has been proposed that these can be attributed to social learning. A number of studies with captive chimpanzees have sought to determine whether they are able to maintain a behavioural tradition within a group which has spread via social learning. In contrast to the majority of these previous studies, which have used two-action tasks, the findings reported here describe the social transmission of the two methods for operating a bidirectional task. The 'Slide-box' has a door on the front which can be pushed either to the left or right revealing a food reward. A chimpanzee from group L was trained to push the door to the left while another from group R was trained to push the door to the right. These chimpanzees were reintroduced to their group members who, in turn, observed the trained 'models' and operate the Slide-box themselves for up to nine hours. Despite the arbitrary nature of the task, the chimpanzees in group L pushed the door to the left significantly more than those chimpanzees in group R. Conversely, the chimpanzees in group R pushed the door to the right significantly more than those in group L. This differential spread between the two groups is a potential indicator that the chimpanzees learnt how to operate the device as a result of observing their conspecifics.

8.1 Introduction

Investigating the spread of novel behaviours within a group of captive chimpanzees has a long history (Menzel *et al.* 1972; Tonooka *et al.* 1997; Huffman & Hirata 2004). However, a limitation of these early studies is that they neither involved a second experimental group, nor a control group for comparison. To answer such criticisms, more recently Whiten and colleagues have published a series of experiments using an ‘open diffusion’ study with two experimental groups of chimpanzees and an additional third set of control chimpanzees for comparison (Whiten *et al.* 2005; Hopper *et al.* 2007; Whiten *et al.* 2007; see also *Chapter 3*). These two experimental groups were seeded with a chimpanzee proficient in one of two methods for solving a task, while chimpanzees in the control condition were provided with no such demonstration. Which method individuals in each experimental group used was recorded and this was compared to both the actions of (i) the model and (ii) those of control individuals.

Hopper *et al.* (2007; *Chapter 3*) replicated the original Whiten *et al.* (2005) study using the Pan-pipes apparatus. Hopper *et al.* found, like Whiten *et al.*, that the chimpanzees in the group seeded with the ‘Lift’ method for operating the Pan-pipes, used Lift significantly more than chimpanzees in the alternate group (seeded with ‘Poke’). Additionally, Whiten *et al.* (2007) expanded on the open diffusion paradigm further by testing and demonstrating both within-group and group-to-group transmission with two different apparatuses; the ‘Probe-task’ and the ‘Turn-ip’.

Whiten *et al.* (2007) described their findings as the first evidence for such inter-group diffusion in a non-human species and that such transmission may help to explain the

spread of behavioural variants observed among wild chimpanzees in Africa (Whiten *et al.* 1999).

The Pan-pipes (Whiten *et al.* 2005; Hopper *et al.* 2007), and also the Probe-task and Turn-ip (Whiten *et al.* 2007), are described as two-action tasks. The two-action method, as described in *Chapter 1*, was originally designed to control for both local and stimulus enhancement (Dawson & Foss 1965; Zentall *et al.* 1996). Originally, the two-action method involved a single manipulandum that can be operated in two different manners. It should be noted that, one criticism of the apparatuses applied by Whiten and colleagues in their open diffusion experiments was that they do not represent true two-action tasks. To gain the reward from the Pan-pipes, for example, two access points are manipulated for the two distinct methodologies (Lift and Poke) hence why it was termed ‘two-action’.

In addition to the two-action method, the second method often used to test social learning, is the bidirectional method (Collins 1988) in which a single manipulandum can move in one of two directions; usually left-right or up-down. Heyes & Dawson (1990) developed this for rats which observed conspecifics magazine-trained to push a vertical bar either to the left or right to gain access to a food reward. This design controls for stimulus and local enhancement as contact is made with the same area of the apparatus, regardless of the action. Additionally, unlike with the two-action design, the acting individual’s body posture should be comparable for both methods and therefore it is more likely that the observer pays attention to the action rather than the model’s body as a cue.

From the aforementioned strengths of the bidirectional task, this open diffusion experiment employed the ‘Slide-box’ apparatus (Hopper *et al.* submitted; *Chapters 6 and 7*). Previously, the Slide-box was used to adapt the methodology of Klein &

Zentall (2003) to investigate emulative-learning by chimpanzees by chimpanzees and children (as reported in *Chapters 6* and *7*). After observing a conspecific push the door on the Slide-box in one direction 58 times to gain a food reward, chimpanzees strongly matched the action (median proportion match = 1.00). This study aims to determine whether such a high fidelity of matching would be maintained when chimpanzees are tested in a group. It is predicted that if one group were seeded with 'Push-left' and a second with 'Push-right' two behavioural traditions would be created and maintained reflecting the results of previous open diffusion studies (Whiten *et al.* 2005; Bonnie *et al.* 2007; Hopper *et al.* 2007; Whiten *et al.* 2007).

Whiten *et al.* (2005) described that the chimpanzees in each experimental group used the same method as that used by the trained expert when operating the Pan-pipes. The Slide-box, in contrast, is potentially much simpler to operate and solve. To operate the Slide-box a door on the front of a cube can either be pushed to the left ('Push-left) or to the right ('Push-right') to reveal a food reward. Such a simple action may be vulnerable to corruption as shown with *the No-info Condition* reported in *Chapter 6* in which three of the eight chimpanzees were able to solve the task, despite being given no instruction. Conversely, when no instruction was provided for chimpanzees for the Pan-pipes, only one of the total 56 chimpanzees that have been tested were able to solve it (Whiten *et al.*; Hopper *et al.* 2007; *Chapters 3* and *4*).

Despite the positive findings of previous open diffusion studies (e.g. Whiten *et al.* 2005), when chimpanzees are tested in an group setting with the Slide-box, its simplicity may render it open to corruption and the spread of traditions more unlikely. Notwithstanding this, that each group will show a trend to use the method with which it is seeded (Push-left or Push-right) it is predicted and supported by the recent findings of Bonnie *et al.* (2007). They reported that chimpanzees maintained

behavioural traditions between two experimental groups, despite the arbitrary nature of the introduced task. Chimpanzees could put a token into either a 'pipe' or 'bucket' to gain a reward and each group was seeded with a chimpanzee trained in one of these methods. Regardless of the inconsequential rules of this task, the chimpanzees showed evidence for social learning and both groups maintained the method with which they had been seeded.

Ultimately, from the previous research detailed (Whiten *et al.* 2005; Bonnie *et al.* 2007) it is predicted that when two groups are seeded with the two alternative methods for operating the Slide-box, the chimpanzees in each group will use the same method as that used by the model. Because it is relatively simple for chimpanzees to learn the Slide-box through trial-and-error learning, if two captive traditions were to emerge across the two groups tested, this would provide extremely powerful evidence for social transmission of task-learning.

8.2 Methods

a. Experimental design

Subjects	23 chimpanzees
Apparatus	Slide-box (bidirectional task)
Conditions	2 group open diffusion Group L seeded with Push-left (n = 10) Group R seeded with Push-right (n = 13)
Independent variable	Direction of door push seeded
Dependent variable	The direction in which the observing group members pushed the door of the Slide-box

b. Participants and testing environment

The chimpanzees were housed in two groups, L and R, at MDACC. Group L comprised of 6 females and 4 males aged 26 - 6 years (mean 16.8 yrs) while group R comprised of 7 females and 6 males aged 44 – 7 years (mean 24.7 yrs). Table 8.1 provides detailed demographic information. Chimpanzee models (see the Procedure below) were trained in one half of their inside-cage, measuring 2.4m x 2.4m x 1.8m, while group testing occurred outside in their corral with a 21.3m diameter (see *Chapter 3*, Figure 3.1a).

Group L		Group R	
Female ID (age/yr)	Male ID (age/yr)	Female ID (age/yr)	Male ID (age/yr)
MU (26)	AX (21)	RH (44)	PA (36)
SO (18)	MA (14)	JU (41)	CA (35)
BE (12)	PE (19)	ME (42)	MR (15)
AA (22)	GA (6)	AP (26)	AU (15)
LE (9)		CO (22)	RU (11)
TI (21)		HA (16)	CH (11)
		SI (7)	

Table 8.1 The demographic information for the chimpanzees. Those in group L were housed in corral 7 and group R in corral 2 (see *Chapter 3*, Figure 3.1a).

c. Apparatus

The Slide-box, a bidirectional task was employed for this experiment. Please refer to *Chapter 6* (Figure 6.1) for a full description.

d. Procedure

(i) Training

A dominant female was selected from each of the two test groups based on the rationale described in *Chapter 3* and on observations of wild chimpanzees (Biro *et al.* 2003). MU, (26-years-old) was the model for group L and for group R, CO (22-years-old) was selected. Both chimpanzees were trained in isolation from their group, using positive reinforcement training. MU was trained to push the door to the left and CO to

the right. Each model was considered proficient once they pushed the door in the designated direction 30 times in succession.

(ii) Testing phase

The demonstrator chimpanzees were presented with the Slide-box in the presence of their group members in the outside corral of their housing. At all times, the Slide-box was on the outside of the cage and the chimpanzees could access it by reaching through the bars to slide the door. Initially, only the model chimpanzees were allowed access to the apparatus so that the observing chimpanzees all had a chance to see the Slide-box being used by the expert model, if other individuals attempted to use it the experimenter (LMH) pulled it out of reach. For both groups, this observation phase took two 20-min sessions.

After the observation phase the chimpanzees entered the open diffusion testing phase in which any chimpanzee was allowed to operate the Slide-box. This continued for 20 hours or until all the group members had successfully retrieved a reward 30 times. Following this, the open diffusion phase for group L lasted seven hours and for group R it lasted 9.5 hrs, with each test session lasting between 1 – 3 hrs.

(iii) Coding

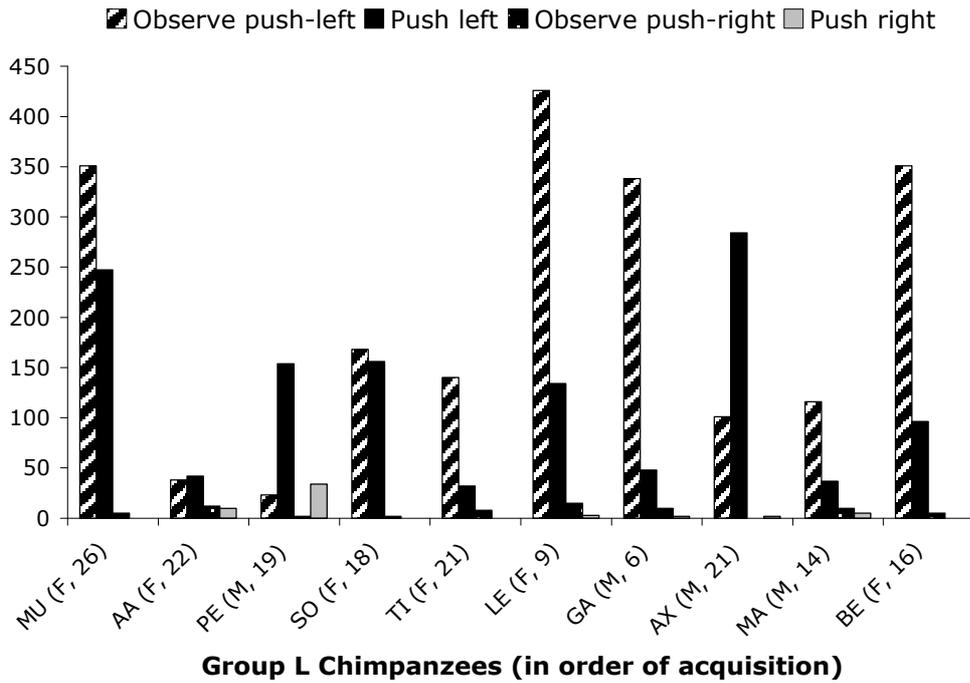
All test sessions were recorded on a Sony miniDV digital handycam (DCR-HC35E). A running commentary was provided by the experimenter (LMH). Which chimpanzee

operated the Slide-box and which chimpanzees observed each successful use of the Slide-box was noted. It was coded in which direction the door was slid when done sufficiently to gain a reward and with which hand the chimpanzee used to achieve this. An 'observing' chimpanzee was defined as one within 1 m of the Slide-box with their body oriented towards the apparatus.

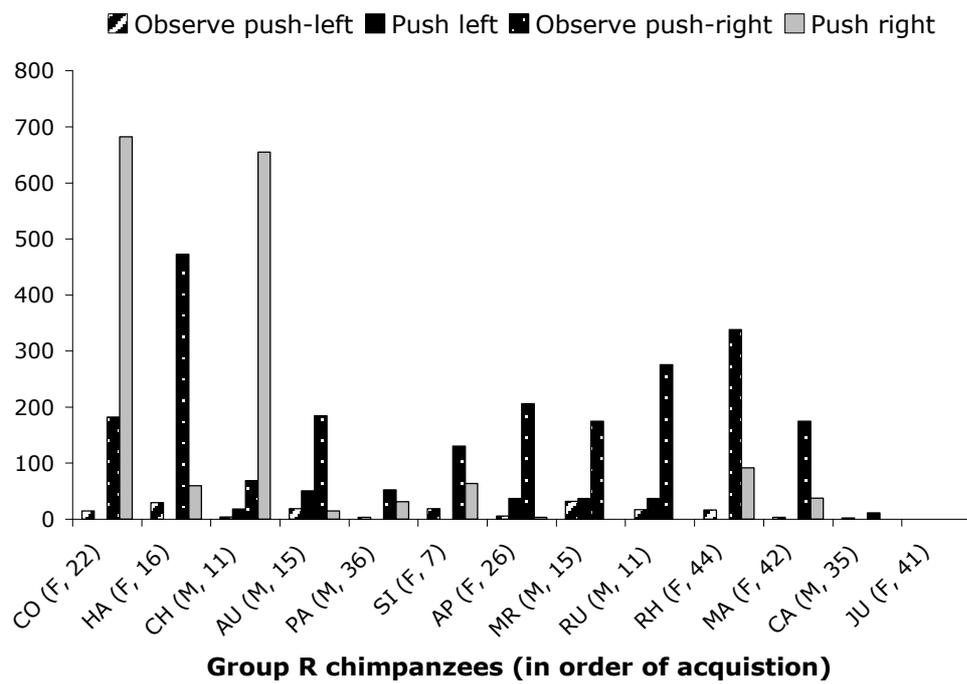
8.3 Results

All chimpanzees in group L (Figure 8.1a) and all but two chimpanzees in group R (Figure 8.1b) successfully operated the Slide-box the requisite 30 or more times. For all further analysis the responses of only those chimpanzees in group L ($n = 10$) and group R ($n = 11$) that successfully operated the Slide-box shall be included.

a



b



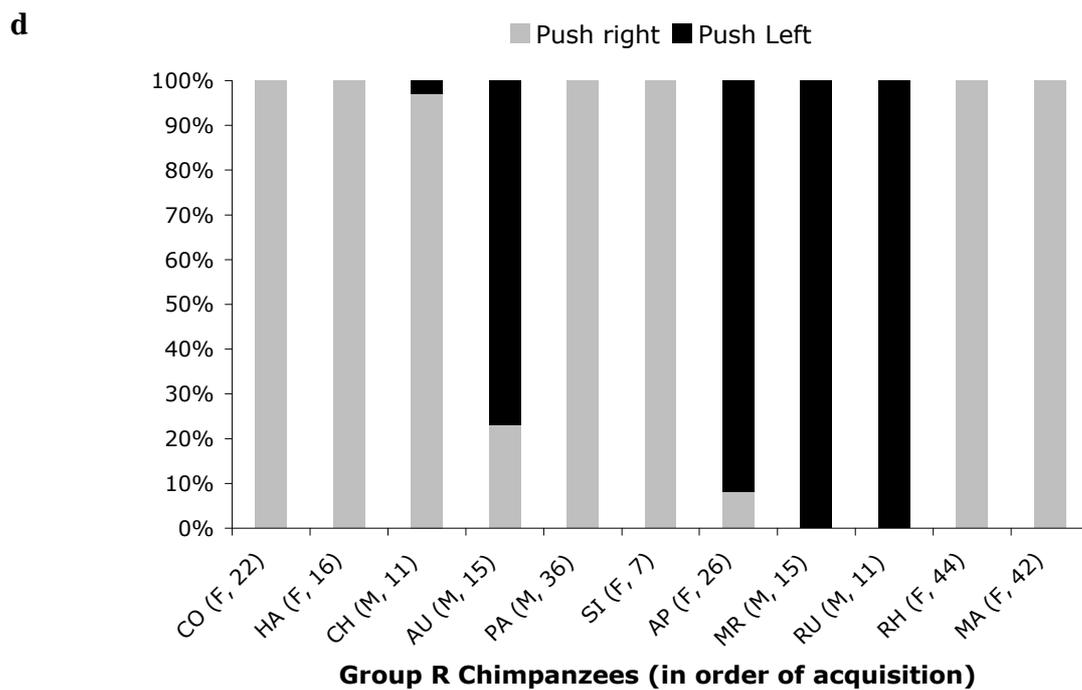
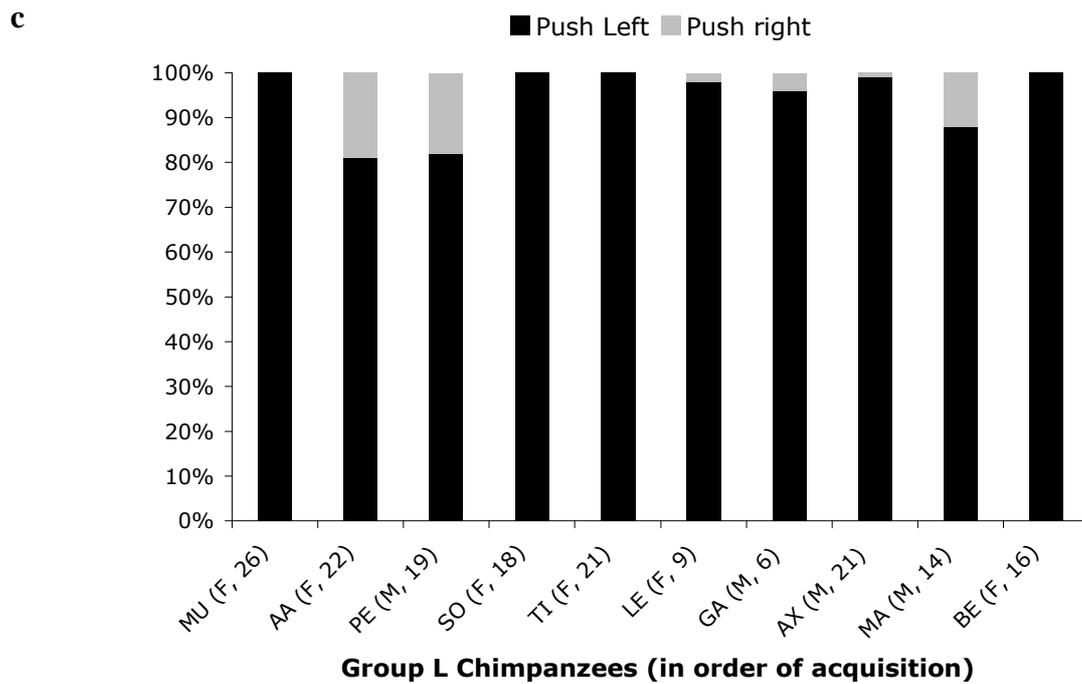


Figure 8.1 (Including previous page) What was seen by, and the subsequent responses, of chimpanzees in group L (a) and group R (b). Additionally, the proportion of matching responses made to the left and right by the chimpanzees in group L (c) and group R (d) are depicted. Each chimpanzee ID code is followed by sex (M, F) and age (years).

a. Matching demonstration in groups L and R

For group L the proportion of Push-left responses was calculated; ‘proportion Push-left’ = [number of Push-left/(number of Push-left + Push-right)]. This was significantly higher for group L (median proportion Push-left = 0.99, IQR = 0.10) than group R (median proportion Push-left = 0.00, IQR = 0.85; two-tailed Mann Whitney U test: $U = 8.5$, $n_1 = 10$, $n_2 = 11$, $P \leq 0.001$).

Likewise, for group R, the proportion of Push-right responses was calculated which was significantly higher for group R (median proportion Push-right = 1.00, IQR = 0.85) than group L (median proportion Push-right = 0.02, IQR = 0.10; two-tailed Mann Whitney U test: $U = 21.5$, $n_1 = 11$, $n_2 = 10$, $P \leq 0.05$). Overall, the chimpanzees in both groups used the same method as that demonstrated to operate the Slide-box as shown in Figures 8.1c and 8.1d.

b. Comparison of level of matching between groups L and R

There was no significant difference in the level of matching by observers to the demonstrated-direction between the two groups (two-tailed Mann Whitney U test: $U = 52.0$, $n_1 = 10$, $n_2 = 11$, $P \geq 0.05$), however this nonsignificance might be a result of the low statistical power.

c. Relation between direction of door-pushes made and observed door-pushes

A Spearman's correlation between the proportion of the Push-left responses by chimpanzees in Group L (median proportion = 0.99, IQR = 112.0) and the proportion of times they observed group members push the door to the left (median proportion = 0.97, IQR = 191.0; Spearman's correlation: $r_s = 0.64$, $P \leq 0.05$ 2-tailed).

The same pattern was not found for group R when a Spearman's correlation was calculated in the same manner. The proportion of Push-right responses (median = 1.00, IQR = 69.0) was not significantly related to the proportion of times they observed a fellow chimpanzee push the door to the right (median = 0.94, IQR = 88.5; two-tailed Spearman's correlation: $r_s = 0.23$, $P \geq 0.05$).

d. Hand-use

When the chimpanzees operated the Slide-box it appeared that it was more motorically simple for them to use the opposite hand to the direction which they pushed the door. For example if they pushed the door to the left, they appeared to use their right hand on most occasions whilst when they pushed it to the right they seemed to use their left hand more. However this potential pattern was not fully borne out.

When chimpanzees (across both groups) pushed the door to the left they were more likely to use their right than left hand (binomial test: $P \leq 0.01$), but when they pushed the door to right they were no more likely to use their left, than right hand (binomial test: $P \geq 0.05$).

To test this further, ‘proportion opposite’ was calculated for Push-left and Push-right across both groups. Thus, when chimpanzees pushed the door to the left, the proportion of times the chimpanzees used their right hand was calculated and compared to the proportion of times chimpanzees used their left hand to push the door to the right. There was no significant difference between the proportion that chimpanzees used the opposite hand when operating the Slide-box with Push-left (median = 0.80, IQR = 0.12) and Push-right (1.00, IQR = 0.46; two-tailed Mann-Whitney U test: $U = 144.0$ $N_1 = 15$, $N_2 = 15$, $P \geq 0.05$).

8.4 Discussion

Members of group L, which had been seeded with a chimpanzee trained to push the door of the Slide-box to the left, pushed the door to the left significantly more than the chimpanzees in group R. Additionally, the chimpanzees in group R, seeded with a chimpanzee trained to push the door to the right, also did so significantly more than the chimpanzees in group L. As was predicted, these two captive traditions reflect those previously reported (Whiten *et al.* 2005; Bonnie *et al.* 2007; Whiten *et al.* 2007).

The clear social learning effect demonstrated by groups L and R was more marked than that shown by chimpanzees at MDACC tested previously with the Pan-pipes (Hopper *et al.* 2007, *Chapter 3*). This is all the more robust given the simplicity of the Slide-box, which had an increased potential for chimpanzees to discover the alternative method for retrieving the reward than that used by the model. Maintaining similar incidental patterns of behaviour was also found by Bonnie *et al.* (2007) who

concluded that “chimpanzees are capable of duplicating a modeled sequence of initially arbitrary actions...to sustain different conventions” (p. 371).

The chimpanzees opened the Slide-box by pushing the door in the same direction as that used by their group’s respective models thus creating two behavioural traditions. Additionally, the level of matching to the demonstrator at a group-level was similarly high for both group L and group R with no significant difference found between the two. The Slide-box was selected for this experiment because it is a bidirectional task and the two methods for accessing the food reward were thought to be equally simple for the chimpanzees, so no bias would override potential transmission. That both groups showed the same high level of matching to the demonstration supports the supposition that both Push-left and Push-right were equally simple for the chimpanzees and thus the use of the Slide-box for such open diffusion experiments

When a trained model chimpanzee is introduced into a group they were allowed to operate the Slide-box in front of their group-mates for 40 minutes before the observing chimpanzees could access the apparatus. This was done to ensure that all chimpanzees saw the demonstrated method before using the Slide-box themselves. However, throughout the open diffusion testing phase the chimpanzees see further ‘demonstrations’ made by group members acting on the Slide-box, not all of which corresponded to the original demonstrated direction. Therefore it was predicted that the proportion of match-to-demonstrator responses would correlate with the proportion of actions made by fellow chimpanzees in the same direction. As predicted, for chimpanzees in group L the total proportion of Push-left responses that the group made as a whole was related to the proportion of times they observed a fellow chimpanzee push the door to the left. However for group R this was not the

case. As Figure 8.1 shows the chimpanzees in group R deviated more from the demonstrated method than did chimpanzees in group L and saw more non-match-to-demonstrator actions. Yet despite this corruption the group as a whole still showed significant matching to the demonstrated action comparable with group L.

For the chimpanzees it appeared physically more parsimonious for them to use their left hand to move the door to the right and to use their right hand to move it to the left. Indeed, it was found there was a significant correlation between using the 'opposite' hand to push the door to the left but not to the right. Chimpanzees have been described as having population-level handedness with a predominance of right-handed chimpanzees (Hopkins & Morris 1993) which is borne out by the higher level of those chimpanzees using their right hand when pushing the door. Despite this, it appears that the effects of social learning overrode any handedness preferences because the chimpanzees were more likely to push the door in the demonstrated direction than would be predicted if a handedness bias were at play. Further, chimpanzees with apparently a dominant handedness preference would use the more awkward method of using the same hand to move the door in order to match the demonstration rather than the motorically more simple way of simply pushing the door in the alternate direction. For example, in group R, CO and HA always used their right hand, yet continued to push the door to the right, even though it appeared to have been easier to slide the door to the left. Such conformity to social learning reflects the 'matching' defined by Whiten *et al.* (2005) in their sub-categories of social conformity. However these conclusions should be taken with caution as those chimpanzees in group R did show a greater level of deviance from the Push-right method introduced into the group (Figure 8.1d). Had the power of these data been great this deviation from the introduced behaviour may have been evidenced.

The strong preference to match the demonstrated direction had been observed previously when chimpanzees were presented with the same Slide-box in a dyadic situation (Hopper *et al.* submitted, *Chapter 6*). In such a scenario it was found that the chimpanzees matched the demonstration (median proportion match = 1.00). The level of matching in this current experiment was comparably high (Group L median proportion match = 0.99; Group R = 1.00). This demonstrates the strong social effect of social learning whereby even a relatively simple task is used in the same manner as that demonstrated and that this is maintained within a dynamic group of chimpanzees, not purely in the relatively stable setting of two chimpanzees isolated from their group members.

The two groups show significant levels of matching in the direction of door pushed by the group as a whole to that demonstrated. However not all chimpanzees pushed the door in the demonstrated direction all the time and one reason for this deviation is a notable point of interest. A number of the chimpanzees from group L, including LE, GA and AX and also CH from group R (see Table 8.1 for demographic details) on a few occasions pushed the Slide-box door in the opposite direction to that seeded and that which they predominantly used as individuals. This switch was often preceded by another observing individual attempting to usurp control of the Slide-box from them. The chimpanzee using the apparatus, at such a time would move their body between the observer and the apparatus, to block the observer's access to the Slide-box. The upshot of such a postural change was to cause the operating chimpanzee to switch the hand with which they operated the Slide-box and thus to move the door in the opposite direction. So such a change of direction in door-pushing was, on these occasions, a by-product of a tactic to prevent other

chimpanzees from gaining access to the Slide-box rather than an independent investigation of the task and subsequent corruption of the method.

This open diffusion experiment demonstrates that chimpanzees have the ability to maintain socially-learnt traditions of even a simple, arbitrary behaviour. Additionally it provides further evidence to support the use of the bidirectional method when testing for social learning in such scenarios.

Chapter 9: Observational Learning by Chimpanzees from a Video Demonstration

Summary

Video playback has been used with a variety of species in a range of experimental designs. It lends itself particularly well for use with chimpanzees as their vision is comparable to that of humans and the chimpanzees tested here often receive video presentations as enrichment. Video stimuli are particularly appropriate for social learning experiments because tight control can be maintained over the demonstration presented and repeated demonstrations can be given. Video footage of a chimpanzee operating the Slide-box apparatus by sliding a door to the right was presented to ten chimpanzees. After viewing the sequence, the observers were given free access to the Slide-box and a significant number were able to operate the device. Additionally, of those chimpanzees that were successful, significantly more pushed the door to the right than the left, thus matching the demonstration.

9.1 Introduction

Since the 1970s (Jenssen 1970) video-images have been used to varying degrees of success with a range of species in a number of experimental designs. The advancement and availability of video-manipulation technology in recent years has

facilitated its use and the range of its applications (see D'earth 1998; Rosenthal 1999; Rowland 1999 for reviews). Video stimuli have many potential beneficial uses. One is that the stimuli remain constant across all trials and for all subjects tested, allowing tight control to be maintained.

A second commonly cited reason for employing video playback is that the stimuli can be altered reliably through computer animation and manipulation or edited to show specific behavioural sequences. Clark & Uetz (1990) termed this process of manipulation 'videosection', which can refer to both morphological and temporal alterations made to the video sequence (Rosenthal 1999). Such stimuli manipulations have been used successfully with a variety of species including guppies (Nicoletto & Kodric-Brown 1999), spiders (*Schizocosa ocreata*, Uetz & Smith 1999) and chimpanzees (Morimura & Matsuzawa 2001).

Conversely, one limitation of using video footage is that, unlike with a live model, the subject is unable to interact with the video recording. Consequently, observing subjects may not perceive the stimuli to be realistic and so may not pay attention, or fully respond, to it. Ord & Evans (2002) overcame this when testing male-male Jacky dragon (*Amphibolurus muricatus*) displays. They designed a computer algorithm which allowed the experimenter to edit recorded video footage of a male's display in real-time whilst it was being presented to a male conspecific. Ord & Evans were therefore able to show footage which appeared to react to the behaviours of the observing test subject, resulting in more naturalistic responses from the observing Jacky dragons.

A second limitation of using video footage as a stimulus is that television screens have been developed for human vision, which is not necessarily suitable for all species. The refresh-rate for cathode ray tube (CRT) television screens in America is

60 Hz (National Television Standards Committee, NTSC) whilst in Europe it is 50 Hz (Phase Alternating Line, PAL and *Séquentiel couleur à mémoire*, SECAM) both of which are suitable for human's critical flicker-fusion (CFF) of 60 Hz (Landis 1954). Some animals however have a CFF which is faster than that of humans (D'earth 1998 provides a comprehensive overview). Animals with a faster CFF observe the screen flicker and thus may be unable to detect the image on the screen. Thin film transistor liquid crystal displays (LCD) can be utilised to overcome such limitations (Mottley & Heyes 2003; Ophir & Galef 2003). Mottley & Heyes found that budgerigars (*Melopsittacus undulates*) copied a conspecific that removed a stopper from a box to gain food rewards when this was either a live model or video footage of a model on thin film transistor LCD.

In addition to the refresh-rate of televisions, the colour-display has also been designed for human vision and may not accurately reflect all the colours of the filmed stimuli. Many insects are able to detect ultraviolet wavelengths (Briscoe & Chittka 2001) represented on a CRT television monitor, so the subject may not recognise the image as intended. Despite this, jumping spiders (*Maevia inclemens*) responded to video images presented both in black-and-white (Clark & Uetz 1990) and colour (Clark & Uetz 1992).

Chimpanzee vision is very similar to that of humans (Landis 1954) having the same CFF (60 Hz) and being trichromatic. This suggests that they should perceive a moving image on a television screen in the same manner as humans. Indeed, video stimuli have been used with chimpanzees in a variety of experimental paradigms including tests of self-recognition (Eddy *et al.* 1996; Hirata 2007), memory abilities (Morimura & Matsuzawa 2001) and understanding of causal relations (Cacchione & Krist 2004; O'Connell & Dunbar 2005). Chimpanzees have also shown the ability to

use video footage as a reference for real-world events in order to locate out-of-sight items (Poss & Rochat 2003).

For social learning experiments, the theme of this dissertation, video stimuli could potentially be a highly usable resource for testing the underlying mechanisms of transmission because they allow for tight control over the presented demonstration and are particularly applicable to testing in a captive environment. Captive populations are often small and there are rarely multiple groups of a particular species. In such cases using video footage of a trained demonstrator allows for repeated use of the same model, which can be shown to different groups without the need for translocation. It also reduces the number of animals used as models, thus maintaining a higher pool of animals in the test population. Price & Caldwell (2007) showed footage of one colobus species (*Colobus polykomos*) to a second (*C. guereza kikuyuensis*) housed at Paignton Zoo, UK, allowing all of the already two small populations of observing individuals to act as test subjects.

The use of video stimuli additionally allows the experimenter to guarantee that all observers are given the exact same demonstration including the assurance of an equal number of viewings of the desired act and the same level of visual access to the task. When testing chimpanzees in a group setting (*Chapters 3, 4 and 8*) it has been observed that subordinate individuals maintain a distance from dominant group-mates acting on the device, which in turn reduces their exposure to the task and so they are provided with fewer viewing opportunities. Presentation of a video demonstration to individual chimpanzees in the manner described in this study would allow all subjects to receive the same number and comparable quality of demonstrations.

Chapter 4 of this dissertation describes a series of experiments run to determine the amount, and format, of information required by a chimpanzee for them to

successfully operate the Pan-pipes. After chimpanzees had been shown a video of a chimpanzee demonstrating the Lift method for the Pan-pipes, at least two, and possibly four, chimpanzees from two of the groups tested learnt Lift. Such preliminary findings provide encouragement and an impetus for more rigorous testing to determine whether chimpanzees can learn from video stimuli.

For social learning experiments, video stimuli allow for the potential propagation of novel behaviours in multiple animals by providing a reliable and consistent model. Such an advantage, coupled with the promising results reported in *Chapter 4*, along with those of other researchers cited above, led to the design of this study. The aim was to investigate the abilities of captive chimpanzees to learn from observing video footage of a conspecific presented on a television screen. It was predicted that chimpanzees, after having observed footage of a conspecific operating a bidirectional device should (i) be able to operate the device when given access to it and (ii) use the same method as that demonstrated.

9.2 Methods

a. Experimental design

Subjects	10 chimpanzees
Apparatus	Slide-box (bidirectional task)
Conditions	Video showing a chimpanzee model pushing the Slide-box door to the right
Independent variable	The provision of a video demonstration
Dependent variable	Ability of chimpanzees to use Slide-box and direction in which they pushed the door of the Slide-box

b. Participants and testing environment

Ten chimpanzees, housed in three groups, at MDACC were used and all were familiar with televisions as part of their enrichment program. The chimpanzee subjects comprised of 5 females and 5 males aged 15 - 37 years (mean 21.7 yrs). Table 9.1 provides further demographic information. Chimpanzees were presented with the video demonstration in one half of their inside-cage, measuring 2.4m x 2.4m x 1.8m. During non-testing times, chimpanzees lived in their social groups and had access to an outside corral with a 21.3m diameter (*Chapter 3* Figure 3.1a).

Male ID (age/yrs)	Female ID (age/yrs)
KO (15)	BE (16)
HO (16)	MX (19)
BA (17)	OO (20)
MA (35)	TY (20)
MO (37)	MY (22)
KM (18)*	

* KM was the chimpanzee used as the model on the video

Table 9.1 The demographic information for the chimpanzees shown the video demonstration.

c. Apparatus

(i) The Slide-box

The Slide-box, a bidirectional task was employed for this experiment. Please refer to *Chapter 6* (Figure 6.1) for a more detailed description.

(ii) The television and miniDV video-camera

The video demonstrations were filmed on a Sony miniDV digital handycam (CDR-TRV27). All video demonstrations were presented on a Zenith full-colour television with an 45 cm screen which was set on a trolley placing the screen 80 cm above the ground.

c. Procedure

(i) Rationale

It was decided, due to the small available sample size, that only one of the two possible directions of door pushes would be shown to all observer chimpanzees. When the Slide-box was used in a previous experiment (*Chapter 6*; Hopper *et al.* submitted) only three of the eight chimpanzees were able to operate it when given no instruction. Of these, three, two chimpanzees pushed the door to the left one pushed the door to the right. As ‘right’ was the direction deemed least-likely to be used spontaneously by the chimpanzees, it was chosen as the direction to be demonstrated.

(ii) Training and filming

An adult male chimpanzee, KM (Table 9.1), trained through positive reinforcement training techniques to push the door on the Slide-box to the right with, was selected as the model for this study. Filming for the video was conducted in the outside Primadome of KM’s cage (*Chapter 3*, Figure 3.1a). He was isolated and presented with the Slide-box on one side of the cage, which he operated whilst being filmed from the far side of the Primadome. The filmed demonstration showed a head-and-shoulders shot of KM operating the Slide-box 58 times as well as a side-view to give a clear image of the grape and KM eating it (Figure 9.2).

a



b



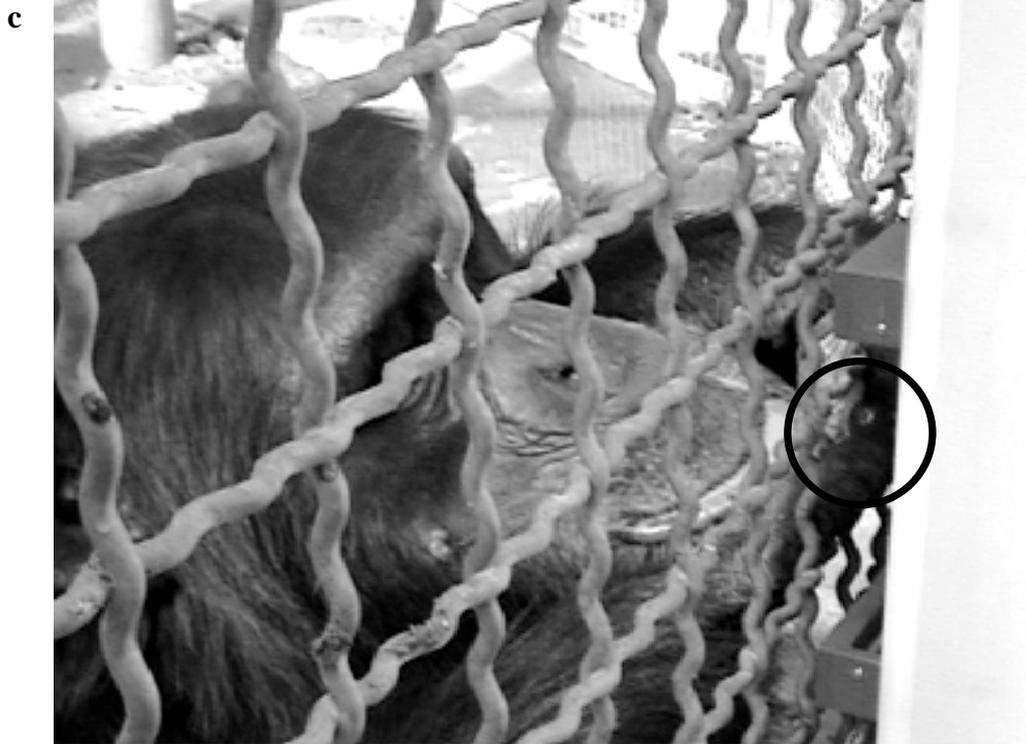


Figure 9.2 (including that on previous page) Stills from the video footage presented, showing model chimpanzee KM (M, 18) operating the Slide-box. Three views were presented which were (a) a wide-angle shot, showing the whole of KM's body and the apparatus, (b) a close-up shot of KM pushing the Slide-box door to retrieve the grape and (c) a side-view of KM retrieving the grape highlighted with a circle) from the Slide-box. This third angle was shown because when filmed from behind when he retrieve the reward, his head occluded the grape and so this third angle was used to show the observer chimpanzees the reward and KM eating it.

(iii) Testing phase

Following the methodology of Klein & Zentall (2003) and that described in *Chapter 6* the video that was presented to the observer chimpanzee showed 58 demonstrations of KM pushing the Slide-box door to the right. Each observer chimpanzee was isolated in their inside caging and the demonstration was displayed on a television as detailed above. Throughout the presentation, the Slide-box was in full view, but out of reach,

of the observer chimpanzee. After the presentation the apparatus was moved within reach of the chimpanzee and they were given a 10-minute free-access period with the Slide-box.

e. Coding

The whole testing period was recorded on a Sony miniDV digital handycam (DCR-HC35E) and a running commentary was provided by the experimenter (LMH). For the free-access period, any successful response by the chimpanzee during the 10-minute period was recorded together with the direction the screen door was pushed. A ‘successful response’ was defined as one where a chimpanzee retrieved a reward from the Slide-box by sliding the door to either the left or right. A chimpanzee, consistent with previous studies (Whiten *et al.* 2005; Hopper *et al.* 2007) was deemed proficient if they were able to operate the Slide-box on 30 or more successive interactions.

9.3 Results

a. General proficiency

Of the ten chimpanzees presented with the Slide-box video demonstration ‘Push Right’ eight responded successfully (Figure 9.3). However one chimpanzee (MX) only responded on three occasions (one response to the right, two to the left), after which she ceased interacting with the Slide-box. It had been decided that a

chimpanzee's response would be classed 'proficient' if it retrieved a reward on 30 successive attempts, therefore MX's response were classed as a 'no response' in further analysis.

That a majority of the chimpanzees were proficient (seven of the ten) compared to the minority able to solve the task when presented with it with no information (3/8) as reported in *Chapter 6*, but this difference is not statistically different (Fisher Exact test: $P \geq 0.05$).

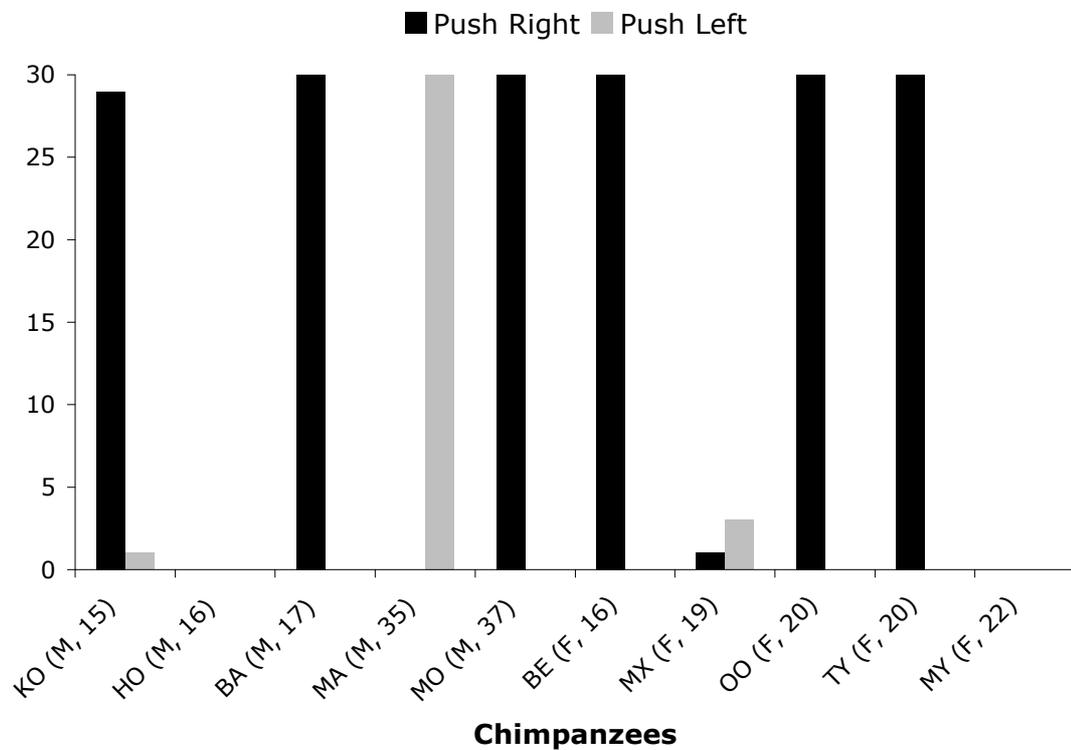


Figure 9.3 The successful responses made by the chimpanzees, capped at 30, in the 10-minute free-access period after the video demonstration in which 'Push Right' was demonstrated by KM. Each chimpanzee ID code is followed by sex (M, F) and age (years).

b. Video model versus live model

When provided with a live model (*Chapter 6*) all eight chimpanzees were able to operate the Slide-box, regardless of whether they pushed the door in the same direction as that demonstrated. The number of chimpanzees who were proficient after having seen the live model was not significantly greater than the number able to operate it after observing the video model (Fisher Exact test: $P \geq 0.05$).

c. Level of matching

This measure of proficiency defined above does not concern the direction in which the chimpanzee moved the Slide-box door and whether that relates to the demonstrated direction of movement. Testing the latter, of the seven chimpanzees that responded 30 times or more, significantly more push-door responses to the right, than to the left, were made (6/7; two-tailed Wilcoxon Matched Pairs Test: $Z = 1.960$; $P \leq 0.05$; see Figure 9.3).

9.4 Discussion

There was no significant difference between the numbers of chimpanzees able use the Slide-box after watching a video of a conspecific compared to those who had observed a live chimpanzee model. Additionally, those chimpanzees who successfully operated the Slide-box after having seen the video demonstration, with just one

exception used the same method as that used by the model on the video.

Chimpanzees thus appear to be able to ‘understand’ an image presented on a television screen and are then able to transfer this to real-world objects, as described by Poss & Rochat (2003). That the chimpanzees not only learnt how to operate the Slide-box but also used the same method as demonstrated suggests that the stimulus was a socially relevant one for them.

It was proposed that video would be a suitable stimulus to present to chimpanzees because their vision is comparable to that of humans, for whose vision television screens were designed. From the positive findings presented here it appears that such a rationale was borne out, and that using a CRT television screen was not a hindrance as it may be when testing other species such as birds. Despite this, a note of caution should be observed. Chimpanzee vision is so similar to that of humans that it may be assumed that because chimpanzees are able to *perceive* an image on a television they can therefore *understand* the display with which they are presented, but this is not always tested for.

Cacchione & Krist (2004) used televisions to present footage of possible and impossible events to determine the chimpanzees’ ability to distinguish causal relations. However, although the authors stated that the chimpanzees were familiar with experimental protocol, no justification for the use of video stimuli with regard to the chimpanzees’ understanding or experience with it was given. There is evidence that children have to learn how to interpret video images (see Troseth & DeLoache 1998 for a review) and so it is not unreasonable to expect that chimpanzees would also have to do so. Experiments, such as the one presented here, testing chimpanzees understanding of video could be made before video is used in other paradigms.

A second limitation of presenting video footage, as described previously, is that the subject is unable to interact with the video stimuli. The chimpanzees tested in the study described here were able to learn from the video of a conspecific operating the Slide-box even though they were unable to interact with the model. It appears that for social learning experiments an interaction between model and observer is not obligatory and so video demonstrations lend themselves to such investigations. Active teaching between chimpanzees is rarely documented (Boesch 1991) and especially not between non mother-infant pairs. Chimpanzee learning appears to be more passive on the part of the expert model (Whiten *et al.* 2004) and this may explain why video footage of demonstrators that, cannot interact with the observer, is as affective as a live model.

Not only was the observer unable to interact with the filmed demonstrator chimpanzee, but the model was also an unfamiliar individual. Despite this, the observers still significantly matched the demonstrated direction when moving the door on the Slide-box. It has been suggested that chimpanzees may be more likely to copy a familiar individual with whom they relate (de Waal 1998), but in this instance it seems that it is not necessary. However, that the demonstrator was a conspecific may have been important for such copying in comparison to footage of a human demonstrator, for example (*c.f.* Chapter 4).

The findings presented here suggest that video is a viable stimulus for use with chimpanzees and is well suited for use in social learning experiments. This study has shown that isolated chimpanzees can learn from observing video footage of conspecifics and an extension of this work would be to present such videos to chimpanzees in a group setting as preliminarily tested by the author (Chapter 4). In support of this, Price & Caldwell (2007) presented video footage of a king colobus

operating an apparatus to groups of Abyssinian colobus. They utilised an apparatus which could be opened with one of two methods; 'push' or 'pull'. The experimenters showed one group of Abyssinian colobus footage of the push method, while a second group was shown the pull method. After 10 demonstrations of the videos with access to the apparatus, the group shown the push-method video used the push method significantly more than the group shown the pull-method video.

Further, group-to-group transmission could be simulated by presenting footage of a chimpanzee to multiple groups following on from the work of Whiten *et al.* (2007). Such an experiment would reflect how novel behaviours are seeded in wild communities of chimpanzees, where it has been proposed that behaviours are introduced to groups by chimpanzees observing an incoming individual which is already proficient in a behaviour pattern novel to the group (Whiten *et al.* 2001). This latter method could be experimentally tested with video stimuli of an unknown chimpanzee and shown to multiple groups of chimpanzees.

With the advancement and availability of video-editing software, it is now relatively simple to manipulate video images which can be employed to determine particular aspects of a demonstration are required for a chimpanzee to learn from it. Both temporal and morphological alterations could be made to the video (Rosenthal 1999) thus varying the number and rate at which demonstrations are presented as well as altering the look of the demonstrator and/or the apparatus. The behaviour of the demonstrating chimpanzee could also be affected in such a way as to make it appear sick or drowsy to enquire whether such a model is deemed 'reliable' by the observer. This could be done by comparing the rate of learning by chimpanzees after seeing an un-manipulated model compared to a model altered to appear sick.

Video manipulations are advantageous because they do not require affecting the live model in a detrimental manner as has been done with Japanese quail (*Coturnix japonica*) which were drugged to induce altered behaviour (Yamazaki *et al.* 2004). These quail were subsequently filmed and presented as models to observing conspecifics to determine whether the observers discriminated against models with altered behaviour compared to those with ‘normal’ behaviour (this was found to be the case).

Ghost conditions have been used both with the Slide-box and Pan-pipes and their use is documented previously in this dissertation in *Chapters 4 – 6* (Hopper *et al.* 2007; submitted). The basic premise of such a condition is to move the pertinent parts of the apparatus to demonstrate the affordances of it to the observing individual without a conspecific model acting on it. Ghost conditions have been employed to tease apart the underlying mechanisms of social learning and to provide an active test for emulative learning (Fawcett *et al.* 2002). Video stimuli offer the potential for creating an alternative to this. One method would be to film a traditional ghost condition – moving the apparatus with fishing line – and present this to the observers with it filmed in such a way as to not show the fishing line or the experimenter moving it. This would produce a ‘cleaner’ ghost condition without the potential contamination of the experimenter attempting to surreptitiously move the device in front of the observer.

Alternatively, a conspecific could be filmed using the apparatus in such a manner that the resultant video footage does not reveal their presence or to not show all of the device. Such footage may reflect a real-life scenario in which the moving parts of the apparatus are occluded by the demonstrator or other observing individuals from the sight of a particular observer (for example, by cutting to a close-up), thus creating a

'natural' ghost condition. Varying degrees of occlusion could be presented to determine exactly how much information an observer requires in order for them to adequately learn the task.

The findings of this experiment suggest that chimpanzees are indeed able to learn from video footage of a conspecific using a particular apparatus and that such stimuli are well suited for future social learning experiments. Not only do videos provide reliable and consistent models but they also allow for the potential for image and temporal manipulation for a wide array of research topics.

Chapter 10: General discussion

The series of experiments reported in this thesis were conducted with both chimpanzees and children to investigate social learning. Both species were tested in a number of comparable scenarios, to determine whether they were capable of learning from conspecifics and maintaining behavioural traditions, and to identify the social learning evidenced by each species. Each experiment was discussed in the relevant chapter, providing potential explanations for the observed behaviours and how the findings related to the discipline of social learning as a whole. This chapter will provide a summary of the reported findings whilst considering them in a broader context. In addition, proposed future studies will be detailed, describing the rationale for them along with brief methodological considerations.

10.1 Overview of results: chimpanzees and children compared in a wider context

a. Dyadic interactions

Both the chimpanzees and children were tested in pairs, in which an observer watched a conspecific model manipulate an apparatus. The chimpanzees and children were studied in this manner with the Slide-box apparatus, from which the reward could be retrieved by pushing the door to either the left or right (*Chapters 6 and 7*). Not only

were all the observers of both species successful in retrieving the reward, but they also pushed the door in the same direction as that used by the model.

In another experiment (*Chapter 5*), children observed a conspecific operating the Pan-pipes apparatus, from which the reward could be gained by using either a Lift or Poke method. Seventeen of the 20 child observers successfully operated the Pan-pipes, all using the same method that they had observed the model use. These dyadic tests show that both chimpanzees and children are capable of matching a model with a high fidelity when tested with problem-solving tasks, which is suggestive of imitation.

Previously, chimpanzees and children have been tested in similar dyadic circumstances observing a conspecific performing a target behaviour or operating an apparatus (see Want & Harris 2002; Whiten *et al.* 2004 for reviews). A variety of studies had previously shown that children were able to copy from observing fellow children (Hanna & Meltzoff 1993; Horner *et al.* 2006; Flynn & Whiten in press) and adults (Meltzoff & Moore 1977; Nagell *et al.* 1993; Tomasello *et al.* 1993*b*; Call & Tomasello 1995; Call *et al.* 2005). This ability was shown even when a delay was imposed between the observation period and the child's response (Barr *et al.* 1996; Hayne *et al.* 2000; Herbert & Hayne 2000*b*).

The majority of these papers describe children imitating either body gestures or relatively simple manipulations of an apparatus. In contrast, the results reported in *Chapter 5* regarding the Pan-pipes, demonstrate that children as young as 3-years-old are capable of faithfully copying a model's method of using a tool. Significantly fewer children discovered how to operate the Pan-pipes when provided with no such information. Despite the apparent complexity of the Pan-pipes for them, the children still adeptly used the tool and in the same manner as that used by the adult.

The chimpanzees, like the children, were able to copy a conspecific which they had observed using the bidirectional Slide-box to gain a reward. The abilities of chimpanzees observing a model in a dyadic situation had been tested before, but often with a human model (for example see Nagell *et al.* 1993; Whiten *et al.* 1996 but see Tomasello *et al.* 1987; Call *et al.* 2005; Tennie *et al.* 2006). Comparisons were drawn between the responses of the chimpanzees who had observed a human with those of children presented with the same task. However such comparisons are limited because only the children watched a conspecific, and for chimpanzees, observing a human may have added another level of complexity to the task. This criticism makes the positive findings of imitation by chimpanzees reported by Whiten *et al.* all the more impressive. More recently, however, more studies are using conspecific models when testing great apes (Hirata & Morimura 2000; Call *et al.* 2005) and it is this tradition that the studies in this thesis follow. The positive findings reported in *Chapter 6* lend further support to the rationale for using conspecific models when testing animals and this should be encouraged in future experiments.

b. Diffusion chains and open diffusion studies

Testing subjects in a dyadic context gives great control over what they can observe, as well as when and for how long they can interact with the test object after observing a model. Additionally, learning in pairs relates to that observed between mothers and their infants. Despite this, testing in this manner has its limitations. It has limited ecological validity as it provides no information about how social learning allows for the spread of a new behaviour among many individuals. The results of experiments

with chimpanzees and children tested in pairs (*Chapters 5 – 7*) provided evidence that they were able to learn from conspecific models with a high level of fidelity. Further studies were conducted employing diffusion chains and open diffusion designs in order to gain an insight into whether each species was capable of maintaining a new tradition across a number of test ‘generations’ (subject-to-subject transmissions).

In the wild, chimpanzees have been observed to show a variety of behavioural variants that differ between communities (Whiten *et al.* 1999; 2001; Whiten 2006) and these have been proposed to have spread within each group via social learning (but see Humle & Matsuzawa 2002; Laland & Hoppit 2003). In order to methodically test the propensity of chimpanzees to learn socially from one another, and to display the maintenance of behavioural traditions, two open diffusion experiments were conducted with the chimpanzees at MDACC. These experiments involved two different apparatuses; (i) a two-action task involving the use of a tool (the Pan-pipes) and (ii) a simpler, bidirectional task (the Slide-box). Such cross-comparisons between the learning of different apparatuses are important because they provide a depth of knowledge about the transmission of behaviours by chimpanzees.

The study reported in *Chapter 3* describes a replication of one previously conducted by Whiten *et al.* (2005). A chimpanzee from one group (group L) was trained how to use the Pan-pipes with the Lift method. It was intended that a second group would be seeded with a similarly-trained individual but to use Poke, however this proved unfeasible. Fortuitously, a chimpanzee in the control group (group C) discovered the Poke method and so this group was allowed to continue interacting with the Pan-pipes for the same length of time as the group seeded with Lift. Although chimpanzees in both groups used Poke, only three chimpanzees in group C used Lift and only on four occasions. Therefore, there was a difference between the

two groups, with those chimpanzees in group L using Lift significantly more than those chimpanzees in group C. The two groups of chimpanzees tested at Yerkes (Whiten *et al.*) had shown a more marked difference, with two traditions emerging with one group predominantly using Poke, and the other Lift. The difference between chimpanzees' responses at Yerkes and MDACC highlights the importance of testing different chimpanzees (at different study centres) but with the same apparatus.

The second open diffusion experiment involved the use of the Slide-box (*Chapter 8*). One group of chimpanzees (group L) was seeded with a chimpanzee trained to push the Slide-box door to the left, while the second (group R) had a chimpanzee trained to push the door to the right. Chimpanzees in group L predominantly pushed the door to the left, significantly more than did chimpanzees in group R. Similarly, those chimpanzees in group R operated the Slide-box by pushing the door to the right significantly more than chimpanzees in group L. This clear effect provides stronger evidence for social learning than the study of chimpanzees, also at MDACC, when provided with the Pan-pipes.

The spread of behaviour, with chimpanzees using the same method as that of their group model when operating the Slide-box, is particularly impressive evidence of social learning because the task is simpler than that of the Pan-pipes and 'vulnerable' to individual discovery and learning. When provided with no information, three of eight chimpanzees tested were able to operate the Slide-box, whereas only one of a total of 50 chimpanzees at MDACC presented with the Pan-pipes in a comparable no-information condition discovered a way to operate it (and this was in a group situation). Despite the simplicity of the Slide-box, very little corruption occurred in each of the test groups, with the majority of chimpanzees using the seeded method.

This provides strong support for social learning in a group situation and reinforces the earlier findings of Bonnie *et al.* (2007).

However, as highlighted by Horner *et al.* (2006), one limitation of open diffusion experiments is that it is problematic to discern who learns from observing whom. All group members could learn from watching the original model or they could learn from later successful individuals. These potential patterns of diffusion within a group reflect those of 'cultural diffusion' illustrated by Whiten *et al.* (2001, Figure 1). To overcome this shortcoming of the open diffusion method, a complementary diffusion chain was run with children (*Chapter 5*). Historically, diffusion chains were originally employed by Bartlett (1932) when testing adults (see also Baum *et al.* 2004; Mesoudi & Whiten 2004). To date, only a few comparable diffusion chains have been conducted and mainly with children (Horner *et al.* 2006; Flynn & Whiten in press; Whiten *et al.* in press) but also a small number of other species including chimpanzees (Horner *et al.* 2006) and birds (Curio *et al.* 1978).

In the experiment reported in *Chapter 5*, one child (A) was shown how to operate the Pan-pipes using Lift after which a second child (B) observed them using it, then child B was allowed to use the Pan-pipes. This pattern of transmission continued, as described previously, with child C watching child B, and child D watching child C, so on and so forth. A diffusion chain, seeded this way, continued along 20 children (19 child-to-child transmissions) with 100% fidelity.

A methodological approach intermediate between the diffusion chain and an open diffusion experiment is the 'replacement method'. It was originally used with chimpanzees by Menzel *et al.* (1972) and has been developed more recently by Laland and colleagues (Laland & Williams 1998; see also Galef & Allen 1995). This

method, as described in detail in *Chapter 1*, could easily be applied in future experiments with children and potentially also chimpanzees.

From the positive results provided in this thesis, open diffusion experiments and diffusion chains have been shown to provide rich detail about social transmission among both chimpanzees and children. The findings demonstrate that both species show a disposition to learn from observing conspecifics and maintaining a behavioural tradition among group members.

c. Ghost conditions

The dyadic studies, diffusion chains and open diffusion experiments provided evidence that both chimpanzees and children were able to learn socially from conspecifics. The dyadic studies, in particular, suggested that chimpanzees and children were capable of imitative learning. To disentangle imitative from emulative learning, ghost conditions were employed. In a ghost experiment, the pertinent moving parts of an apparatus or tool are moved discretely and surreptitiously by the experimenter. The apparatus thus appears to move as if operated by a ‘ghostly’ agent. Tomasello (1990) defined emulation as learning from changes that occur in the environment and a ghost condition provides such information for the observing subjects.

Ghost conditions of the Pan-pipes and Slide-box were provided to the chimpanzees and children. There were both similarities and differences between the responses of the two species after observing such ‘demonstrations’. No chimpanzee learnt Lift from the ghost Lift condition with Pan-pipes, whether they had a baseline

free-access period or not (*Chapter 4*). Additionally, showing the tool in the ghost condition did not enhance their ability to operate the Pan-pipes. Across all these conditions, whether tested in isolation or in their group, only one chimpanzee did Poke on one occasion and it was never repeated. For the Pan-pipes, chimpanzees appeared much better able to learn from observing a conspecific or video footage of a conspecific.

In comparison to the chimpanzees' failure to respond to the ghost conditions with the Pan-pipes, all but one chimpanzee adeptly used the Slide-box after seeing a ghost condition of the door movement to the left or right (*Chapter 6*). Not only were the chimpanzees in the ghost conditions able to operate the Slide-box but a significant number moved the door in the same direction as that of the ghost condition with their first response¹³. Interestingly, this level of matching was comparable to that shown by chimpanzees who had observed a live conspecific model. Although chimpanzees showed this initial tendency to emulate, the pattern of responses was not maintained over the 20-minute response period. These results represent the first evidence of chimpanzees emulating when tested with a ghost condition and are in contrast to those of Subiaul *et al.* (2004) and Hopper *et al.* (2007). However, other evidence for emulation was shown in a previous study which showed chimpanzees the end-states of a particular test apparatus (Call *et al.* 2005).

In contrast to the chimpanzees, when the children were tested with a ghost condition of the Pan-pipes they were no less successful in Ghost condition Lift than in Demonstration Lift, in which they observed an adult model (*Chapter 5*). However this was not the case for Ghost condition Poke in which only two children were able to

¹³ This was true when the responses of the chimpanzees in the Enhanced-ghost and Ghost conditions were collapsed

gain the reward from the Pan-pipes; both used a novel, Push-Slide, method. Despite the reduced matching shown by children in the ghost conditions collectively compared to the demonstration conditions, nine of the 20 children tested in both ghost conditions were still able to operate the Pan-pipes regardless of the method that they used. That nearly half the children tested were able to learn something from the ghost conditions is markedly different from the chimpanzees.

Like the chimpanzees, the children were presented with ghost conditions of the Slide-box (*Chapter 7*). Also like the chimpanzees, with their first responses the children showed significant matching to the ghost conditions when considered together, comparable to that shown by children who had observed a fellow child model. In contrast to the chimpanzees, however, the children showed continued matching not only in the Push-demo condition but also in the Enhanced-ghost condition. These findings about the children's responses to ghost conditions support previous positive findings of children matching to ghost conditions suggestive of emulation learning (Thompson & Russell 2004; Tennie *et al.* 2006) but are in contrast to other previous work, which has found that children are likely to imitate, rather than emulate, even when it is not the most logical method (Horner & Whiten 2005).

The chimpanzees and children responded differently both from one another and across the different conditions. However, they both were able to learn something from at least one of the ghost conditions. To help illuminate these findings and the existing array of definitions for emulation (Byrne 2002a), a new three-tier terminology for emulation was proposed (see *Chapter 5* for full definitions). The responses of the chimpanzees and children were also categorised throughout this thesis with regard to this three-level scheme of emulation (*Chapters 5 – 7*). It is proposed that it could be

applicable to a number of previous and future studies investigating emulative learning, not just by primates, but with any species tested.

The first of the three levels of emulation was comparable with goal and end-state emulation (Level 1). This pertains to the replication of results or goals, revealed through changes in the environment, by an observer as identified originally by Tomasello (1990, see also Whiten & Ham 1992; Whiten *et al.* 2004). Level 2 emulation describes utilising global information by the observers. An example of Level 2 emulation was the chimpanzees who had seen the ghost conditions with the Slide-box, and although they did not continue to match the direction of the door movement they learnt that the door could be moved to reveal the food reward (regardless of direction) more than those chimpanzees in the control condition with no information. The final, Level 3 emulation, is a term to describe ‘specific’ emulation in which not only are the affordances of an apparatus learnt, but also the precise manner in which they move or operate is matched. For a ghost condition with the Slide-box, the observer would not only learn that the door moves to reveal a reward but also, when given a chance to respond, the observer would move the door in the same direction as that in the ghost condition. This highest level of emulation (Level 3) was shown by both chimpanzees and children with their first responses in the ghost conditions of the Slide-box.

This series of experiments adds to previous research which has produced evidence for emulation in children (Huang *et al.* 2002; Thompson & Russell 2004; Tennie *et al.* 2006), apes (Tomasello *et al.* 1987; Toth *et al.* 1993; Call *et al.* 2005; Horner & Whiten 2005) and birds (Huber *et al.* 2001; Klein & Zentall 2003). Both chimpanzees and children showed evidence of emulation, yet this matching only persisted in the responses of the children.

d. Video demonstrations

In addition to the diffusion and ghost studies conducted with chimpanzees, two experiments were also run to assess chimpanzees' ability to observe, and learn from, video footage of a conspecific. The experiments reported through this thesis showed that conspecifics are reliable models for chimpanzees. However, training chimpanzees to act as models can be time consuming and may not always be feasible, for example if the sample pool is small and so the number of subjects must be maximized. In such circumstances video footage of models is appealing. Potentially only one model need be trained and the same video shown to multiple observers. An additional advantage of video footage of a model is that the experimenter can guarantee that all observers see the exact same demonstration. Video footage is a viable option for using with chimpanzees because their vision system is comparable to that of humans, for whom television screens have been designed (Landis 1954; D'eath 1998) and many chimpanzees in captivity are familiar with watching videos as part of the enrichment regime.

In a group situation, tentative evidence for chimpanzees learning from observing a video demonstration of a conspecific using the Pan-pipes was found (*Chapter 4*). To test this finding more rigorously, ten chimpanzees were tested in isolation and were shown video footage of an unknown male chimpanzees operating the Slide-box (*Chapter 9*). A significant number of chimpanzees were able to use the Slide-box after watching the video. Impressively, a significant number of those successful chimpanzees also matched the direction in which the model pushed the Slide-box door on the video.

Video footage has been used before to test a variety of abilities shown by chimpanzees, including memory of images and causal understanding (Eddy *et al.* 1996; Morimura & Matsuzawa 2001; Poss & Rochat 2003; Cacchione & Krist 2004; O'Connell & Dunbar; Hirata 2007). However the findings reported in *Chapter 9* are novel in that, rather than just reacting to or remembering what they had observed, the chimpanzees were able to learn from what they had observed and apply it to a real-life apparatus which had been represented on the television screen.

That the chimpanzees learned from the video footage, is indicative of the potential use of video for chimpanzees in the place of live models, especially when testing social learning. One particular, novel application would be to simulate group-to-group transmission, particularly in an establishment like MDACC where multiple groups of chimpanzees are housed.

10.2 Proposed future research

a. Open diffusion studies

(i) Who observes whom?

In *Chapters 3* and *8* open diffusion experiments were described. The results of these were analysed in terms of which method each chimpanzee used to operate the particular device, and how the two groups in each experiment compared. However, a

detailed analysis of *which* group members each chimpanzee watched, and potential reasons for *why* they may observe specific individuals, was not attempted.

The only analysis approaching such detail was that for the Slide-box open diffusion (*Chapter 8*). In this, the responses of each chimpanzee (Push-left and Push-right) were compared to the proportion of actions in either direction that they observed other chimpanzees in their group performing, to determine whether there was a correlation between the number of each response and the type of actions that they had observed. However, the analysis of the Slide-box open diffusion neither provided detailed information about the particular identities of the chimpanzees that were watched, nor the observer's relationship to them. It might be supposed that chimpanzees would be more likely to observe related chimpanzees than unrelated individuals.

Analysis of the identities of the chimpanzees that others choose to observe would be complex with an open diffusion, because often each chimpanzee observes multiple others. However, to tease apart possible links, the proportion of time that each chimpanzee watched each group member could be calculated. At MDACC, familial histories and relationships for all the chimpanzees are known and documented and such an analysis could be enhanced with this added information. An example might be that chimpanzee CE watched seven chimpanzees throughout the entire open diffusion phase, but of all those observations, one particular chimpanzee (KE) was watched 80% of the time. One could then investigate how factors such as kinship or affiliation predict biases in watching (see *Social learning strategies* below).

(ii) *Social learning strategies*

The proposed analysis described above for the open diffusion experiments is retrospective and would deal with data that has already been collected. Although it would provide information about which individuals each chimpanzee watched proportionally more than other, it fails to provide insight as to *why* a chimpanzee would observe a particular individual. Family relationships may be identified between those observed and those watching them, and also dominance relationships, but such inquiry would be inherently correlational and unable to confirm cause-and-effect relationships.

To remedy these limitations of the open diffusion design, and to extend upon it, further tests could be run in which the initial model could be selected by the experimenter for their particular qualities. In the open diffusion experiments reported in this thesis, an alpha female was always selected as the model based on the report of Biro *et al.* (2003). However, whether other individuals within the group's hierarchy would be equally successful could be formally tested.

Learning a novel behaviour or new information from observing another is a potentially beneficial attribute as it save the time-consuming, and possibly dangerous individual learning by trial-and-error (Bandura 1977). However if the individual that is observed has only out-moded or inefficient information then it could be detrimental to copy them (Boyd & Richerson 1985; 1996; Galef & Whiskin 2004; Galef & Laland 2005; Kendal *et al.* 2005). With this in mind, we might predict observers should select a 'reliable' model to copy and so which individuals an animal selects to observe and copy is of great interest. To test this, open diffusion experiments could be initiated in a variety of novel ways to determine from whom chimpanzees would learn.

Mathematical modeling has been conducted to elucidate which individuals should be copied and when (Laland 2004) and also to identify the potential influence of social learning on identified behaviours (Kendal *et al.* submitted). Studies with chimpanzees have shown that social learning has facilitated the transmission and maintenance of behaviour traditions (Whiten *et al.* 2005; Bonnie *et al.* 2007; Hopper *et al.* 2007; Whiten *et al.* 2007) and also they can imitate rationally, selecting specific information to copy (Buttelmann *et al.* 2007); however, no published study with chimpanzees has empirically tested the reliability of different models.

In these previous open diffusion studies it could be proposed that the chimpanzees copied the model with which the group was seeded, because they were successful at retrieving the reward from the apparatus. This would follow the suggestion of Boyd & Richerson (1985) that individuals would be likely to copy those individuals that were successful, regardless of whether this was maladaptive or not. However this effect is confounded by the fact that the model selected by the experimenter in these experiments was often an alpha female and so it may have been her status, rather than her success, that caused others to copy her actions. In chickens such an effect was supported by the findings of Nicol & Pope (1999) who reported that chickens were more attentive to conspecifics that were relatively dominant to them, rather than those who were subordinate.

In the future, it should therefore be asked: “Are chimpanzees more likely to weight social information provided by another more heavily than their personal information if that individual is more dominant, or deemed to be more successful, than them?”. To answer this, it is proposed that video demonstrations, following on from the work conducted at MDACC (*Chapter 9*), could be utilised to facilitate such study. The video conditions could show various models to test the following factors:

1. An unknown adult male *vs.* unknown adult female
2. An unknown juvenile male *vs.* unknown juvenile female
3. A female with a tumescent swelling *vs.* female with a maximal swelling

To ensure that the responses of the observers are not due to some particular characteristic of the model chimpanzee shown on the video footage, at least two chimpanzees per condition should be used as the model, as was done in *Chapters 6* and *7*. The first two comparisons suggested here, following from the proposal of Boyd & Richerson (1985), are based on previous work that suggests chimpanzees tend to copy those individuals within the group that are older, more competent or more dominant (Biro *et al.* 2003). To investigate this, comparisons between the first two conditions could test the efficacy of adult *vs.* juvenile and male *vs.* female models.

Less work has focused on whether a female's 'reliability' as a model varies during her cycle (Lacreuse *et al.* 2007). Inoue & Matsuzawa (2006) tested a female chimpanzee, Ai, at different stages of her menstrual cycle with cognitive tasks in which she had to put Arabic numerals in ascending order. Inoue & Matsuzawa reported a correlation between poor cognitive abilities and maximal swelling. It may be proposed that reduced cognitive abilities may render a female with a maximal swelling being less observed as a model, however, when conducting open diffusion experiments reported in this thesis the author noticed that females with maximal swellings were often enabled greater access to the apparatus by males, than when they had a tumescent swelling. It would be interesting to formally test whether there was an interaction between the two. Additionally, previous research has been conducted

on the role and status of females within a social group as affected by their swelling (Bloomsmith *et al.* 1991; 1992).

If an effect was found, whereby individuals relied on social information from certain types of individuals rather than others, then further tests would be required to identify factors including whether these 'preferred' individuals are better at the tasks. Vanayan *et al.* (1985) observed that pigeons acquired a new behaviour more quickly after observing a *less* proficient model than a successful one. Zentall (2001) suggested that the consequences of non-reinforced *and* reinforced responses are equally important to observers (see also McGregor *et al.* 2006). Fawcett *et al.* (2002) also reported that those observers who saw the more efficient models were themselves not the most quickly responding across the conditions. However, in contrast to Zentall's reasoning, Fawcett *et al.* suggest that this could be a result of the model's actions being too rapid for the observers to follow.

In summary, the status of a model may depend on a number of factors including the age, sex, ability and (if a female) phase of menstrual cycle of the chimpanzee. Teasing these apart will require a number of conditions all of which could be tested with video demonstrations. The rank of a model within a group should also be tested as a factor determining the efficacy of a model. However this factor, unlike those described previously, could not be tested using video footage. This is because a chimpanzees' rank within a group is specific to the dynamics of their group and a live model should be used for this. The open diffusion experiments reported here have used an alpha female as the model with success, but comparisons could be made with the dominant males and also subordinate chimpanzees of both sexes.

In addition to the effect of the status and/or success of the model on the amount to which they are observed and their behaviour copied, the *number* of animals also

performing the same behaviour may also effect whether an individual also participates or not. ‘Copying the majority’ was another rule proposed by Boyd & Richerson (1985) as to when an individual may copy a behaviour. This could also be tested with the multiple groups of chimpanzees housed at MDACC, as the number of proficient models that each group is seeded with could be varied to determine whether this would affect the reliability with which a behaviour spread. It would be predicted that the more individuals use a particular behaviour, the more likely it would be that it would be adopted by naïve individuals.

b. Testing for emulation

The focus of this thesis was to identify *whether* chimpanzees would learn from one another, and once it was identified that they did, *how* this had occurred. Although ghost conditions were used with success, extensions are required to provide richer detail about how this occurred, or why it did not in certain circumstances.

(i) Ghost condition extensions

The chimpanzees were presented with ghost conditions of the Pan-pipes which both included a tool or did not (*Chapter 4*). In comparison, children were only tested in ghost conditions with the Pan-pipes, with no tool (*Chapter 5*). Although the children were able to operate the device after having seen this better than those in a no-information control, they were less successful than those children who had observed a

fellow human operate the Pan-pipes. The difference between the demonstration and ghost conditions was not just the presence of a live model, but also the involvement of the rod-tool and how it could be used to operate the Pan-pipes.

For chimpanzees, including a tool in a ghost condition had no effect on their ability to operate the Pan-pipes; indeed, no chimpanzee was successful in either condition. However, because chimpanzees' performance was unaffected by the addition of a tool, their responses cannot be used as a predictor for that of children, as both species responded differently in the basic ghost condition. A proposed future extension to the experiment reported in *Chapter 5* would therefore be to provide children with ghost conditions of both the Lift and Poke methods for operating the Pan-pipes, with the inclusion of the rod-tool to indicate its relation to the pertinent parts of the apparatus. All other factors should remain the same, for comparison between the two conditions. It is predicted that those children who observe a ghost-with-tool condition would have greater success with the Pan-pipes compared to those in the no-information conditions and in the basic ghost condition.

(ii) End-state extensions

The end-states of a variety of apparatuses have been included as conditions in a number of experiments with both children and non-human primates (Meltzoff 1985; Bellagamba & Tomasello 1999; Call *et al.* 2005; Huang *et al.* 2006). Such a condition would act as a natural extension to the replication of the methodology of Klein & Zentall (2003) which was reported in *Chapters 6* and *7* with the use of the Slide-

box¹⁴. Both chimpanzees and children, in isolation, could be shown the Slide-box with the start position with the door in the central position and then (out of view of the subject) the door could be moved to either the far left or right position and then re-shown to the subject with the reward sitting at the bottom of the reward-chute. It would be predicted that both species would show an increased inclination to move the door in the direction that they saw it in its end-state.

c. Video demonstrations

The findings reported in *Chapter 9* have provided an indication that chimpanzees are capable of learning from video footage of a conspecific and this knowledge can be applied to a variety of new test scenarios. As described above, video footage of a variety of models can allow for the discrimination of the role of the model and the effect of the status of a variety of models.

Video demonstrations could also be coupled with ghost conditions. Currently, ghost conditions are presented by the experimenter moving the pertinent parts of the apparatus discretely with fishing-line. However such a demonstration is obviously not free from flaws; it could be that the observer sees the fishing-line and their response is inhibited because they are unable to imitate what they have observed as they cannot move the apparatus with the fishing-line. Video footage and video manipulation allows a potential avenue for overcoming this.

¹⁴ I would like to thank Thomas Bugnyar for his help and suggestion of this potential extension to the Klein & Zentall (2003) replication.

The operation of an apparatus could be filmed so that the operator is occluded or out of the shot, so the apparatus appeared to be moving remotely. Subjects could be shown either this form of ghost footage or comparable shots of a live model and the responses of both conditions compared. Not only would these ghost videos be useful when testing non-human animals but also for testing children. Indeed McGuigan *et al.* (2007) replicated and extended Horner & Whiten's (2005) study, finding comparable results despite showing the children films of the demonstrations instead of using a live model.

10.3 Concluding remarks

The experiments reported in this thesis provide further evidence that chimpanzees and children are capable of social learning and maintaining behavioural traditions across multiple transmissions. Further experimental designs were proposed which would provide greater insights to how this transmission occurs, and to whom an observer would likely attend. Additionally, both species were shown to learn by imitative *and* emulative learning, depending on the test conditions. Supplementary ghost conditions and end-state studies, proposed here, would provide further information about *to what* an individual pays attention to, and learns about, when watching a model use an apparatus. Not only was the social learning of chimpanzees tested, but new experimental methods were also explored. Chimpanzees were shown to learn from, and match, video-footage of a conspecific operating an apparatus. Therefore video demonstrations could be used in a number of applications when testing observational learning among captive chimpanzees. In conclusion, the series of studies herein add to

the corpus of literature focusing on observational learning among chimpanzees and children, extending upon it through the use of little-used paradigms such as the ghost condition, and also proposes new ones.

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