

**SOCIAL LEARNING FROM VIDEO  
DEMONSTRATIONS IN CHIMPANZEES (*Pan  
troglodytes*), CHILDREN (*Homo Sapiens*), AND  
RAVENS (*Corvus corax*)**

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## **ABSTRACT**

The capacity for cumulatively complex and constructive technologies is a hallmark of human cognitive ability. Many species use tools, yet the breadth, adaptability, and inventiveness of human tool use distinguishes us. Such complex technological adaptations require the causal understanding to invent and perfect new techniques and the ability to copy perceived behaviours. This has led to considerable research comparing the social learning abilities of chimpanzees and young children on tool-using tasks, yet experimental studies directly investigating tool modification are rare. The studies outlined in this thesis sought to assess the social learning abilities of chimpanzees and children by manipulating both the complexity of a tool modification method and the amount of information available in a demonstration. Video demonstrations of conspecifics were used in lieu of live models, in order to manipulate the quality and quantity of information directly. Both chimpanzees and children presented with complete information about the modification process learned to combine two tools together to make a more efficient tool significantly more than those provided with less information. Unlike chimpanzees, children presented with a more perceptually opaque method of tool modification (twisting and extending an internal rod) were also able to socially learn the task, despite the fact that none of the children in the control condition successfully solved the task. Both children and chimpanzees who solved the task after seeing a demonstration also persisted in using the socially learned method two-weeks later, even when it was no longer necessary. These results identify potent social learning effects in both chimpanzees and children, however, children proved superior to chimpanzees in observationally learning finer manipulative techniques.

This thesis also provides the first analysis of video stimuli in ravens. To assess the feasibility of the methodology, ravens were first presented with different types of video stimuli, varying in terms of the subject identity. Ravens showed a preference for video footage of other ravens over different species of birds. In a second study, ravens who saw a conspecific solve a two-step task were more likely to attempt a solution than those who had not. This represents the first evidence of social learning from a video demonstration in ravens and further supports the use of this medium to dissect social learning mechanisms in a range of species.

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# CHAPTER 1. BACKGROUND INFORMATION

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## 1.1. Introduction

The following chapter provides an overview of the study of social learning and culture, with particular reference to nonhuman primates. First I discuss how it is identified in the wild and dissected experimentally in captivity. Next, I focus on cumulative culture and the methods used to distinguish the types of learning which might drive differences between humans and chimpanzees. This includes an overview of tool use, and then focuses specifically on differences between chimpanzees and children. Finally, I discuss how this thesis aims to explore several gaps in the existing literature using video demonstrations.

## 1.2. Why social learning?

Social learning has fascinated scientists for over a century. Many of the major players in biology and early experimental psychology hypothesized about its function and underlying cognitive processes. While these early works were mainly anecdotal in nature, the scientific study of social learning mechanisms was well underway by the late 20<sup>th</sup> century (Galef, 1988; Whiten & Ham, 1992). Social learning was historically thought of as low-level and relatively cognitively undemanding, and its numerous processes were often lumped under the category “imitation”. Today, social learning is thought of as a collection of different cognitive processes. Although *social learning* in some form is considered common in many species, *imitation* is thought to be a rarer ability, in our own species linked to “characteristically human forms of intelligence, in particular language, culture and the ability to understand other minds” (Hurley & Chater, 2005, p.1).

The study of social learning can be broken down into two broad categories of inquiry. The first approach investigates social learning in terms of how information is transferred from one individual to another as an underlying psychological process. The second approach views social learning on a macro level, in terms of its function as an adaptive mechanism and its interaction with ecological and genetic processes. Learning from others can act as a valuable short-cut to acquiring anti-predator or skilled foraging behaviour, and to help avoid other potential risks associated with trial-and-error learning (Boyd & Richerson, 1988; Galef, 1995; Galef & Laland, 2005). However, despite the range of benefits to be had from learning socially, it is important to note that socially

transmitted behaviour is not always adaptive. The benefits are in part dependent on the rate of change in the environment, and social learners run the risk of acquiring information that is outdated or inappropriate. Ecological and social conditions like group size, resource distribution, and the number of social learners already present in a population can also shape the opportunities for social learning, as well as the costs and benefits (Giraldeau, Caraco, & Valone, 1994; Laland, 2004). Social learning theories have therefore been developed concerning how life history, social gregariousness, and rates of environmental change interact with social learning ability and its application (Lefebvre & Giraldeau, 1994; Lefebvre & Palameta, 1988).

In addition, whereas behavioural variants acquired by individual learning only affect the individual and last for her lifetime, those learned socially can have “population-level consequences” (Boyd & Richerson, 1985), and can bring about changes in cognition or behaviour in shorter periods of time than genetic or individually learned change (Richerson & Boyd, 2005; Tomasello, 1999). The ability to socially learn is an essential prerequisite to the spread of traditions or “culture”. Our cultural abilities have allowed us to populate a more diverse range of habitats, sustain more complex societies, and produce more intricate technologies than other animals (Boyd & Richerson, 1996). Many nonhuman species exhibit social learning, but humans differ in generating an increasingly complex accumulation of changes across generations (Boyd & Richerson, 1996). Exploring cultural cognition in other species can highlight important similarities or differences between humans and other animals. This is useful in tracing the evolution of distinctly human cognition (McGrew, 2004; Whiten et al., 1999), and investigating how culture, as a nongenetic evolutionary process, interacts with biological evolution (Laland, Kendal, & Kendal, 2009; Richerson & Boyd, 2005). Social learning is therefore of interest to a wide range of researchers, spanning several fields of study. The literature on social learning and culture is immense, and covers an ever increasing range of species (see Laland & Galef, 2009 and Price, Caldwell, & Whiten, 2010 for recent reviews).

From the earliest studies in the opening years of the twentieth century, nonhuman primates (hereafter “primates”) have been a focus of much of this research. Primates have relatively long periods of juvenescence, which when coupled with their often complex societies and large social groups can make social learning a valuable adaptation. Primates

also share the most recent common ancestors with humans, so that studying their behaviour is potentially useful in attempting to understand the evolution of both shared and uniquely human traits. Some of the earliest candidates for culture or traditions in nonhuman animals were recognised at primatology field sites. Thorough field observations of monkeys and apes in free-ranging populations have revealed examples of complex behavioural repertoires present in some groups and absent in others. In addition, empirical tests of primate cognition in the laboratory have found striking evidence of social learning in primates. Nevertheless, the study of “culture” in primates and other animals remains highly contentious, with disagreement over what specific social learning mechanisms are at work, and whether these types of learning are adequate to support culture. Field researchers identify putative cultural traits in wild populations, and new techniques are making it easier to trace the spread of behaviours. Others seek to test social learning in captivity, specifically addressing how different social learning mechanisms underlie certain behaviours.

### 1.3. Social learning in free-ranging populations

Much of the contention surrounding questions of culture in other animals stems from differing definitions. The greatest divide in the literature concerns how to define “culture”. Although behavioural scientists tend to view social learning in nonhuman animals as a precursor to culture, there is still much disagreement about how to define and label culture in different animal species (Laland & Hoppitt, 2003). These definitions hinge on the precise nature of the transmission of information. In the broadest sense, any behavioural variation between groups that is not the result of genetic processes is deemed cultural (Lumsden & Wilson, 1981). At the other extreme, definitions limit culture to humans by suggesting that behaviours must be acquired through imitation, or even that they must include teaching or language (Tuttle, 2001; Washburn & Benedict, 1979). A distinction is often made between “behavioural traditions” and “culture”, with the term tradition more readily applied to behaviours seen in nonhuman animals.

Despite this terminological variation and potential confusion, there are several basic components commonly discussed in the literature. A very useful definition of “traditions” is laid out by Frigaszy and Perry (2003) as “enduring behaviour patterns

shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group” (p. 3). This highlights the importance of several key variables: the proportion of group members displaying the behaviour, the stability of the behaviour over time, and the process through which the behaviour is acquired. It is largely agreed upon that the behaviour should be common in the population and stable across generations (Matsuzawa, Biro, Humle, Inoue-Nakamura, & Tonooka, 2001; van Schaik, 2003). The means through which the behaviour is acquired is more debatable, not only because it is difficult to pinpoint how behaviours are learned in free-ranging populations (socially versus individually), but also because the specific social learning process necessary to sustain the spread of “cultures” is not agreed upon. It is also not clear how many of these behavioural variants or traditions should be present to warrant the label culture. For some, a single behavioural variant suffices. A large and diverse number of animals display single variants (for example vocal dialects in birds and cetaceans: Catchpole & Slater, 1995; Janik & Slater, 1997, 2003; Noad, Cato, Bryden, Jenner, & Jenner, 2000, and foraging techniques in monkeys - Kawai, 1965a, rats - Aisner & Terkel, 1992, and insects - Worden & Papaj, 2005).

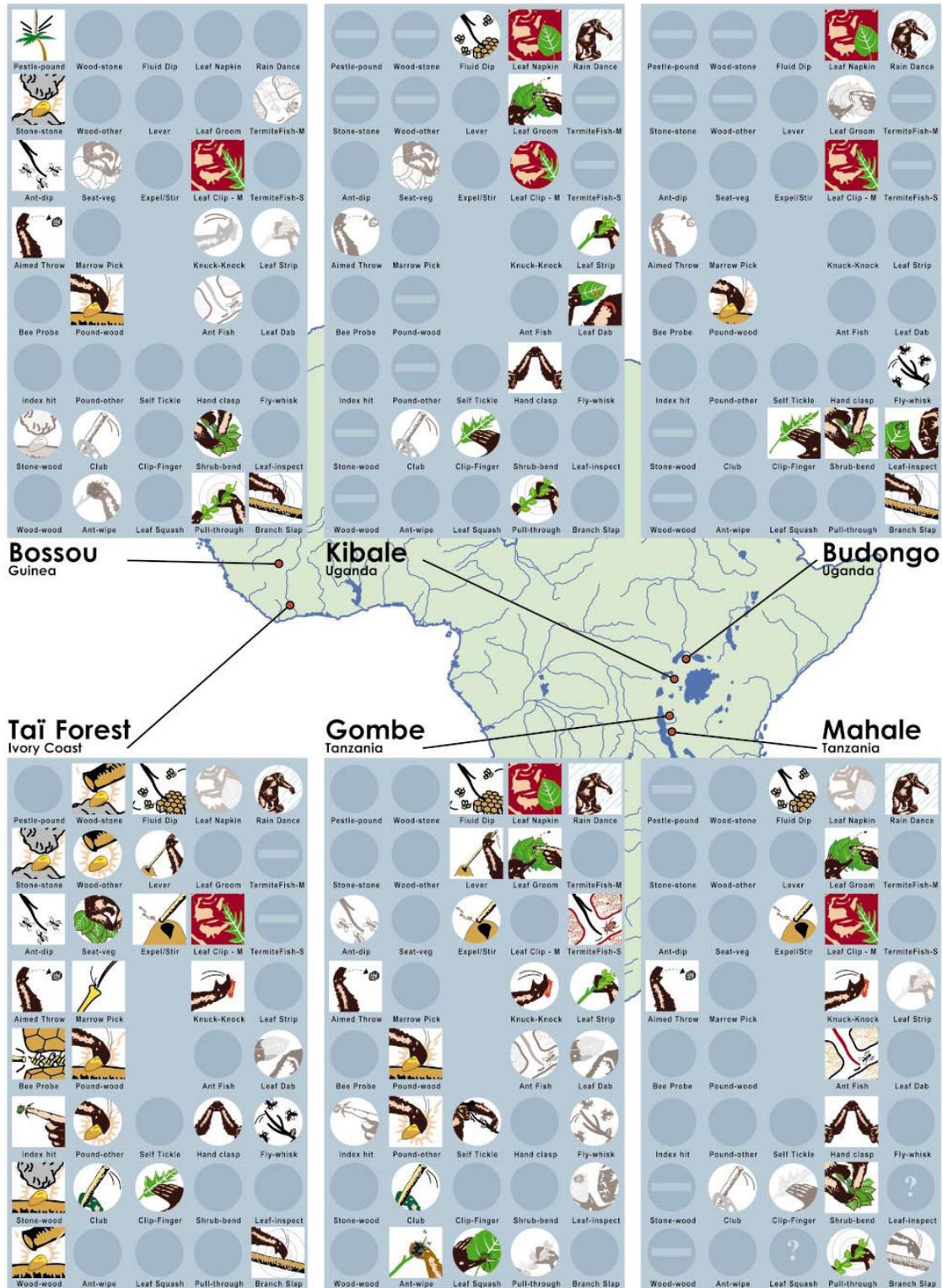
In contrast, Whiten and van Schaik (2007) urge that a population must be exhibiting an assemblage of traditions in order to be described as cultural. Chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and capuchin monkeys (*Cebus capucinus*) qualify under these criteria (Perry, Baker et al., 2003; van Schaik, 2003; Whiten et al., 1999), possibly some cetaceans (Rendell & Whitehead, 2001) and perhaps one corvid species, the New Caledonian crow (*Corvus moneduloides*, Hunt & Gray, 2003). The difficulty with such field observations is determining whether or not variants are definitely socially transmitted. It is most commonly inferred that such behaviours are spread by social learning because they diffuse through the group too rapidly to be explained by genetic or ecological factors. The subject can be tackled in part by gathering data together across field sites for a given species, examining the ontogeny of foraging techniques, analysing the rate of the spread of new behaviours throughout a group, or experimentally manipulating free-ranging populations.

### 1.3.1. Cataloguing differences between field sites

The first report of a primate tradition came from the food processing techniques employed by the Koshima troop of Japanese macaques (*Macaca fuscata*). The spread of sweet potato and wheat-washing was traced from its innovation by Imo, a young female, to her close associates, and finally through almost half of the rest of the troop (Itani & Nishimura, 1973; Kawai, 1965b; Nishida, 1987). Since then, long term observations at several field sites have found behavioural differences in populations of other species with no apparent ecological or genetic explanation. As early as 1973, Jane Goodall suggested that chimpanzee food extraction techniques were likely to be socially learned behavioural traditions (Goodall, 1973). Later, McGrew (1992a) provided the first major synthesis for chimpanzee cultures, by cataloguing numerous behavioural differences across chimpanzee study sites.

These approaches involve identifying local variants with patchy geographic distributions and then attempting to rule out environmental or genetic explanations. Recently, the heads of the most long-term chimpanzee study sites went a step further and pooled their data to look for differences in behaviour patterns between groups. After ruling out behavioural differences with possible genetic or environmental explanations, they identified 39 “cultural variants” covering a range of behaviours from tool use to social and courtship styles (Whiten et al., 1999, 2001). They ranked the occurrence of these behaviours at each site, and found that some were customary (occurring in all or most able-bodied members of at least one age-sex class) at some sites and absent at others (Whiten et al., 1999). The presence or absence of these cultural variants made up an overall profile for each chimpanzee community, and no two of these cultural profiles were identical (see Figure 1.1).

**Figure 1.1 Charting chimpanzee behavioural variation in the wild** (taken from Whiten et al, 1999). Each chimpanzee community is characterised by an overall profile of cultural variants, present in some groups and absent in others.



This systematic approach has since been used in other primate species. Van Schaik et al., (2003) surveyed six different orangutan field sites in Sumatra and Borneo, identifying 24 putative cultural variants. As with chimpanzees, these included a range of behaviors, from foraging techniques, including tool use, to social signals. Local variants have also been found in white-faced capuchin foraging techniques, social customs, and games (Panger et al., 2002; Perry, Baker et al., 2003) and in stone-handling behaviours in Japanese macaques (Huffman, Nahallage, & Leca, 2008; Leca, Gunst, & Huffman, 2007). Such variation is not restricted to primates. Although the same approach has yet to be completed across sites, dolphins (*Tursiops aduncus*) exhibit evidence of behavioural traditions across domains as well (Mann & Sargeant, 2003; Rendell & Whitehead, 2001). In addition, New Caledonian crows (*Corvus moneduloides*) show evidence of complex, layered behavioural variations involving tool use that may be cultural (Hunt & Gray, 2003).

Several of these behaviours provide particularly convincing evidence of culture because they are purely social in nature, making an ecological explanation for intergroup differences unlikely. Leca et al. (2007) also showed that variability in stone-handling behaviour in Japanese macaques was not related to the availability of stones. In addition, phylogenetic analyses have concluded that behavioural variation between groups of chimpanzees cannot be sufficiently explained by genetic differences (Lycett, Collard, & McGrew, 2007; although see a recent analysis which suggests that genetic differences cannot be ruled out completely - Langergraber et al., 2010). Determining differences between local conditions may not be a straightforward process, however, and has been criticized for not ruling out ecological explanations well enough (Laland & Hoppitt, 2003). In the case of chimpanzee tool-use, for example, it may not only be a matter of checking that the appropriate tools are accessible across sites, but differences might be confounded by the availability of alternative resources which may lessen the necessity of a particular behaviour (Matsusaka et al., 2006). In addition, ant dipping behavior, one of the cultural variants identified by Whiten et al. (1999), can possibly be explained by the species of the prey. Gombe and Tai chimpanzees use two different methods for extracting ants from their nests. Chimpanzees at Bossou, however, employ both techniques,

depending on the species of ant, which vary in terms of aggressiveness (Humble & Matsuzawa, 2002) although see (Humble, 2006; Möbius, Boesch, Koops, Matsuzawa, & Humle, 2008; Schönig, Humle, Möbius, & McGrew, 2008) for an analysis of the behavior that reveals both cultural and environmental forces at work).

### 1.3.2. Micro studies: Tracing the spread of behaviours

The spread of behaviours can also be investigated on a micro level to determine whether or not such variants are acquired via social learning processes. Ethologists can trace the spread of a new behavior through a group if they are fortunate enough to see its innovation. If social learning is taking place, close associates of the innovator should learn the behaviour first. Such a process was possible in the case of the sweet potato washing in the Koshima macaques. The close associates of the innovator, Imo, developed the behaviour first, and then their relatives and associates, and so on. Similar patterns were found with stone-handling behaviors in Japanese macaques; the behaviour spread laterally to the innovator's frequent playmates, and then vertically from mothers to offspring (Huffman, 1986; Huffman & Quiatt, 1986; Leca et al., 2007). If it is not possible to trace the spread of a new behaviour, proximity data can provide a useful tool to detect if social learning is taking place. Van Schaik et al. (2003) found that the percentage of time orangutans spent in association with others was significantly related to the number of cultural variants they displayed. Similarly, capuchin monkeys who spend the most time together use similar foraging techniques (Agostini & Visalberghi, 2005; Panger et al., 2002; Perry, Panger et al., 2003). Three social behavioural variants were also analyzed separately across capuchin field sites. These behaviours were particularly useful because they were largely participated in dyadically. The behaviour could therefore be traced from one monkey to another in the dyad, and then after the second monkey participated in another dyad, traced further across transmission chains (Perry, Baker et al., 2003). As a result of their distinctive and sparse social contacts, orangutans also provide a unique opportunity to trace the spread of such behaviours on an individual to individual level (Russon, 2003).

The spread of behaviours can also be detected by scrutinising their development in individual animals. The most obvious source of social information for young individuals is their mothers. If the behaviour of the offspring matches that of the mother

more closely than that of unfamiliar (spatially distant) adults, it is suggestive of social learning. Lonsdorf and colleagues traced the development of termite fishing in young chimpanzees. Young females spend significantly more time interacting with and observing their mothers during termite fishing bouts than do young males. They not only master the technique a year earlier than males, but also tend to adopt techniques similar to their mothers (Lonsdorf, 2006; Lonsdorf, Eberly, & Pusey, 2004). Likewise, immature orangutans adopt nearly identical diets to their mothers (Jaeggi et al., 2010) and detailed observations in young rehabilitant orangutans over several years suggest that close associates display similar foraging strategies (Russon, 2003). In dolphins, mothers and daughters have similarly sized behavioural repertoires, and display significantly correlated foraging techniques (Mann & Sargeant, 2003).

Even if social influence is occurring, it is difficult to determine to what extent. Individual learning might still explain a sizeable portion of the behavioural similarities. For example, those in proximity to a given innovator are consequently in proximity to the appropriate tools or food and may therefore be more likely to discover similar techniques through their individual explorations (Tomasello & Call, 1997). In the classic potato-washing tradition, those individuals who were close associates of Imo may have been in proximity to both potatoes and water as a consequence. They may therefore have developed the behaviour largely through individual trial-and-error learning. Individuals may also be facilitated through observation of others to interact with certain salient objects, but might not be engaging in imitation.

### 1.3.3. Modelling diffusion patterns

Patterns of diffusion throughout groups can also be investigated on a macro level; in this case it is not who is learning from whom that is the primary focus, but rather, the rate at which the behaviour spreads. In this way, statistical tools can be used to generate specific probabilities which can then be matched against data from free-ranging populations (Laland et al., 2009). Most early diffusion data assumed that if social learning is occurring, the number of individuals displaying the behaviour should increase at an accelerated rate. This is because over time, more and more opportunities are available to learn as more individuals adopt the behaviour. Under this reasoning the spread of potato-washing in Koshima macaques is unlikely to be explained by social

learning, as the rate of behaviour increased steadily, rather than accelerating (Galef, 1990; Tomasello, 1999). However, more recent theoretical analyses suggest that asocial learning can also generate acceleratory curves under some conditions. The addition of factors such as the proportion of skilled individuals to scroungers in a group, or the nature of the relationships between skilled and naïve individuals can also affect the shape of the distribution curve (Caldwell & Whiten, 2006; Laland, Richerson, & Boyd, 1996). Recent theoretical models taking such factors into account hold much scope for identifying cultural transmission in the future (Hoppitt, Boogert, & Laland, 2010; Laland et al., 2009).

#### 1.3.4. Field experiments

The clearest way to disambiguate the type of social transfer occurring is through controlled experimentation, which has proved difficult in the wild and has largely been pursued with captive animals. However, it is possible to determine if social learning, rather than individual learning, is occurring by experimentally manipulating populations of animals. Cross-fostering (moving individuals out of their natal groups into new ones at a formative age) and translocation (swapping entire groups across environments) experiments showed that behaviours were socially transmitted in rats and fish (Helfman & Schultz, 1984; Terkel, 1995; Warner, 1988). Thornton & Malapert (2009) trained meerkats to find food from different locations and thus showed experimentally that the behaviour was socially learned, although resulting group differences were ephemeral. Unfortunately such experiments have not been feasible with populations of larger free-ranging species to date, probably for both logistical and ethical reasons. One alternative is to artificially enhance the possibility of a new innovation by introducing new materials to a group. Biro et al. (2003) followed the development of nut-cracking in the Bossou population of chimpanzees (Guinea, West Africa) for 16 years. They then introduced novel nuts to the group and traced the spread of the behaviour from one female who had likely had experience with the nuts prior to her emigration. Gruber, Muller, Strimling, Wrangham, & Zuberbuhler (2009) presented wild chimpanzees in two different communities (Sonso and Kanyawara, Uganda) with artificial honey dipping devices (logs drilled with holes). Chimpanzees in these two populations differed in that Kanyawara chimpanzees already used sticks to dip for honey, and Sonso chimpanzees did not, but

did frequently use leaves as tools. The authors found that Kanyawara chimpanzees applied this stick dipping technique, whereas Sonso chimpanzees did not, although they occasionally used leaves. The authors concluded that the chimpanzees were relying on cultural information; however it is difficult to rule out individual learning, since the original mechanism which led to the acquisition of the behaviour is still not clearly established. Regardless of the potential problems, these studies provide a unique combination of an ecologically valid environment and the benefit of some experimental control, offering a promising avenue for future research (Whiten & Mesoudi, 2008).

#### 1.4. Experimental studies: Identifying social learning mechanisms in captivity

##### 1.4.1. Defining social learning mechanisms

Controlled experiments with captive populations provide a useful complement to field observations by allowing researchers to determine if a given species is capable of social learning, and therefore might be exhibiting cultural variants in the wild. They can also help determine what mechanisms of social learning animals are employing. As mentioned previously, there is still disagreement in the literature as to what specific social learning processes are necessary to sustain stable behavioral traditions or culture in the wild (Galef, 2009; Laland & Janik, 2006; Whiten, Horner, & Marshall-Pescini, 2003). Some suggest that many processes of social learning can support cultures in wild populations (Laland & Hoppitt, 2003). Under this definition there is evidence of culture in a large range of species (Boyd & Richerson, 1996; Laland & Hoppitt, 2003; Laland & Janik, 2006; Lefebvre & Palameta, 1988). Others argue that for behavioural variants to be truly cultural, they must be supported by imitation or teaching (Galef, 1992; Piaget, 1945; Tomasello, Kruger, & Ratner, 1993 ). If an animal is still relying heavily on its own interaction with the environment, information can be lost during social transmission and less stable behavioural traditions may result. In addition, while social learning in any form can potentially support behavioural variation between groups, these are likely to be behaviours that individuals can learn on their own. Social learning simply allows them to be acquired faster. Imitation, however, might be key to cumulative cultural evolution - cultural change which “accumulates over many generations leading to the evolution of behaviours that no individual could invent” (Boyd & Richerson, 1996, p. 78).

Cumulative cultural evolution has allowed humans to develop an amazing array of complex technologies, societies, and institutions that distinguish us as a species. Evidence for cumulative culture in other animals is either exceedingly rare or nonexistent (Boyd & Richerson, 1996). The attempt to distinguish imitation from other forms of social learning has therefore driven much of the research in nonhuman animals (Byrne & Russon, 1998; Galef, 1988; Heyes, 1993; Heyes & Galef, 1996; Whiten & Ham, 1992; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Zentall, 2006).

Caldwell & Whiten (2002) provide a comprehensive definition of social learning that “occurs when the behavior, or presence, or the products of the behavior, of one individual influence the learning of another” (p. 193). This definition covers a wide range of processes, from learning about what food to eat by scrounging on materials left over from a group member, to copying specific sequences of body movements. The primary distinction between social learning mechanisms lies with what features of a “demonstration” are most salient in determining an observer’s subsequent behaviour (Heyes, 1993; Whiten & Ham, 1992). Observing a particular behaviour in a conspecific could simply trigger a behaviour already existing in the natural repertoire of the observer, often referred to as contagion, priming, social or response facilitation (Byrne & Russon, 1998; Zentall, 2003, 2006). Alternatively, the behaviour of the model could facilitate interaction in a number of ways that lead to an increased possibility of the observer learning the specific solution through trial-and-error learning. Examples of this type of social learning are stimulus or local enhancement, where the attention of the observer is drawn to relevant objects or locations (Whiten et al., 2004; Zentall & Galef, 1988).

Social learning is generally considered imitative if the observer is attending to and replicating the specific actions of the demonstrator and there is little influence of the environment on the observer’s behaviour. However, as with culture, definitions of imitation vary. Some argue that the observer must have an understanding of the intentions behind the outward behaviour in order to be truly imitating (Tomasello, 1999; Tomasello et al., 1993 ). Others adopt the more general approach that if alternative mechanisms are ruled out, imitation is likely to be occurring (Zentall, 2006). One distinction which might be particularly important in comparing humans and other animals is that between emulation and imitation. Tomasello, Davis-Dsilva, Camak, and Bard (1987) provided the

first analysis of what later came to be known as *emulation* after finding that chimpanzees would reproduce the final result of a modeled action, but not the exact technique used to achieve it. Emulative learning is defined as the “process whereby an individual observes and learns some dynamic affordances of the inanimate world as a result of the behavior of other animals and then uses what it has learned to devise its own behavioral strategies” (Boesch & Tomasello, 1998, p. 592, also see Wood, 1989). In this instance, the observer is reproducing the results of another’s actions, rather than copying the details of those actions, and is thus still heavily relying on individual learning to reach a solution. Call and Carpenter and (2002) go one step further, breaking down a demonstration into three possible sources of information: actions, results, and goals. Demonstrators replicating the action are said to be mimicking, those copying the results emulating, and those replicating the final goal employing goal emulation. Only those copying all three are imitating (Call & Carpenter, 2002). Imitation in this sense, or the “reproduction of both the behavior and its intended results” (Boesch & Tomasello, 1998, p. 599), may be limited to humans, and is rather difficult to test in other animals (Galef, 2009).

#### 1.4.2. Identifying social learning mechanisms in the lab

Given the distinctions outlined above, several key components are necessary in designing experimental controls to help identify specific mechanisms. In order to rule out response facilitation or contagion, the task should be relatively novel. This can be accomplished either by using novel actions, or improbable sequences of actions. Distinguishing between emulation and imitation has perhaps caused the most difficulty, as both processes can often lead to similar behaviours in the observer. In addition, it is difficult to strike a balance between applying tight experimental controls and still affording as natural a learning environment as possible. Inventive experimental designs are helping to tackle these problems, as discussed below.

##### *a. Do-As-I-Do.*

“Do-as-I-do” experiments address imitation specifically, because they involve copying arbitrary, novel body actions and not the results of actions on a given task. Chimpanzees (Custance, Whiten, & Bard, 1995) and one orangutan (Call, 2001) were first trained to respond with the same action as the demonstrator, and then presented with a set of different facial, postural and manual actions. Independent coders of the data were

able to identify behavioural matches significantly above chance, however, in even the best performance (by the orangutan) behaviours classed as “fully imitated” reached only 58%. Capuchin monkeys were tested on a slightly different set of actions involving body movements and interactions with objects. Although they were facilitated to touch certain objects after observing their human demonstrators do so, they did not copy the actions involved (Fragaszy & Visalberghi, 2004). While the evidence from apes is suggestive of imitative ability in at least some individuals, the behaviour was trained extensively and does not reflect spontaneous interactions. Myowa-Yamakoshi & Matsuzawa (2000) found that five chimpanzees with no prior training rarely reproduced demonstrated actions spontaneously. In addition, the majority of primates tested on these tasks are human-reared, and there is evidence to suggest that the process of enculturation might affect their performance (Call & Tomasello, 1996). These tests therefore might offer evidence of what apes can do, but do not necessarily reflect what they would do when faced with a more natural situation.

*b. Foraging/Problem solving tasks.*

Foraging tasks typically allow an observer to watch a demonstrator perform a task and retrieve a reward, and then offer the observer the opportunity to perform the task. In this sense, the behaviour of the observer is spontaneous, rather than trained, and might better address the role of social learning in task acquisition. The development of the two-action task (Dawson & Foss, 1965) achieved great success at isolating specific social learning mechanisms, and is widely used across a diverse range of taxa (for example: common marmosets, *Callithrix jacchus* - Voelkl & Huber, 2000; chimpanzees - Tennie, Call, & Tomasello, 2006; rats, *Rattus norvegicus* – Ray & Heyes, 2002; Japanese quail, *Coturnix japonica* - Atkins & Zentall, 1996; pigeons, *Columba livia* – Zentall, Sutton, & Sherburne, 1996; budgerigars, *Melopsittacus undulatus* - Mottley & Heyes, 2003). In two-action tasks, an animal can achieve the same reward in one of two different ways, either by using different body parts or by manipulating a device in one of two discrete ways. One experimental group is typically shown one solution, a second group an alternative solution, and ideally, a third group receives no prior demonstration. If the observer produces behaviours which match the demonstrated behavior, it is said to have socially learned. Where the subject is interacting with the same part of the apparatus to

achieve the reward, the behaviour is unlikely to be explained by stimulus enhancement or local enhancement. One of the few tasks claiming “true imitation” in a primate species used such a methodology. Marmosets presented with film canisters which could be opened with either the hand or the mouth matched the behaviour they had seen demonstrated (Voelkl & Huber, 2000). This was considered strong evidence of imitation because the specific body actions of the demonstrators were copied. If the marmosets were attempting to replicate the effects of the actions, rather than the actions themselves, they might be expected to use their hands and mouths equally.

Despite this, critics of the two-action methodology suggest that many of the results may be explained by *object movement reenactment* (OMR) a form of emulation. “Ghost conditions”, where the device moves in the absence of a demonstrator, have helped to ascertain whether the observer is replicating the movement of the device (OMR) rather than the action of the demonstrator (Klein & Zentall, 2003). Results using this method are mixed. For example, chimpanzees presented with a door which could be pushed or pulled to obtain a reward, did not copy the movement of the door in a ghost condition, or the method used by a live demonstrator (Tennie, Call, & Tomasello, 2006). In contrast, chimpanzees presented with a door which slid either to the right or left did initially copy the movement of the door in the ghost condition. When presented with a more difficult tool-use task, however, they failed to learn from the ghost condition (Hopper, Lambeth, Schapiro, & Whiten, 2008; Hopper et al., 2007). This is a striking finding, considering previous tests have shown that chimpanzees can learn from watching a live model demonstrate the same task (Whiten, Horner, & de Waal, 2005).

Behaviours thought to be socially learned in the wild typically involve complex, hierarchically organized procedures. Multiple-step tasks might therefore be particularly informative tests of imitation in captive populations (Byrne & Russon, 1998). “Artificial fruits” necessitate the removal of several defenses in order to open a box and retrieve a reward. In these tests, either the solution at each step or the sequence of steps (e.g. poke or twist a bolt, then lift or turn a handle) creates a novel string of behaviors (Whiten, 2002; Whiten, Custance, Gomez, Teixidor, & Bard, 1996). This methodology has been used in a range of primate species with mixed results. Of the apes tested, chimpanzees and western lowland gorillas (*Gorilla gorilla gorilla*) were found to significantly match

the techniques they had observed (Stoinski, Wrate, Ure, & Whiten, 2001; Whiten et al., 1996), and orangutans were facilitated to solve the task and showed a tendency to match, albeit to a lesser degree (Custance, Whiten, Sambrook, & Galdikas, 2001; Stoinski & Whiten, 2003). Chimpanzees also showed a significant tendency to match the specific sequence of behaviors used (Whiten, 1998). Of the monkeys tested, both common marmosets (Caldwell & Whiten, 2004) and capuchin monkeys (*Cebus apella* - Custance, Whiten, & Fredman, 1999) produced some of the actions they saw demonstrated.

#### 1.4.3. Experimental methodologies: Dyads to diffusions

Captive experiments typically strive to strike a balance between ecological validity and tight experimental controls, depending on the type of information sought. Many tests are performed dyadically, that is with one individual demonstrating to another, away from the rest of the group. This is useful when a high degree of control is required over the amount of information seen by the observer, in order to determine what social learning mechanisms animals have the capability to employ. Such tests might not be the best means to establish which of these mechanisms might be responsible for the acquisition and spread of traditions in the wild, however, particularly over longer periods of time. Diffusion experiments across communities of individuals allow researchers to test whether a particular behaviour is maintained long enough to be spread to other group members. In such experiments, a novel behavior is seeded into a group by training an individual to solve a task in a particular way and then reintroducing her to the group as a demonstrator. Such designs are most powerful when coupled with the two-action methodology, so that one group gets a specific solution, the other an alternative, and the third no demonstration. Seeded behaviors on a tool use task spread through two groups of chimpanzees, with a third control group not learning either solution. Further, these behaviours remained in place two and nine months later (Whiten et al., 2005). “Open group” diffusions of this nature have been successfully repeated in groups of chimpanzees (Whiten et al., 2007), colobus monkeys (*Colobus guereza*, Price & Caldwell, 2007), macaques (de Waal & Johanowicz, 1993) and capuchins (Dindo, de Waal, & Whiten, 2009).

Linear diffusion chains break down the chain of transmission in a group to its individual links. In such tests, one animal acts as a model for a naïve observer, who in

turn becomes the model for a new observer and so on. This allows researchers to identify where corruption might occur. Such a method has been used with chimpanzees and human children (Horner, Whiten, Flynn, & de Waal, 2006) as well as tufted capuchin monkeys (Dindo, Thierry, & Whiten, 2008). Diffusion experiments have the potential to act as replications of behavioural traditions in the wild, and provide a useful middle-ground between observations in the field and dyadic social learning experiments.

### 1.5. Cumulative culture: A human adaptation?

Despite compelling evidence for behavioural traditions in primates, cultures in other animals remain far distant in their complexity from the diverse array of technologies, languages, religions and so forth that make up human cultures. Such complex cultural assemblages are dependent on cumulative cultural evolution. It has been hypothesized that the capacity for cumulative culture in nonhuman animals is limited by their social learning abilities (Tomasello, 1999). Comparative studies investigating differences between humans and other animals can help to illuminate key social learning differences which might drive the human advantage (Matsuzawa, 2001b). Tool use is often the focus in captive studies for obvious reasons: human tool use is incredibly complex and reliant on cumulative culture. Such complex technology requires the ability to innovate new techniques and to copy behavioural patterns to a high degree of fidelity (Tomasello, 1999). Captive studies can therefore help determine if a given species has the requisite causal understanding to innovate new techniques. They can also address if social learning differences are at play by comparing species. The bulk of this research focuses on differences between chimpanzees and children. Chimpanzees are not only our closest living relatives (along with bonobos) but are also the most proficient tools users in the wild, displaying a wide collection of cultural variants as discussed above. Differences between chimpanzee and human social learning abilities are therefore particularly enticing to those interested in cumulative culture.

#### 1.5.1. The Focus on tool use

The ability to make and use tools has long been considered a main driving force in the development of distinctly human intelligence (Byrne, 1997). Humans are the most proficient tool users in the animal kingdom, and the complexity, breadth, adaptability,

and inventiveness of our tool use distinguishes us (Baber, 2003). Tools act as an intermediate step in our interactions with the world, and require motor coordination and planning. Furthermore, along with the variation and complexity of human communication systems and social structures, human tool technology and industries cannot be explained by biological evolution alone; there has simply not been enough time for forces such as genetic variation and natural selection to have shaped differences (Richerson & Boyd, 2005). Until recently, tool use was thought to be restricted to our species. Although first mentioned by Darwin (1874) a description of tool use in a nonhuman animal did not re-emerge until the 1960s when Jane Goodall reported that chimpanzees used tools to gain access to termite mounds (van Lawick-Goodall, 1968). Since then the number of animals found using tools in the wild has increased greatly and includes species across three phyla and seven classes (Bentley-Condit & Smith, 2010), depending on how tool-use is defined. Tools can be used in a variety of contexts: foraging (e.g. food extraction/preparation/capture), physical maintenance (e.g. used to affect appearance or body), social purposes (e.g. mate attraction, agonistic displays), predator defense, or nest-building (Beck, 1980; Bentley-Condit & Smith, 2010; St Amant & Horton, 2008). Primates and Passeriformes are distinguished by displaying tool use across several categories of behaviour. In particular, apes and corvids use tools in a variety of contexts for a range of purposes. When tool modification or manufacture is considered, defined as “adapting a naturally occurring object by simple means to improve its performance” (Napier, 1980, p. 115), the list narrows even more.

Tool manufacture can be broken down into four broad modes as described by Beck (1980). Most tool manufacture in the wild consists of detachment (or removing one object from another or the substrate) and subtraction (modifying an object to better serve as a tool by removing objects - Beck, 1980). The combination of two or more elements is rarer, as is the restructuring of material to create a functional tool. In addition, most tool use involves the use of one tool directed towards the final goal; tool sets or composites, defined as “two or more tools having different functions that are used sequentially and in association to achieve a single goal” are much rarer (Sugiyama, 1997, p. 23). This can involve using different tools in sequence (sequential tools), or in combination (associate tools) to achieve an end result. In both instances, although separate tools are used in

combination, each one is directed toward the final goal; metatools, or secondary tools, differ in that one tool is directed towards another in order to increase the efficiency of that tool. Evidence of meta-tool use in free-ranging animals is very sparse, and largely anecdotal (Sugiyama, 1997).

Tool composites and tool manufacture involving reshaping and combining materials are fundamental features of human tool technology. Such tool-use requires a high level of coordination and flexibility, and possibly also foresight and knowledge of causal relationships (Limongelli, Boysen, & Visalberghi, 1995; Tomasello & Call, 1997). Although there is considerable complexity in many types of animal tool-use, the only other species to display similar behaviours consistently in the wild and captivity is the chimpanzee (Panger, 2007). The use of tool sets, especially metatools, however, is much rarer in wild chimpanzees than are simpler tool using behaviours. This may be because such behaviours are simply not necessary in the environment and involve expending too much energy when food is more readily available elsewhere. It could be that they are too cognitively complex to be learned through trial-and-error, or the behaviour may be too complex to be transmitted socially if chimpanzees are emulating rather than imitating. Alternatively, we have not been watching them long enough for such behaviours to emerge (McGrew, 1992a). The reasons as yet are unclear, but are particularly important when it comes to considering the “ratchet effect” found in human cultures.

*a. Captive tests of physical cognition in chimpanzees*

Captive studies of spontaneous understanding of physical causal mechanisms in chimpanzees can help rule out the possibility that cognitive restraints are responsible for the paucity of certain types of tool use in the wild (Mulcahy & Call, 2006b; Povinelli, 2000; Visalberghi & Tomasello, 1998). The main areas of focus are tool selection, insight, and means-end tool use. Studies of tool selection in chimpanzees have met with mixed results. Povinelli (2000) found that when presented with two rakes, only one of which was correctly oriented with the food, chimpanzees failed to consistently choose the correct rake. In addition, when presented with appropriate and inappropriate tools for a given task, they did not choose correctly above chance. In contrast, other studies have found that chimpanzees can select an appropriate tool based on diameter (Visalberghi,

Fragaszy, & Savage-Rumbaugh, 1995) and even abstract modalities like rigidity (Manrique, Gross, & Call, 2010).

In order to further identify insightful tool use, chimpanzees have also been assessed in their ability to avoid an obstacle. The most widely used test is the trap-tube. In this task a reward can be pulled or pushed out of a tube with a stick-like tool. Depending on where the reward is placed, it is beneficial to push or pull the food in one direction over another to avoid losing it in the trap (a hole in the tube from which the reward cannot be retrieved). Although there is some evidence that apes are capable of learning the task, the results are mixed (Limongelli et al., 1995; Mulcahy & Call, 2006b; Povinelli, 2000). Some chimpanzees performed well, even when potential confounds like procedural rules (e.g. always push away from the trap) were controlled for, while others did not perform at all or did so at chance levels. Part of this discrepancy might be the result of task design, and slight variations have led to better success in apes (for example one vs. two available tools – Grindt, Meier, & Call, 2008, the opportunity to pull in rather than push away grapes – Mulcahy & Call 2006b, or removing the necessity of the tool altogether – Seed, Call, Emery, & Clayton, 2009). Taken together, results make it difficult to pinpoint whether chimpanzees are relying on sophisticated strategies or trial-and-error learning (Seed et al. 2009, Call 2010).

Means-end studies look at whether or not chimpanzees are capable of using one tool to act upon another to achieve a distant goal (Santos, Rosati, Sproul, Spaulding, & Hauser, 2005). Humans are quite adept at this type of tool use, often using complex sequences of means-means-ends, and although this behaviour has been observed in wild chimpanzees (for example: a push-pull stick attached to a leaf sponge, Sugiyama, 1997) it is very rare. In his classic studies, Köhler (1925) tested chimpanzees' ability to combine objects to obtain out of reach rewards. Although several individuals were able to reach a reward by stacking one box, stacking two to reach a higher reward presented more of a problem. One individual also managed to construct a longer tool from two separate pieces in order to reach a reward, however it is difficult to gauge if this was a spontaneous response. In addition, Povinelli (2000) found that when presented with the opportunity to retrieve a reward by using one tool to pull in another, or by discriminating between a set of tools that are either functionally connected or merely touching, chimpanzees did not

fare well. Conversely, Mulcahy, Call and Dunbar (2005) found that gorillas and orangutans were able to use a shorter tool to gain access to a longer one, thus enabling them to reach a reward.

Studies specific to tool modification are equally mixed. Bania, Harris, Kinsley, and Boysen (2009) replicated a study completed by Povinelli (2000), wherein chimpanzees were provided with assembled or disassembled tools (sticks with t-bar hooks on the ends). They were then presented with different tasks which required the tool in either the assembled or disassembled form. While Povinelli and colleagues' earlier study found that the modifications of the chimpanzees did not relate to the causal structure of the problem (Povinelli, 2000), the replication found that the adult chimpanzees tested consistently modified the tool in the appropriate fashion, demonstrating a functional understanding of the tools and the task (although two infant chimpanzees performed less consistently). Bania et al. (2009) explain this difference as a result of the early rearing history of the subjects, arguing that the enculturated environment of the chimpanzees in their study (enculturated here defined as extensive human interaction) gave them an advantage.

The evidence thus far is inconclusive; chimpanzee responses on causal tool-use tests differ greatly between individuals. The lack of a consistent picture could stem from rearing histories, or inappropriate designs, and new inventive techniques have found that slight variations in design could rule out certain chimpanzee propensities which may have overshadowed causal understanding (Call, 2010).

#### *b. Emulation versus imitation in chimpanzees and children*

Direct comparisons between chimpanzees and children seek to determine if the lack of cumulative culture in other species is a result of differences in the quality or quantity of social learning. Research claiming positive results for imitation in chimpanzees has been criticized for not ruling out emulation well enough, and well-controlled experiments have found differences between chimpanzees and children on social learning tasks. Much of this research concludes that children replicate perceived behaviour to a higher level of fidelity than do chimpanzees, and this has led to the description of children as imitators and chimpanzees as emulators (Tennie, Call, & Tomasello, 2009; Tomasello, 1999). Although there is a body of evidence to support this

claim (see Call, Carpenter, & Tomasello, 2005; Tomasello & Call, 1997; Tomasello, Davis-Dasilva, Camak, & Bard, 1987; Whiten et al., 2004 for examples), the reasons for this difference have only recently begun to be dissected experimentally. Essentially, the difference between humans and chimpanzees could be a qualitative one: chimpanzees emulate simply because they do not have the cognitive capacity to imitate. Children on the other hand may be “hardwired” to imitate, and this is what allows them to learn complex behaviors that they would not be able to learn on their own (Lyons, Young, & Keil, 2007). Alternatively, chimpanzees might be choosy copiers, only seeking external information if they cannot solve a task through individual learning. In this sense, the difference is quantitative, and chimpanzees and children might be applying different strategies under different conditions (Boyd & Richerson, 1996). Furthermore, emulation has often been used as a label for a whole host of cognitive mechanisms (essentially anything that is not imitation in some cases) and has only recently been tested for directly (Byrne, 2002a) .

Causal understanding of a given task might influence an individual’s social learning strategy. For example, if an animal is shown one of two demonstration techniques, but is able to work out the basic requirements of the task, it may emulate rather than imitate. Emulation of this type has been classed as “a kind of imitation” (Zentall, 2006, p. 346) in which “the organism is not bound to reproduce the actions of the model, but reorganizes the relationships between model and copy to its own ends” (Mitchell, 1987, p. 207; see also Gattis, Bekkering, & Wohlschläger, 2002). In this sense the observer perceives the result as a goal, attainable by other means. There is some evidence that chimpanzees will use their own methods to solve simple bi-directional tasks (Tennie et al. 2006), but copy more faithfully on complex tool using tasks (Hopper et al., 2008; Hopper et al., 2007; Whiten et al., 2005). The fact that other primates, with arguably less cognitive savvy, do copy on such simple tasks (common marmosets - Bugnyar & Huber, 1997; colobus monkeys, *Colobus guereza*, Price & Caldwell, 2007) lends credence to this assertion.

These results are suggestive, but studies that directly manipulate the amount of causal information available in a given task are necessary to determine if different learning strategies are in place. Nagell, Olguin, and Tomasello (1993) presented

chimpanzees and children with one of two demonstrations for raking in a food reward. In the complete demonstration, the model flipped the rake over to the effective “edge” position and raked in the reward. In the partial condition, the model’s rake was placed in the “edge” position, while that of the observer was in the ineffective “rake” position (spokes down). Observers in this condition were not able to see the crucial step of flipping the rake over prior to retrieving. Although children tended to copy the model’s behaviour in both conditions, chimpanzees tended to use the more efficient method (flip the rake over) regardless of the demonstration. Chimpanzees were therefore adopting the more effective strategy.

Horner and Whiten (2005) presented chimpanzees and children with a task in which a tool was used to act on a box in a sequence of two main actions. One of these was required to solve the task, but the other was causally irrelevant. Horner and Whiten found that chimpanzees tended to copy both actions when the task was perceptually opaque (there was no visible information about the causal irrelevance). When the task was transparent, they performed only the necessary action. Children, on the other hand, always tended to perform the irrelevant action, even when they could potentially see it was not necessary. In both of these instances, chimpanzees thus adopted the more efficient strategy of emulating. At first glance, it would seem as though chimpanzees are varying their copying fidelity based on their ability to understand the causal features of the task, and might be better at judging the most effective strategy. Children, conversely, (regardless of whether or not they are aware of the most functional solution) are applying a blanket copying strategy. The reason may be that although this strategy is sometimes ineffective, it might generally allow children to copy information they would not otherwise be able to learn on their own. Alternatively, their motivation to copy might be purely social (e.g. bond forming), and there is evidence to suggest that children learn better from socially interactive models (Hayne, Herbert, & Simcock, 2003; Nielsen, Simcock, & Jenkins, 2008). However, Lyons et al. (2007) found that three to five year olds imitated unnecessary actions, even when the demonstrator was no longer present. Lyons et al. (2007) suggest that children are not just imitating as a purely social exercise but have a predisposition to encode the actions of an adult demonstrator as “causally meaningful”. This socially gained causal information then overrides the child’s own

causal view of a task. Regardless of the underlying process, this propensity might allow humans to learn causally opaque actions commonly involved in human technology. Conversely, chimpanzees might be limited to socially learning those tasks which are within reach of their own causal understanding (Tennie et al., 2009).

There is also evidence that children do not always apply a blanket “copy” strategy, but rather imitate flexibly, behaving much more like chimpanzees on some tasks. Chimpanzees and children were presented with demonstrators using an unusual body part to operate a device, in either a “hands free” condition – in which they presumably had the free choice to use their hands, or a “hands occupied” condition – in which the demonstrator’s hands were constrained in some way. Both chimpanzees and children copied the body action more in the “hands free” condition, suggesting that they had some understanding of the rationality behind the demonstrator’s behaviour (Buttelmann, Carpenter, Call, & Tomasello, 2007; Gergely, Bekkering, & Király, 2002). In addition, differences were found between the responses of three and five-year old children on a tool use task using irrelevant and relevant actions. When presented with degraded information in a video demonstration (a version showing only a demonstrator’s hands), three year olds omitted irrelevant actions, whereas five year olds copied both relevant and irrelevant actions (McGuigan, Whiten, Flynn, & Horner, 2007b). The results of the research taken together are suggestive of an important cognitive shift, perhaps in relation to the development of shared intentionality, or theory of mind, in children. The majority of tests reporting “rational imitation” have tested infants or toddlers. Tests finding more striking evidence of over-imitation typically involved three to five year old children (although there are some exceptions - Nagell et al., 1993).

#### 1.5.2. Direct tests of cumulative culture

Very few studies to date have directly tested cumulative culture. Such tests can determine if a given animal is capable of the most basic aspect of cumulative culture - the ability to socially learn an efficient modification. They can also help test the theory that imitation is required for such transmission in humans. Marshall-Pescini and Whiten (2008) first had chimpanzees socially learn how to obtain a reward using a simple method demonstrated by a familiar human. They were then shown a more complex method, which allowed them to retrieve a higher quality reward. While chimpanzees tended to

stick to the simple method, a majority of children, tested later, upgraded to the more efficient method (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). This result would seem to provide evidence of a limit for chimpanzees in “ratcheting” up to the next modification. One possible explanation is that chimpanzees were applying a “copy if dissatisfied approach”; they still obtained a reward using the simpler method, and were consequently not sufficiently motivated to move onto a more complex method (Hirata & Morimura, 2000; Laland, 2004). Human demonstrators were also used with both chimpanzees and children, so children might have been more socially motivated to copy the demonstrator, regardless of the reward.

In a series of recent studies, Caldwell and Millen (2008) have directly tested cumulative culture in adults. Participants were asked to construct paper airplanes or towers built from spaghetti and modeling clay. Researchers then simulated the creation of new “generations”, by gradually replacing older participants with naïve participants over time. In one study, the amount of information available to the groups was manipulated, so that in some active instruction was encouraged, and in others, information was limited to actions or end results only. In each of these groups, the resulting products (e.g. the height of the spaghetti tower) were superior in the later generations than in early generations, suggesting that emulation (seeing end results only) was sufficient for increasingly effective modifications to take hold. This is an important result, and suggests that imitation might not be the key distinction driving cumulative culture in humans that it has often been assumed to be.

## 1.6. Future directions

### 1.6.1. The complexity of the tool

As discussed, tool use is an excellent vehicle with which to investigate cumulative culture in humans and other animals in a captive environment. Experimental studies have helped explain the absence or presence of behaviours by focusing on causal understanding or social learning abilities in captive animals. Despite this, there are still several gaps in the literature worthy of further exploration. For one, although several studies have used complex tasks involving hierarchical steps (Marshall-Pescini & Whiten, 2008; Whiten, 2002; Whiten et al., 1996; Whiten, Flynn, Brown, & Lee, 2006;

Whiten et al., 2007) the complexity of the task itself is typically manipulated, while the required tool remains relatively simple. Observational learning of complex tool modification has yet to be investigated in any detail. An individual will not likely face increasingly complex food defences in her lifetime, but might benefit from constructing a complex tool with which to more efficiently extract food. The ability to modify and to build tools from multiple parts is also fundamental to human cumulative technology. The complexity of the tool itself, or the ways in which an individual can modify the tool, might therefore be better variables to manipulate. Additionally, human technological advances are a result of a flexible combination of causal understanding and social learning, yet few studies have directly investigated the interaction between these two processes in either human or nonhuman animals.

#### 1.6.2. The use of video demonstrations

Secondly, although the results have undoubtedly been instructive, conclusions based on comparative studies in children and chimpanzees should be approached with caution. In order to guarantee tight experimental controls, human demonstrators are often used for both chimpanzee and child participants (Boesch, 2007, 2008; De Waal, Boesch, Horner, & Whiten, 2008). Conspecific demonstrators are particularly relevant in social learning experiments, but it is difficult to control for discrepancies across demonstrations when using live animal models. Video playback offers a potential compromise by allowing for the use of ethologically relevant conspecific models, while still granting precise control over the quality, quantity and type of information available in the demonstration (Carpenter & Nielsen, 2008; Emery & Clayton, 2004a). For example, as previously described, “ghost conditions” are very useful methods of deciphering between emulation and imitation, but they involve unexpected, often surreal situations, and might affect an individual’s performance. With the use of video playback, varying degrees of information can be presented in ways that might be more intuitive.

Video playback has been used in animal behaviour experiments since the 1960s, largely developed to address visual signalling (D’Eath, 1998). Video footage can be manipulated to test a range of behaviours including predator or prey recognition, audience effects, and courtship behaviours, and has been used with a wide variety of species (for example: Jacky dragons, *Amphibolurus muricatus*, Ord, Peters, Evans, &

Taylor, 2002; jumping spiders, *Maevia inclemens*, Clark & Uetz, 1990; green swordtails, *Xiphophorus helleri*, Trainor & Basolo, 2000; bonnet macaques, *Macaca radiate*, Plimpton, Swartz, & Rosenblum, 1981; three-spined sticklebacks, *Gasterosteus aculeatus*, Rowland, Bolyard, Jenkins, & Fowler, 1995; for a review see D'eath, 1998; Fleishman, McClintock, D'eath, Brainard, & Endler, 1998).

Video playback has been used to test social learning less frequently. McQuoid and Galef (1993) found an enhanced preference for specific feeding dishes after presenting Burmese red junglefowl with video footage of conspecifics eating out of these dishes. Further, they found an enhanced preference for the dish when the video showed the junglefowl actively feeding, as opposed to videos showing them either immobile or active near the dish. The two-action task methodology has also been applied successfully using video demonstrations. Budgerigars presented with video footage of a conspecific solving a two-action task tended to match the demonstrated solution, using either the same action (lifting or pushing - (Mottley & Heyes, 2003) or the same body part (pecking or stepping - (Richards, Mottley, Pearce, & Heyes, 2009). In an earlier experiment, I and my colleague Christine Caldwell presented two groups of Abyssinian colobus monkeys (*Colobus guereza*) with video footage of a King Colobus monkey (*Colobus polykomos*) either pushing or pulling a door to retrieve a reward. We found very high rates of matching the demonstrated method, in some cases even 100% (Price & Caldwell, 2007).

### 1.6.3. Further cross-species comparisons

Lastly, overemphasis on chimpanzees does not provide a complete view (McGrew, 1992a) and might even be misleading if applied in isolation to hominid evolution (Sayers & Lovejoy, 2008). This is particularly important regarding the study of tool use. The complexity and frequency of tool use varies considerably across species; it is instructive, therefore, to test for both convergent evolution and divergent evolution. For example, corvids demonstrate cognitive abilities comparable to primates in many domains (Emery, 2006) despite not sharing a common ancestor for over 280 million years (Emery & Clayton, 2004a). In fact, one of the most convincing examples of possibly cumulative technology is from a nonprimate species – the New Caledonian crow (Hunt & Gray, 2003). Tool use also varies between closely related taxa (Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009) and some animals that have not been observed to use

tools in the wild do so frequently in captivity. It is therefore difficult to tell whether tool use is reliant on specialized cognitive abilities, or on common processes shared with non-tool-users. Recent tests have made headway by testing non-tool using species on the same causal cognition tasks normally applied to tool-users (Santos, Pearson, Spaepen, Tsao, & Hauser, 2006). Additionally, studies with nonprimate species typically either test individual learning of tool use, or social learning on non-tool tasks. Captive experiments investigating social learning of tool-use are less frequent, and would prove very instructive with both tool and non-tool using species.

### 1.7. Conclusion

This thesis strives to explore the gaps laid out in the previous section and includes a series of experiments using video playback of conspecifics to investigate social learning on complex foraging tasks. Despite an abundance of studies comparing social learning abilities in chimpanzees and children, very few specifically address tool modification or construction. Given the importance of social learning to human tool technology, this seems an important step to better understand potential differences between ourselves and the next best tool users in the animal kingdom, chimpanzees. In addition, video demonstrations have been used successfully in a variety of species, and have great potential for manipulating demonstration quality. Despite this, they have yet to be exploited with regard to chimpanzee social learning. In addition, while they have been tested in children in comparison to live models, their effectiveness has not been tested in chimpanzees. Chapters two and three focus specifically on the social learning of tool modification in chimpanzees and children, with reference to potential similarities and differences in how they learn and apply their knowledge. In order to test the efficacy of the video playback methodology, chapter two also includes a section directly comparing video and live demonstrators on the same task in chimpanzees. Chapter four details two exploratory experiments in a non-tool, non-primate species, the common raven (*Corvus corax*). The first experiment tests the video demonstration methodology in ravens by measuring behavioural reactions to a series of different video stimuli. The second investigates social facilitation on a proto-tool task. Chapter five draws conclusions based on the research, and presents suggestions for future scientific exploration.

## **CHAPTER 2. SOCIAL LEARNING OF TOOL MODIFICATION IN CHIMPANZEES**

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## 2.1 Introduction

Complex tool use is a distinctive feature of human cognition, characterised by multiple sequential steps, understanding of causal relationships, and rapid expansion of increasingly complex technological additions, or cumulative culture. However, many other species display a range of tool-using abilities, and recent discoveries in the field include examples of tool use in nonhuman species previously thought to be restricted to humans (Hunt & Gray, 2003; Pruetz & Bertolani, 2007). As previously discussed, chimpanzee tool use, in particular, has many similarities to behaviours found in humans; it is widespread, (Whiten et al., 1999) it may require years of practice to master (Biro et al., 2003; Matsuzawa et al., 2001) and recent archaeological evidence suggests that some forms have a history of centuries at least (Mercader et al., 2007). Furthermore, distinct patterns of tool use in chimpanzee groups have recently been described as “cultural” behaviours, maintained by social learning with no apparent ecological, environmental or genetic explanation (Boesch & Tomasello, 1998; McGrew, 1992b; Schöenig, Humle, Möbius, & McGrew, 2008; Schönig et al., 2008; Whiten et al., 1999).

Free-ranging chimpanzees also use tool-sets, or more than one tool used sequentially for a single task (Boesch & Boesch, 1990; Brewer & McGrew, 1990; Deblauwe, Guislain, Dupain, & Van Elsckker, 2006; Sanz, Morgan, & Gulick, 2004). For example, chimpanzees have been observed using a particular tool to perforate an ant nest or bee hive, and then a more slender stem to dip inside and harvest the food resource (Brewer & McGrew, 1990; Sanz & Morgan, 2009; Sanz, Shönig, & Morgan, 2010). There is also some evidence to suggest that tool sets are specialized for particular situations. Chimpanzees in the Goualagou Triangle, Republic of Congo, for example, use different tool combinations for ant predation than they do for termite or honey gathering (Sanz et al., 2010). Further, chimpanzees of Bossou, Guinea combined certain stones as hammer and anvil more often than expected by chance (Carvalho, Biro, McGrew, & Matsuzawa, 2009), suggesting that they might recognise a collection of elements together as a single tool composite.

Despite this complexity, there is minimal evidence of modifications to tool technology over time - the “ratcheting effect” so evident in human cumulative culture (Boesch & Tomasello, 1998; Sanz, Call, & Morgan, 2009; Tomasello et al., 1993 ). In

addition, whereas human tool manufacture often involves reshaping and combining materials, chimpanzee tool manufacture in the wild mostly involves subtraction or removal of materials (Beck, 1980), and tool construction involving more than one raw component is lacking. Recently, Sanz, Call and Morgan (2009) presented evidence that chimpanzees deliberately modified the end of fishing probes before collecting termites. Their experimental analyses suggest that this “brush-tip” method renders the dipping tool more effective and the absence of this behaviour in other populations of chimpanzees implies that it is not necessarily species-specific, but is most likely acquired during ontogeny. It is still unknown specifically how the behaviour is acquired (i.e., whether through trial-and-error, social learning, or a combination of the two), however, and further exploration is warranted. There is some evidence of wild chimpanzees using one tool (a “metatool”) to render another tool more effective (for example using a stone as an anvil prop to create an even surface, or using a push-pull stick attached to a leaf sponge to assist in retrieving water), but such behaviour is rare and has not spread as simpler tool using behaviour has (Matsuzawa, 1994, 2001a; Sugiyama, 1997). Combinatorial technology is likely to be more cognitively demanding than other forms because the second tool acts as an intermediary step between the main tool and a goal (Santos et al., 2005). The spread of such technology in the wild requires the cognitive ability for innovation, the capacity for social transmission, and an ecological niche affording technological fixes (van Schaik, Deaner, & Merrill, 1999; van Schaik & Pradhan, 2003). It may be that developments of this nature are not seen in wild chimpanzees because their ecological niche does not call for them. Alternatively, the limit may lie in physical cognition (e.g. understanding causality), or the behaviour may be too complex for chimpanzee social learning abilities (Boesch & Tomasello, 1998).

In the following experiments I assessed whether captive chimpanzees could socially learn how to modify a tool one of two ways. Building off of the classic Köhler (1925) study, one technique involved constructing a composite tool from two components. The second required structurally reshaping a tool. I also investigated how much information chimpanzees required to solve the task and how well they understand the function of the modification process. Further, I explored if such complex information could be transmitted via video footage of a conspecific model. Videos are often used as a

form of environmental enrichment with captive chimpanzees (Bloomsith & Lambeth, 2000; Rumbaugh, Washburn, & Savage-Rumbaugh, 1989), and match-to-sample tests show that chimpanzees can discriminate between different types of movies (for example: different chimpanzees in the movies, or fluid movies versus those with sudden changes, Morimura, 2006; Morimura & Matsuzawa, 2001). Additionally, chimpanzees have been shown to use information from a video to find hidden objects (Poss & Rochat, 2003). Experiments using video in lieu of live models on a manipulative social learning task are lacking, as is their efficacy in comparison to live models on the same task.

## 2.2. Subjects and housing

A total of 74 chimpanzees acted as subjects. All were housed at The Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M. D. Anderson Cancer Center in Bastrop, Texas, U. S. A. Chimpanzee enclosures were comprised of outdoor domes measuring 10.4 m in diameter, and four inner housing compartments measuring 2.4 x 2.4 m and 1.8 m high.

During 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 testing has been approved by the University of Texas Institutional Animal Care and Use Committee. Positive reward shaping was used to train all chimpanzee models. Observer chimpanzees were tested opportunistically where possible, by opening the inner doors and allowing them to come inside if they chose. If a chimpanzee showed distress at any time, the session was immediately terminated and subjects were reintroduced into their social groups.

## 2.3. Pilot study

In order to determine an appropriate level of complexity, as well as test the durability of the tools, I completed a pilot study divided into two parts.

### 2.3.1. Subjects

Fourteen adult chimpanzees (10 male and 4 female) participated in the study. They were housed in three social groups as outlined in Appendix A.

### 2.3.2. Apparatus

The tool set consisted of two elements. The first was a 39 cm long hollow polycarbonate tube containing an internal nylon rod which protruded 3 cm out of one end. The second element, a 28 cm rod, could be inserted into an 8 cm hollow opening on one end of the polycarbonate tube, creating a 59 cm long stick. Alternatively, the tool could be elongated to 59 cm by twisting on the protruding end of the internal rod and extending it (See Figure 2.1). Thus, a more efficient tool could be manufactured by either combining two elements, or reshaping one of the tools.

For the initial food retrieval task (“Poke” apparatus) a grape was suspended in a small plastic cup 1 m above the ground along a wire attached to two metal poles. The cup measured approximately 7.5 cm wide by 5 cm deep and had a small hole cut on either side measuring approximately 2 cm by 2 cm. The grape could be dislodged by either pulling down on the top of the cup or by poking the cup so that it spun on the wire axis. The grape then fell into a funnel which was attached to a metal feeding tube 61 cm in length which fed into the enclosure. This was secured with a metal clamp so the device could not be pulled further into the cage, and the whole device was attached to a wheeled cart so it could be easily placed against the enclosures (See Figure 2.2).

**Figure 2.1. Tool set**



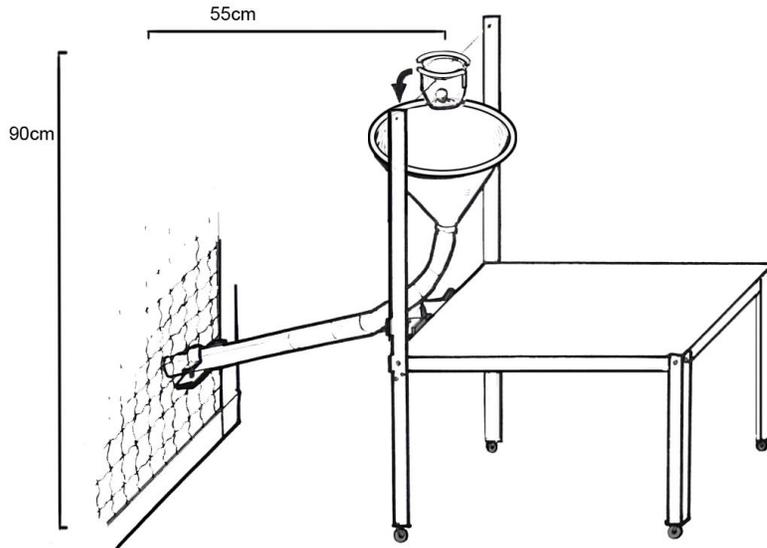
Unmodified Tool Components



Alternative Method (top)

Combine Method (bottom)

**Figure 2.2. “Poke” apparatus**



Grapes could be dislodged by poking the cup until a grape fell into the funnel, through the tube, and into the enclosure.

### 2.3.3. Method

Nine chimpanzees from groups Q2 (2 males, 4 females) and Q4 (3 males) were tested using the original apparatus (See Appendix A). Individuals were initially isolated from the rest of their group in the outside or inside section of their enclosure depending on their level of comfort with each area. The feeding tube was inserted into the caging so that the grape was suspended approximately 55 cm in a direct horizontal line from the edge of the enclosure, requiring either the combined or extended tool as described above. Each subject was given 20 minutes to interact with one set of tools and the “Poke” apparatus. Each group as a whole was then provided with two sets of tools and given 20 minutes to interact with the apparatus.

With three of the chimpanzees from the above group (Q4) and an additional five male chimpanzees (Q3) I also explored a potentially easier food retrieval task. Each subject was isolated in the outside portion of their enclosure and provided with one set of tools. Grapes were placed on the ground 20 cm outside of the enclosure and could be obtained by raking through the caging with either unmodified tool component. Subjects

were given 5 minutes of access to grapes in this manner after which the food was moved 55 cm away, requiring the use of the longer modified tool. If subjects were unsuccessful, the grapes were once again moved within reach of the unmodified tool components for 5 minutes, and then once again out of reach for 5 minutes. Both groups were then given access to two sets of tools as a whole and the grapes were placed out of reach for the entire 20 minutes. All sessions were videotaped and all interactions with both the set of tools and the device noted (See Appendix B).

#### 2.3.4. Preliminary results

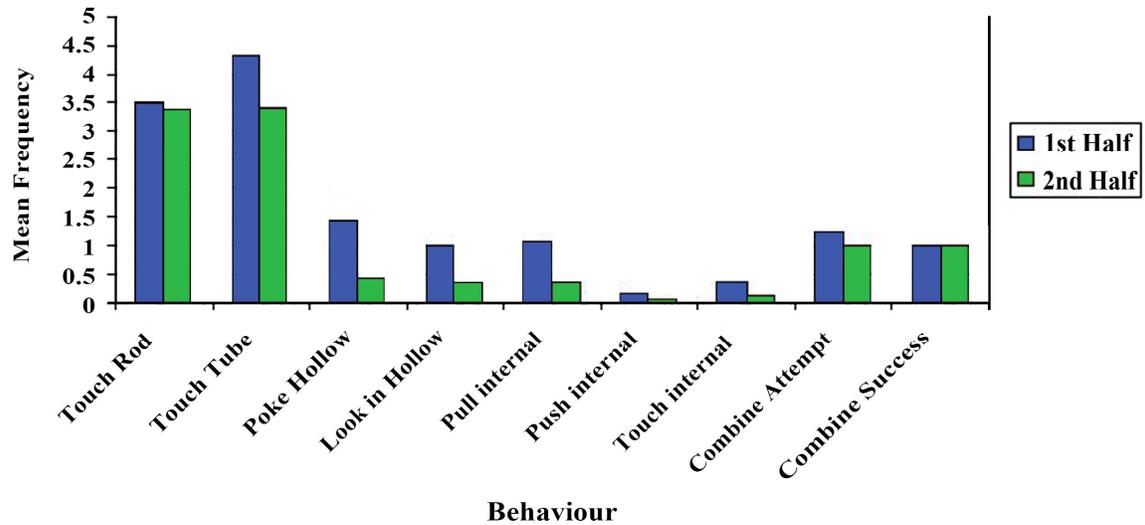
None of the nine chimpanzees provided with the original retrieval device (Poke Apparatus) attempted to dislodge a grape with either a provided tool or a tool of their own. Six out of nine individuals interacted with the hollow end of the tube (either by looking inside or inserting a finger or tongue). Seven also tried to pull or push on the tip of the extendable part of the tool component, although none made the twisting action required to extend it. The majority of these interactions were pull attempts (89%, 20 out of 23). Two (one male, one female) spontaneously slotted the two tool components together to create a longer tool; the female did so in her individual and group sessions, the male only during his individual session. All subjects made contact with the metal feeding chute, eight out of nine attempting to fish inside it with one of the tools.

Of the eight subjects in the Rake condition, six successfully raked in grapes using one of the two provided tools when the grapes were placed at the shorter distance away from them. Four out of these six subjects made some attempt to rake in the grapes when they were placed further away, but none successfully modified the tools. No subject put the tools together (including the one individual that had done so previously with the original retrieval device). Two subjects found their own longer tools (sticks lying on the ground of the enclosure) and used these to successfully rake in grapes placed farther away. When these were removed, they continued to try unsuccessfully with the unmodified tool components.

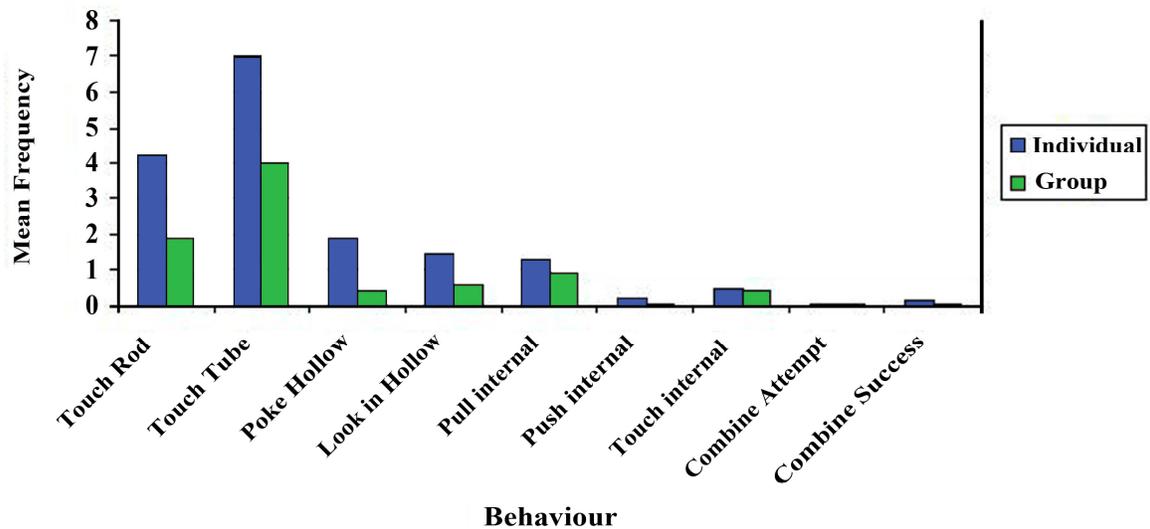
In both cases, the data were summarised in 10 minute sections to ascertain whether the length of the sessions was appropriate. Most interactions (64% for those in the Poke condition, 65% for those in the Rake condition) took place during the first 10 minutes, with some subjects not interacting with the tools at all in the latter half of the

session (See Figure 2.3). Mean frequencies of interaction were also higher per subject in the individual sessions rather than the group sessions (see Figure 2.4). The two subjects who combined the two tools, however, did so for the first time in the last 10 minutes of their individual sessions (See Appendix C for mean rates of behaviour for all subjects).

**Figure 2.3.**



**Figure 2.4.**



\* The means were calculated using only the Poke Condition scores for Q4

### 2.3.5. Discussion of pilot study

The tools were used to try to retrieve grapes only during the Rake condition, suggesting that the Poke apparatus may not have had intrinsic affordances for the chimpanzees. There was also no evidence of insightful tool use. None of the chimpanzees made a connection between combining the tools and their potential use to reach far distant grapes. In fact, even the subject who had put the two tools together in the Poke condition did not think to do so to reach the grapes when they were placed farther away in the Rake condition. In addition, although the majority of interactions took place during the first 10 minutes, the two chimpanzees who combined the two tools did so later in the session, suggesting that 20 minutes is an appropriate session length. Testing individually away from the group did not inhibit interaction with the tools, with subjects interacting more with the tools when housed individually, rather than in their social groups. Based on this information, testing individually was deemed appropriate, and the simpler raking method was chosen for the main study.

## 2.4. Experiment 1

### 2.4.1. Subjects

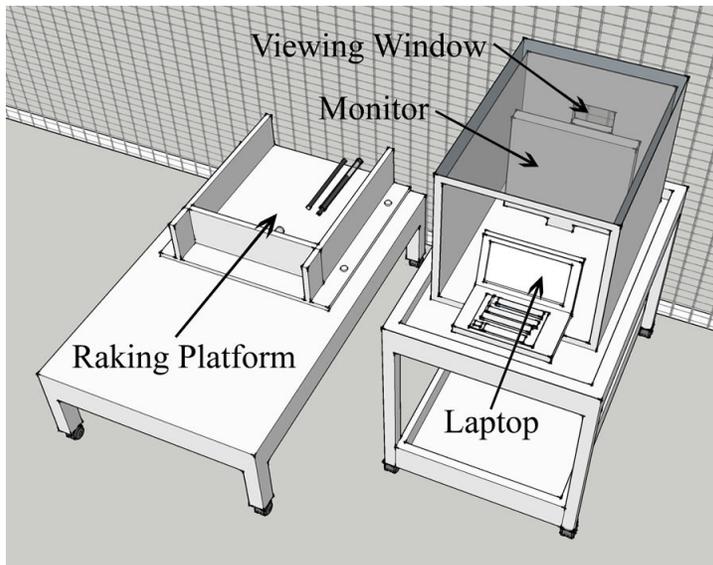
Fifty chimpanzees (25 male and 25 female, mean age = 25.5, SD = 9.42, range = 9 – 46 years) housed at the University of Texas M.D. Anderson Cancer Center (Bastrop, Texas) participated in the study (see Appendix D for demographic data). One additional male chimpanzee from the Center acted as the demonstrator for all conditions (age = 24 years). Participants resided in social groups of five to 14 individuals with access to four inner housing compartments and were tested in one half of their inside enclosure, measuring 2.4 x 2.4 x 1.8 m<sup>3</sup>. All regulations as laid out in section 2.2 were followed.

### 2.4.2. Apparatus

The same tool composite as described above was used. The raking platform consisted of a 50 cm by 55 cm acrylonitrile-butadiene-styrene (ABS) tray placed atop a wheeled cart measuring 1.22 m by 74 cm wide and 31 cm high. Grapes were placed 55 cm back from the edge of the platform against a 13 cm high wall. Video footage was played on a laptop connected to an external 19” LCD monitor, so that the experimenter had visual access to what the chimpanzees were seeing at all times. The monitor was

enclosed in a viewing box measuring 48 cm wide by 45 cm high and 67 cm long so that the screen was placed 23 cm back from the edge and was visible through a viewing window measuring 13 cm by 7.6 cm. The entire monitor/viewing box was placed on top of a wheeled cart 61 cm wide by 91 cm long. When fully assembled on the cart, the base of the viewing window measured 83 cm from the ground (see Figure 2.5).

**Figure 2.5. Experimental set-up**



At the start of the experimental session, the food retrieval platform was placed flush to the edge of the enclosure as depicted above. The monitor was directly attached to the laptop seen pictured, so that all video demonstration clips could be watched simultaneously by the experimenter.

### 2.4.3. Method

#### *a. Baseline*

All subjects were first provided with baseline raking sessions to ascertain individual raking abilities. Subjects were provided with a grape placed approximately 30 cm out of reach on the platform and sticks of adequate length. Once two grapes were successfully retrieved, the session ended.

#### *b. Video demonstrations*

One adult male chimpanzee (not a member of the group of any other subject) acted as the model for all demonstration conditions and was trained using positive reward

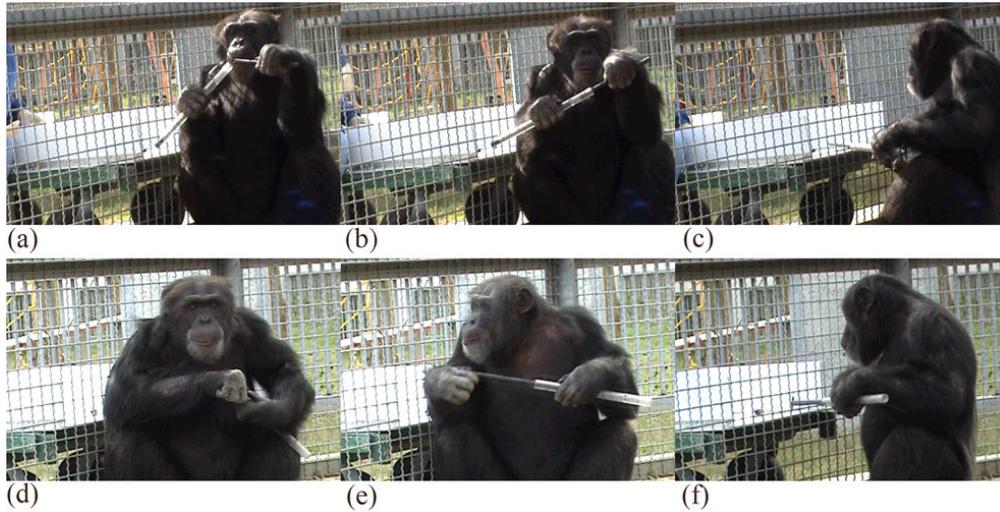
shaping. Video footage was captured on a Sony Handicam (DCR HC35E) then digitised and edited using Adobe Premier Pro 2.0. All demonstration clips consisted of a combination of alternating close up and far away shots captured from the same angle. Each clip lasted approximately 25 seconds and clips were looped continuously with a 1 second pause between close and far away shots.

*c. Experimental sessions*

Subjects were assigned to one of five demonstration conditions: Combine-and-Retrieve, Retrieve-Only, Video Control, No-Video Control, and Alternative Method. In all but the No-Video Control, video footage was presented. Subjects in the Combine-and-Retrieve condition had access to video footage of an unfamiliar chimpanzee slotting the nylon rod into the hollow end of the complex tool, thereby creating a longer tool, and retrieving a food reward off the platform. The Retrieve-Only condition involved the chimpanzee model retrieving the reward with a combined tool, but the modification process was omitted. In the Video Control condition the model was eating the food reward in the absence of tools or platform. Chimpanzees in the No-Video Control condition received no prior video demonstration. In the Alternative Method condition, chimpanzees saw the model reshape the tool by twisting the end of the complex tool, extending an internal rod, and then retrieving a reward (See Figure 2.6).

Subjects were isolated from their social group in one half of their inside housing area. Video footage of the appropriate demonstration was shown for approximately 6 minutes, totalling 16 demonstrations. During this time the raking platform was visible but not accessible. After the pre-session, the platform was pushed flush with the cage with a food reward placed 49 cm out of reach, and the tool set handed to the chimpanzee. An additional 48 demonstrations were played simultaneously for the entire 20 minute test session. Subjects were given access to the platform and the tool set for up to a total of three 20 minute sessions or until they solved the task. As soon as a subject had successfully modified the tool and retrieved a reward, the session was over, giving each chimpanzee only one opportunity to obtain a reward.

**Figure 2.6. Demonstration stills from the Combine and Alternative Method Conditions**

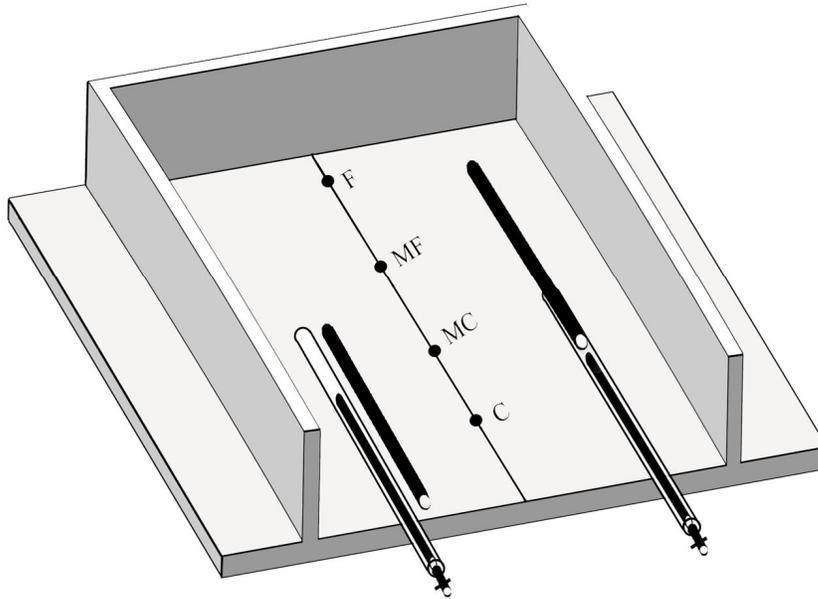


Demonstration stills taken from the Combine Method (a,b,c) and the Alternative Method (d,e,f). Stills show the sequence of actions for combining: picking up and positioning both components (a), slotting the two components together (b), and retrieving the reward (c) and for the alternative method: twisting the black end of the complex component (d), extending the internal rod (e), and retrieving the reward (f).

#### *d. Post-sessions*

Successful subjects (who had successfully modified the tool and retrieved a reward) were tested away from their group two weeks after their final session. Each trial started with the presentation of the tool components immediately following the placement of a grape at one of four different locations on the platform: Close (13cm), Mid-close (22cm), Mid-far (36cm), and Far (49cm; see Figure 2.7). Close and Mid-close rewards could be retrieved easily with the unmodified components, Mid-far rewards required the longer, polycarbonate tube, and Far rewards could only be retrieved by combining. Rewards were placed in each location four times, for a total of 16 presentations. Presentation order was randomised across subjects. All chimpanzees had previously been trained to return objects in response to a “give” hand gesture (open hand palm up), and returned the tools prior to the next grape presentation.

**Figure 2.7. Post-Session reward distances**



The reward distance positions for the Post-Session, accompanied by the uncombined components and a combined tool. A reward was placed in each position four times: F = Far Distant, MF = Mid-Far, MC = Mid-Close, C = Close.

#### 2.4.4. Coding and reliability

In coding videotapes, subjects were assigned a score on a scale of interaction for both combining and using the alternative method (0 = no interaction, 14= complete modification and retrieval; see Table 1). Ten randomly selected trials were coded independently by an additional rater and overall scores assigned on both the combining and alternative method indices. Inter-rater reliability was assessed using Spearman's rank order coefficient, yielding 0.90 for the combining index and 1.00 for the alternative method index.

**Table 2.1. Combine and Alternative Method Indices**

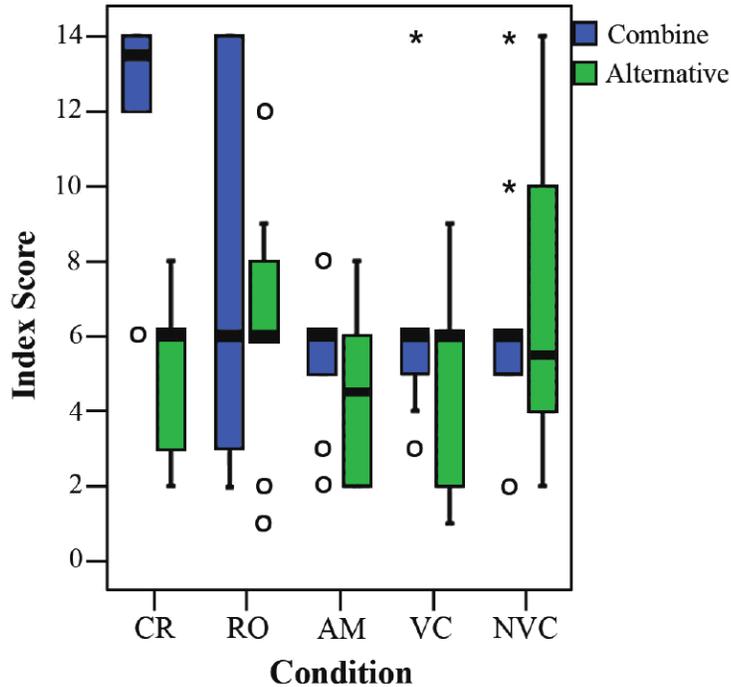
<i>Combine Index</i>	<i>Score</i>	<i>Alternative Method Index</i>
Successful retrieval with the combined tool.	<b>14</b>	Successful retrieval with alternative method.
Combine tools successfully, retrieval attempt with combined tool.	<b>13</b>	Successful modification (twist and extend), retrieval attempt with modified tool.
Combine tools successfully, retrieval attempt with either or both unmodified components.	<b>12</b>	Successful modification, retrieval attempt with either or both unmodified components.
Combine tools successfully, no retrieval attempt.	<b>11</b>	Successful modification, no retrieval attempt.
Combine attempt with hollow (correct) end, retrieval attempt with either or both unmodified components.	<b>10</b>	Twist and pull attempt (unsuccessful modification), retrieval attempt with either or both unmodified components.
Combine attempt with hollow end, no retrieval attempt.	<b>9</b>	Twist and pull attempt, no retrieval attempt.
Combine attempt with black (incorrect) end, retrieval attempt with either or both unmodified components.	<b>8</b>	Twist attempt, retrieval attempt with either or both unmodified components.
Combine attempt with black end, no retrieval attempt.	<b>7</b>	Twist attempt, no retrieval attempt.
Insert finger into hollow end, retrieval attempt with either or both unmodified components.	<b>6</b>	Pull attempt, retrieval attempt with either or both unmodified components.
Insert finger into hollow end, no retrieval attempt.	<b>5</b>	Pull attempt, no retrieval attempt.
Look into or mouth hollow end, retrieval attempt with either or both unmodified components.	<b>4</b>	Bite or hand touch to black end, retrieval attempt with either or both unmodified components.
Look into or mouth hollow end, no retrieval attempt	<b>3</b>	Bite or hand touch to black end, no retrieval attempt.
Retrieval attempt with either or both unmodified components.	<b>2</b>	Retrieval attempt with either or both unmodified components.
Contact, but not retrieval attempt	<b>1</b>	Contact, but no retrieval attempt
No contact	<b>0</b>	No contact.

## 2.4.5. Results

### *a. Experimental sessions*

Overall there were significant differences in the level of combining across groups (Kruskal-Wallis test,  $\chi^2(4) = 13.07$ ,  $p = 0.01$ ). Subjects who saw the Combine-and-Retrieve demonstration scored significantly higher on the combine index (Median = 13.5) than those in the Video Control (Median = 6, following Siegel & Castellan, 1988; critical value = 18.2; significant at  $p = .05$  – see Appendix E.), No-Video Control (Median = 6,  $p = .05$ ), or Alternative Method (Median = 6,  $p = .05$ ) conditions (see Figure 2.8). There was no significant difference between the Retrieve-Only condition and any other condition (Median = 6,  $p > .05$ ), with the level of combining in this condition (4 combiners) lying between that in the Combine-and-Retrieve (8 combiners) and the Control conditions (1 combiner in each condition). The same analyses were completed on the scores for the Alternative method and no significant differences were found (Kruskal-Wallis test,  $\chi^2(4) = 3.61$ ,  $p = 0.46$ ). Two subjects from the No-Video Control condition, and one from the Retrieve-Only condition, did manage to modify the tool using this method, but only one of these (from the No-Video Control Condition) successfully retrieved a reward. The other two individuals successfully made and used a combined tool to retrieve a grape.

**Figure 2.8. Median Combine and Alternative Method Scores**



The median scores and interquartile ranges on both the Combine Index and the Alternative Method Index for the Combine-and-Retrieve (CR), Retrieve-Only (RO), Alternative Method (AM), Video Control (VC), and No-Video Control (NVC) Conditions ( $n = 10$  in each group). Boxes represent the interquartile ranges, and whiskers the maximum and minimum values which are not outliers (values between 1.5 and 3 times the interquartile range, marked by circles) or extreme cases (values over 3 times the interquartile range, marked by asterisks).

Further analyses were run to test the relationship between the amount of time chimpanzees spent watching the video and the Combine score they achieved. Chimpanzees were coded as watching only when they were directly gazing into the viewing box. For those in the Combine-and-Retrieve Condition, the time spent watching the video footage (in seconds) prior to access with the tools was significantly positively correlated with the Combine scores (Spearman's correlation:  $r_s = 0.566$ ,  $N = 10$ ,  $p = 0.04$ , one-tailed). For those in the Retrieve-Only condition, the time spent watching before the session was not significantly related to the Combine Index score ( $r_s = 0.194$ ,  $N = 10$ ,  $p = 0.29$ , one-tailed). Given that the session ended upon successful retrieval of a reward,

some sessions were longer than others (offering the opportunity to observe video footage longer) therefore the same analyses were not conducted for the time spent watching during the session.

Intriguingly, three of the eight chimpanzees who learned to combine in the Combine-and-Retrieve condition, and one of the four chimpanzees in the Retrieve-Only condition, nevertheless failed to retrieve a reward. In the case of one Combine-and-Retrieve condition individual, her combined tool fell apart during the retrieval process and she did not attempt to retrieve again. The other three individuals combined the tool, in some cases several times, but then pulled them apart and attempted to retrieve the reward using the separated components. This suggests that while they had learned to combine the components, they did not understand the utility of doing so.

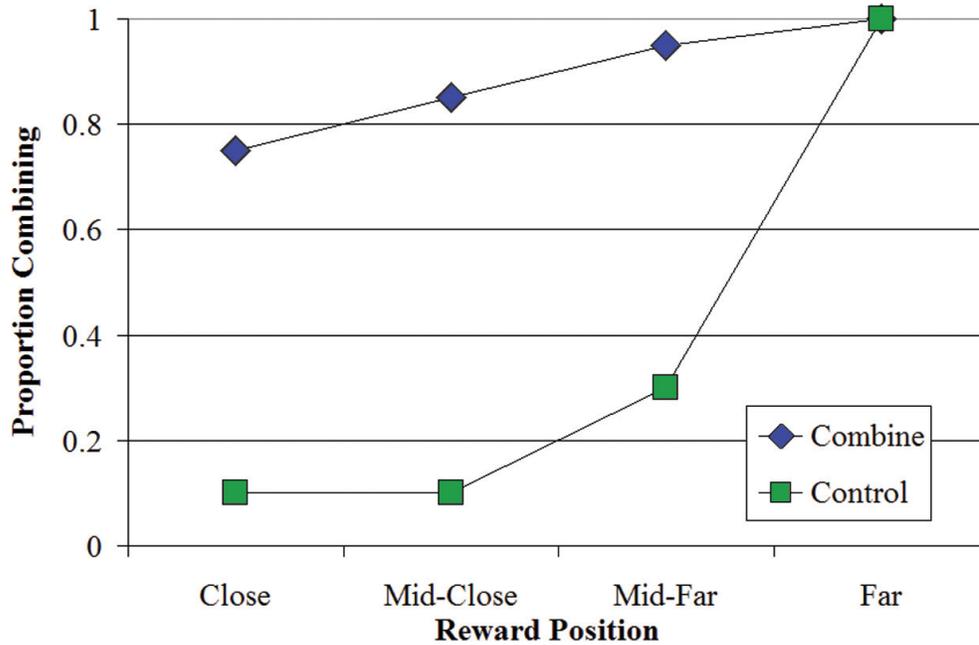
*b. Post-sessions*

In order to ascertain whether or not chimpanzees understood the function of combining, those individuals who solved the task (combined and retrieved the reward) were given a follow up test two weeks after their final session. The one individual who had successfully extended the tool and retrieved a reward using the alternative method did not make any attempts during the post-session using either method and was subsequently excluded from the analysis. Those who solved the test after seeing video footage of the combining process (Combine-and-Retrieve,  $N = 5$ ) combined significantly more in the Close, Mid-Close, and Mid-Far reward positions (when the unmodified tools could be used), than those who had solved the test without first seeing the combination process (Retrieve-Only  $N = 3$ ; Video Control  $n = 1$ ; No-Video Control  $N = 1$ ; Mann-Whitney  $U = 1$ ,  $p = 0.02$ ). Although the sample size was very small, for the purposes of comparison to the studies later completed with children, an additional analysis comparing only those in the Combine-and-Retrieve and Retrieve-Only conditions was run on the proportion of combining responses to the “Close” reward position only. Those who had seen the combining process combined significantly more in the close position ( $N = 5$ , Median = 1) than those who saw the end results of the process only ( $N = 3$ , Median = 0; Mann Whitney  $U = 0.50$ ,  $p = 0.036$ ).

Subjects who had not seen the combining demonstration switched between using the unmodified tools and the combined tool depending on the distance of the reward

(Close versus Far positions, Wilcoxon test,  $z = -2.12$ ,  $p = 0.034$ ), whereas those in the Combine-and-Retrieve condition did not switch significantly between the two techniques (Wilcoxon test,  $z = -1.63$ ,  $p = 0.102$ ; see Figure 2.9).

**Figure 2.9. Proportion of post-Session combining responses**



The overall proportion of combining in the Post-Session across the reward distance positions. Those subjects who solved the task after seeing a model combining the two components (“Combine”: Combine-and-Retrieve,  $N = 5$ ) tended to combine more, even when unnecessary as compared to those who had not seen a model combining (“Control”: Retrieve-Only,  $N = 3$ , Video Control,  $N = 1$ , No-Video Control,  $N = 1$ ).

#### 2.4.6. Discussion

Chimpanzees who saw a conspecific combining two tool elements and retrieving a reward fared significantly better than those in all conditions aside from the Retrieve-Only condition. This result provides the first experimental evidence of chimpanzees socially learning how to manufacture a tool by combining separate elements. Such a result suggests that the spread of similarly complex tool manufacture in free-ranging chimpanzees is unlikely to be blocked by cognitive deficits in social transmission.

Additional inferences can be made about the types of social learning involved. Chimpanzees in the Retrieve-Only condition did not differ significantly from those in the control conditions, suggesting that the chimpanzees were attending to the combination process itself, rather than the product of that process. However, the level of combining in this condition did not differ significantly from the Combine-and-Retrieve condition either, indicating that seeing a conspecific using a completed tool, but not seeing the process itself, was enough to facilitate some chimpanzees to solve the task on their own, but this was not so for the majority.

None of the chimpanzees in the Alternative Method condition learned how to retrieve a grape. Although this task did not involve combining two tool components together, it is arguably more perceptually opaque. Reshaping a tool by twisting and extending an internal rod might be beyond the capabilities of the average chimpanzee's physical cognition, and additionally may be too subtle to learn socially. Although many individuals across the conditions tried to pull on the end of the tool, only three out of the 50 succeeded in twisting the end to elongate the tool, and only one was successful at using the tool to retrieve a reward. It may be that for the majority, chimpanzee understanding of "folk physics" does not extend to such mechanisms. If chimpanzees are relying heavily on their own individual problem solving skills in addition to information gleaned through observation, a task outside of chimpanzee physical cognition abilities may be less easily facilitated by a demonstration.

Understanding of the function of the combining process was limited in several chimpanzees. Although they learned how to combine the two components together, three participants in the Combine-and-Retrieve condition failed to grasp the function of combining. In addition, in the Post-Session, those individuals who saw the combination process tended to combine even when the reward was within reach of the unmodified components. This is especially intriguing given that the combining process was more time consuming and the elongated tool more awkward to use with a reward in the close position. Nevertheless, although combining is less effective in the two close positions, it always works and thus does not require a re-evaluation of distance at the start of each trial. In two recent studies, chimpanzees have been found to persist in an acquired

method, even when presented with a demonstration of a more effective technique (Hrubesch, Preuschof, & Van Schaik, 2008; Marshall-Pescini & Whiten, 2008).

However, if chimpanzees are merely employing a conservative strategy, then both groups tested in the Post-Session should use the combine method equally. All subjects entered the Post-Session having retrieved a reward using the combine method once; the only difference between the two groups was whether or not they saw a conspecific model combining the two components. The five individuals who did not see the combination process constructed tools selectively, only combining when the reward was out of reach of the unmodified components. They therefore demonstrated the capacity to develop an efficient solution through individual problem-solving skills, and seemed to have a causal understanding of the task. It may be that those who socially learned to combine the tools did not understand the function of combining and were blindly copying what they had seen. Alternatively, seeing a conspecific combine the tools may have had an inhibiting effect on insightful behaviour, and chimpanzees were adopting a conformist strategy. Either way, these results suggest that socially learning a task, rather than learning through individual exploration, can have a potent effect on maintaining a particular method among chimpanzees, even at the cost of efficiency.

The question remains as to why combinatorial tool behaviours like these, although observed on rare occasions in the wild, do not spread. The number of available demonstrators or quality of available demonstrations may be a crucial limiting factor. The rare instances of combinatorial tool construction in the wild typically involve low-ranking individuals (Sugiyama, 1997). These individuals might be more likely to perform such tasks because they have more restricted access to prime foods, and as low-ranking group members they are then less likely to act as salient models for other group members (Laland, 2004).

The number of available demonstrators may also be limited by a disparity between the development of advanced physical cognition and the social tolerance of potential demonstrators. Social tolerance can play an important role in the spread of new behaviours (Matsuzawa, 1999; van Schaik et al., 1999). Adults are highly tolerant of infants, allowing young chimpanzees to observe their mother and other adults in close proximity (Hirata & Celli, 2003; Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2006).

Free-ranging chimpanzees typically become proficient at extractive tool use between the ages of four and seven years (Biro et al., 2003; Hirata & Celli, 2003; Lonsdorf, 2006; McGrew, 1977), and there is evidence for a critical age in the development of more advanced tool use, such as nutcracking, between the ages of three and five (Matsuzawa et al., 2001). Individuals who do not learn during these years do not become proficient later. The few instances of metatool use (e.g. an anvil prop used to level a surface on which to pound nuts) have been observed solely in individuals over the age of 6.5 years (Matsuzawa, 2001a). Such tasks involve not only manual dexterity and motor control, but also demand sophisticated physical cognition. It is possible that when chimpanzees reach an age at which they are physically and cognitively capable of performing these higher level techniques, they may be too old to have access to sufficiently tolerant demonstrators.

The video demonstrations used in the current study allowed adult chimpanzees to observe a skilled conspecific perform a task without fear of repercussion. They witnessed repetitions and precise details of the actions involved. Those chimpanzees in the Combine-and-Retrieve condition who spent more time watching the video prior to attempting the task themselves scored higher on the Combine Scale. In the Retrieve-Only condition, when subjects were able to see the final result of the combination process, but not the process itself, the level of combining was roughly midway between the Combine-and-Retrieve and Control conditions. This might be more akin to the amount of information they would be able to see as adults in the wild, given the presence of skilled users. Without access to precise details, observers may gain a global idea of the task, but may experiment with their own methods to solve it. As a consequence, it might be difficult for new technological additions to spread through the group due to an information “slippage effect” (Boesch & Tomasello, 1998). If these innovated additions are particularly subtle or complex, they might not spread at all.

## 2.5. Experiment 2: Video versus live demonstrations in chimpanzees

In order to examine the efficacy of the video demonstrations directly, live conspecific models were trained to demonstrate the Combine-and-Retrieve method to an additional group of chimpanzees.

### 2.5.1. Subjects

Four socially tolerant high-ranking individuals (based on husbandry staff and experimenter observations) were selected from amongst those who solved the task in Experiment 1 to act as demonstrators (2 from the Combine-and-Retrieve condition; 1 from the Retrieve-Only condition; 1 from the Control condition). Ten additional chimpanzees acted as subjects (mean age = 27.30, SD = 12.88, range = 12-45; see Appendix F. for demographic and grouping information).

### 2.5.2. Method

Individuals were isolated from their social groups in demonstrator/observer dyads. Demonstrators were trained so that they predictably combined the two tools, retrieved a grape, and returned the tools to the experimenter 16 times in 10 minutes. Observers were allowed access to the demonstrations in the same compartment after which the demonstrator was removed and the observer provided with a tool set. As before, subjects were given up to three 20-minute sessions to retrieve a reward from the platform (see Figure 2.10 for the demonstration set-up).

**Figure 2.10. Live demonstration set-up**



A still showing a demonstrator (right) combining the two tool components prior to retrieving a grape from the platform. The observer (on the left) is touching the tools while the demonstrator combines.

### 2.5.3. Results

Of the 10 chimpanzees tested, only three combined the tool components and successfully retrieved a reward. An additional two individuals successfully combined the tool components together, but were not able to retrieve a reward (one attempted with the combined tool; one un-combined the tools and then attempted to retrieve with the unmodified tool components). As before, all chimpanzees were assigned a score on the Combine Index. There was no significant difference between the levels of combining in the Live Demonstration condition (Median = 11) and the Combine-and-Retrieve video demonstration condition (Median = 13.5, Mann Whitney  $U = 35$ ,  $p = 0.28$ ), or between the Live Demonstration condition and the Control condition (Median = 6, from Experiment 1), although this was approaching significance (Mann Whitney  $U = 25$ ,  $p = .06$ ).

As before, further analyses were conducted to test the relationship between the time spent watching demonstrations and the achieved score on the Combine Index. “Watching” was defined as the amount of time spent in proximity (1 m) to the demonstrator with the head visually oriented toward the demonstration. There was no significant correlation between the time spent watching the live demonstration and the score on the Combine Index ( $r_s = -0.218$ ,  $N = 10$ ,  $p = 0.27$ , one-tailed).

### 2.5.4. Discussion

Those chimpanzees presented with familiar group-mates as demonstrators fared no better than those presented with video footage of an unfamiliar male. In fact, those who watched live demonstrators did not perform significantly better than those with no demonstration at all (in the Control condition of Experiment 1). This suggests that the video methodology is not only adequate for social learning, but that there might also be a slight benefit. One explanation is that observers in the Live Demonstrator condition might have been distracted by attempts to scrounge or beg for food from the demonstrator, and thus were not attending as carefully to the technique. Alternatively, subjects in the video conditions might have benefited from simultaneous access to demonstrations while exploring with their own set of tools. In the Live Demonstrator condition it was necessary to choose sufficiently dominant demonstrators who could monopolize the tools and platform. This subsequently necessitated the removal of the

demonstrator from the compartment during test sessions (to give the observer a chance) and thus did not allow for simultaneous access to demonstrations. However, in a few instances the model was sufficiently tolerant to remain in the enclosure and continue demonstrating while the observer had access to her own set of tools (in an additional fourth session). Even in this instance observers were still unsuccessful ( $N = 2$ ).

Social dynamics between the demonstrator and observer might constrain possibilities for social learning (Coussi-Korbel & Fragaszy, 1995), and free-ranging animals are known to attend more to specific types of demonstrators, namely older or skilled individuals (Biro et al., 2003; Lonsdorf, 2006; Ottoni, de Resende, & Izar, 2005). This undoubtedly plays a role in captive experiments, yet social dynamics between observers and demonstrator are typically mixed across conditions. Video demonstrations afford the opportunity to control for or directly test the effect of demonstrator type (varying the rank, age, sex, familiarity, or even species of the model). In Experiment 1, the model was unfamiliar to all observers, thus controlling for relatedness and social dynamics, at least in part (although it is difficult to determine specifically how much information about the demonstrator chimpanzees were able to obtain from the video footage). The unfamiliarity of the male and the novelty of the stimulus could have also helped draw the observers' attention, and most subjects in Experiment 1 were quite keen to watch the video footage, many of them reacting as they might to another chimpanzee (i.e. using similar vocalisations and displays).

Regardless, the fact that subjects socially learned from an unfamiliar male at least as well as they did from familiar group-mates is suggestive. It lends support to the idea that social tolerance is a key limiting factor of social learning, with access to demonstrations restricting opportunities. If provided with the opportunity to observe, adult chimpanzees might learn complex new skills from a range of individuals.

## 2.6. Conclusion

Chimpanzees are the most proficient non-human tool users in the wild, and use an array of tools for diverse purposes. Yet, there is still little evidence that tool technology builds much over time, with new additions leading to greater technology, as happens in humans. These experiments show that captive chimpanzees are cognitively capable of

socially learning a technological addition to an existing tool behaviour. Those who saw the complete process, rather than just the end result or products of the process, performed the best. Further, chimpanzees who socially learned the task continued to use the new method faithfully, even when unnecessary. However, social learning in chimpanzees was restricted to one particular method, and when exposed to a more subtle method of tool manufacture, chimpanzees were not able to socially learn. In order to test for social learning differences directly, I applied a similar methodology with human children, as detailed in the following section.

**CHAPTER 3. SOCIAL LEARNING OF TOOL  
MODIFICATION IN CHILDREN**

### 3.1. Introduction

Human tool use is universal and may hold a special place in human cognition. For example, there is evidence that brain damage can selectively impair understanding of tools, leaving other faculties unharmed (Hillis & Caramazza, 1991; Johnson-Frey, 2004), and that children categorise tools differently than they do other objects (Brown, 1990; Keil, Smith, Simons, & Levin, 1998). Tool use develops at an early age and by the second year children routinely use some tools (e.g. spoons or chopsticks) prevalent in their culture (Lockman, 2000). Although it is largely agreed upon that human tool use is supported by social learning, until recently the specific learning processes underlying its acquisition were not dissected experimentally (Want & Harris, 2001). Developmental studies specific to tool use tended to focus on sensorimotor skills (for example: grip precision, Connolly & Dagleish, 1989) or physical cognition, seeking to pinpoint the earliest age at which children could solve basic causal problems (Bates, Carlson-Lunden, & Bretherton, 1980; Piaget, 1954; Richardson, 1932).

The majority of developmental social learning studies, perhaps as a result of restrictions imposed by motor development (Barr, 2002), test simple actions on objects or body movements, rather than more complex sequences or tool use. In addition, until recently, learning processes in the developmental literature were often lumped together as “imitative”. This broad label can cloud important developmental changes in the way children learn (Nielsen, 2006). Recently, the more stringent criteria typically used to assess social learning in nonhuman animals have been applied in developmental studies (Jones, 2009; Want & Harris, 2002). As detailed in Chapter 1, such work has unveiled potential developmental shifts in the reliance on social learning versus individually acquired information in children.

While the desire to differentiate learning processes has led to more complex tests of social learning in children, the complexity typically derives not from the specific actions themselves, but from sequences of actions. Most studies either do not involve tools (for example: removing a series of “artificial fruit” defenses - Whiten, 1996; Whiten et al., 1996, or selecting a series of pictures on a touch screen - Subiaul, Lurie et al., 2007; Subiaul, Romansky, Cantlon, Klein, & Terrace, 2007), or they involve simple tools and actions (for example using a stick or rake to poke or shift other objects Flynn &

Whiten, 2008; Horner & Whiten, 2005; McGuigan & Whiten, 2009; Nielsen, 2006; Whiten et al., 2006). As with tests on nonhuman tool use, the complexity of the tool is rarely manipulated. In particular, social learning of tool construction or modification is largely overlooked in the developmental literature. Given that human social learning abilities are thought to fuel the cumulatively complex technologies prevalent in human societies, it seems important to test how children socially learn about the fundamental elements of tool modification and construction.

As a companion to the preceding experiments, the following study uses a similar methodology to investigate social learning on a tool modification task in children. The purpose of the study is twofold. First, from a developmental perspective, it seeks to decipher the nature of the learning mechanisms underlying the acquisition of a technological modification in children. Second, from a comparative perspective, it aims to test how such processes might differ from chimpanzees.

Previous research suggests that by 18 months children have the motor skills and cognitive capacity to use simple tools as agents on other objects (Meltzoff, 1995). Given the complexity of the task, children aged 2.5 to 4.5 years were chosen (Want & Harris, 2002). If there is a cognitive shift favouring increased copying within this age range, a positive correlation between copying fidelity scores and age should be present. If, as discussed in previous chapters, there are fundamental differences in the type of information children glean from a demonstration in comparison with chimpanzees, it is anticipated that children will be able to socially learn both the combine and alternative method techniques. Furthermore, if children learn more from the actions (imitation) than the results of actions (emulation), they should perform better in the Combine-and-Retrieve condition.

Video footage of a conspecific model was chosen in lieu of live demonstrators, as before. In addition to the methodological benefits of video demonstrations detailed in previous sections, video playback has the extra advantage of controlling for social interactions with the demonstrator, so it is better at isolating salient features in the demonstration itself, rather than the effects of social engagement (Nielsen et al., 2008). Video footage has been used to explore a range of abilities in children (for example: problem-solving - Deocampo & Hudson, 2005; Schmitt & Anderson, 2002; language

acquisition - Kcmar, Grela, & Lin, 2007; and self-recognition - Povinelli, Landau, & Perilloux, 1996; Suddendorf, Simcock, & Nielsen, 2007). Children have been found to learn from video demonstrations on social learning tasks in previous studies (Huang & Charman, 2005), albeit to a slightly lesser degree than live models in some cases (see Flynn & Whiten, 2008, for an example).

### 3.2. Participants

A total of 44 2.5- to 4.5-year-old children (mean age = 40.32 months, SD = 8.14, range = 29-54 months, 22 male, 22 female) were recruited from nursery schools in Fife, Scotland, UK for the main study (see Appendix G). Head teachers were contacted first and then met in person to discuss the planned tests (See Appendix H for sample parental consent forms and letters). All testing was completed by E. Price, for whom a cleared Scottish Police background check had been obtained. E. Price first met with the children in their classrooms until they were comfortable accompanying her to the testing room. If at any time participants expressed discomfort or a desire to return to their classrooms, the session ended.

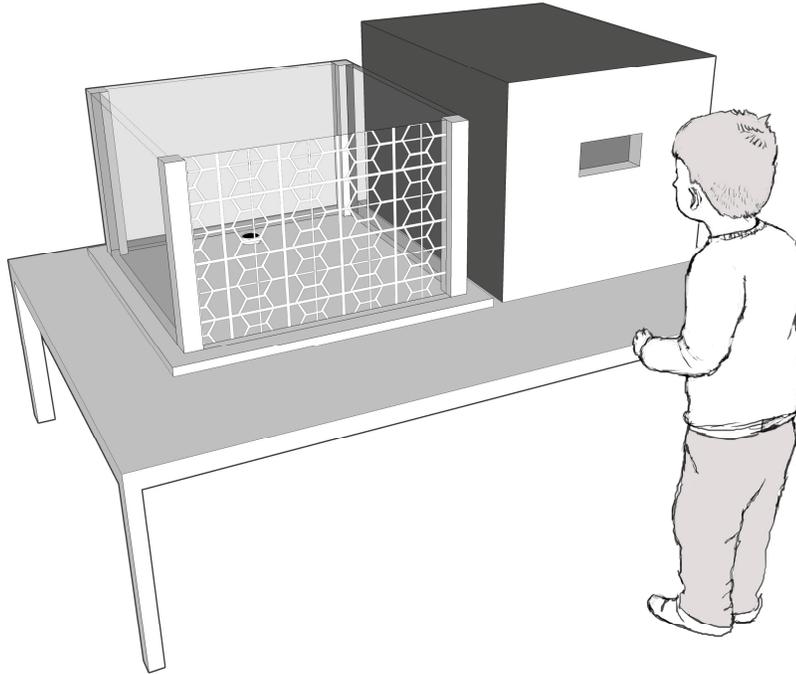
### 3.3. Method

#### 3.3.1. Apparatus

The same tool set as described in the preceding chapter was used. The raking platform was enclosed by hard clear plastic on all three sides and the top (50 x 50 x 36 cm – see Figure 3.1). A reward could be retrieved by inserting the tools into the front of the box which consisted of 4 cm square metal mesh, covered by flexible plastic 2.5 cm mesh. The back of the raking box could be slid upwards, allowing the researcher to replace the rewards once they were retrieved (in the post-sessions only). As before, all video footage was played on an external LCD monitor attached to a laptop so the experimenter had simultaneous access to the demonstrations. The video monitor and laptop were enclosed in a hard, opaque plastic shell measuring 48 cm wide by 45 cm high and 67 cm long so that the screen was placed 23 cm back from the edge and visible through a viewing window measuring 13 cm by 7.6 cm. During all sessions the raking platform was placed atop a table so that it was roughly .5 metres off the ground. The

viewing box was placed 3-5 cm beside the platform so that the viewing window was approximately 1 metre high (see Figure 3.1 for a diagram of the experimental set-up).

**Figure 3.1. Experimental set-up**



As with chimpanzees, the raking platform was placed next to the viewing box, so that children had simultaneous access to video demonstrations. All video footage was played on an external monitor attached to a laptop, and could be viewed by the experimenter.

### 3.4. Procedure

#### 3.4.1. Pilot data

Five children aged 2.5 to 3.5 years were given the opportunity to interact with the tool components and raking box in order to test the experimental set-up. The original 4 cm square holes proved too large, allowing children to fit their entire hand into the box and reach the reward without combining the tool in some cases and resulting in the alterations described above (placement of mesh over the holes). None of the five children modified the tools using either method during their 20-minute sessions, and became disinterested early on, typically after five minutes. For this reason, 10-minute testing sessions were chosen.

#### 3.4.2. Baseline

In order to familiarize participants with the experimental set-up and ascertain individual raking abilities, all participants were given baseline sessions. During these sessions, only the raking box was present, with a reward placed 30 cm from the opening at the front. The reward consisted of a sticker placed atop a plastic bottle cap, so that it slid easily along the surface of the platform. Children were escorted to the testing chamber from their classroom and asked “Can you see the sticker? Would you like to see if you can get it?” and handed a 50 cm long black tool. Once the sticker had been retrieved, a new sticker/bottle cap was placed on the platform. Once children had successfully retrieved two stickers, the session ended.

#### 3.4.3. Video demonstrations

Video footage was taken of an unfamiliar adult modifying the tools and retrieving a reward. As before footage was captured on a Sony Handicam (DCR 35E) and then digitised and edited using Adobe Premier Pro 2.0. Demonstration clips consisted of close-up and far-away shots of the procedure. All clips lasted approximately 25 seconds and were played on a continuous loop with a one second pause between close and far away shots.

#### 3.4.4. Experimental sessions

The 44 participants were each assigned to one of four video demonstration conditions: Combine-and-Retrieve, Retrieve-Only, Alternative Method, and Control (omitting only the Video Control condition used in the chimpanzee study). As before, the

Combine-and-Retrieve condition showed the model sitting in front of the platform, picking up the two tools, slotting them together and then retrieving a reward. The Retrieve-Only condition showed the model picking up the two tools and combining them off screen (so that this process was not visible to the observer) and then retrieving a reward with a completed tool. The Alternative Method condition showed the model twisting and extending an internal rod and then retrieving a reward. No prior video was played to those assigned to the Control condition.

Children were visited in their classroom and asked if they'd like to come and play a game with the experimenter. They were then taken into a testing room where the video and raking boxes were placed on a table as described. The sticker was already in place inside the raking box, and no tools were present at the start of the trial. After 10 demonstrations had played for approximately 6 minutes (as compared to 16 demonstrations seen by chimpanzees), children were asked if they'd like to see if they could get the sticker and were presented with the tool set. They were then given up to 10 minutes to retrieve the sticker from the raking box. If participants asked for assistance they were told "See if you can get the sticker, you can do whatever you want". Once the session was over, participants were returned to their classrooms.

#### 3.4.5. Post-sessions

Those children who successfully modified the tool components (using either method) and retrieved a sticker were tested again two weeks later. This time only the raking box was present in the testing room. Stickers were placed at one of two locations five times for a total of ten reward presentations. "Close" stickers were placed 13 cm from the edge of the platform, and "far" stickers, 49 cm. After the reward was put in place, the tool set was handed to the participant and they were given up to two minutes to attempt to retrieve it. Once participants successfully retrieved a reward, another sticker was placed on the platform by the experimenter. If no attempt was made during the two minutes, the reward was removed and placed again. If an attempt was made, children were given an additional two minutes to successfully retrieve the reward. During all testing sessions, the experimenter stood behind the raking box.

### 3.5. Coding and reliability

All sessions were videotaped using an unobtrusively placed Sony Handicam and were later coded by E. Price. As before, participants were assigned a score on a scale of interaction for both Combining and using the Alternative Method (see Table 1, Chapter 2). To assess inter-rater reliability, ten randomly selected trials were coded by an independent observer, yielding 0.99 for the combine index and 0.89 for the alternative method index (Spearman's rank order coefficient,  $N = 10$ ,  $p > 0.001$  and  $p > 0.0001$  respectively, two-tailed).

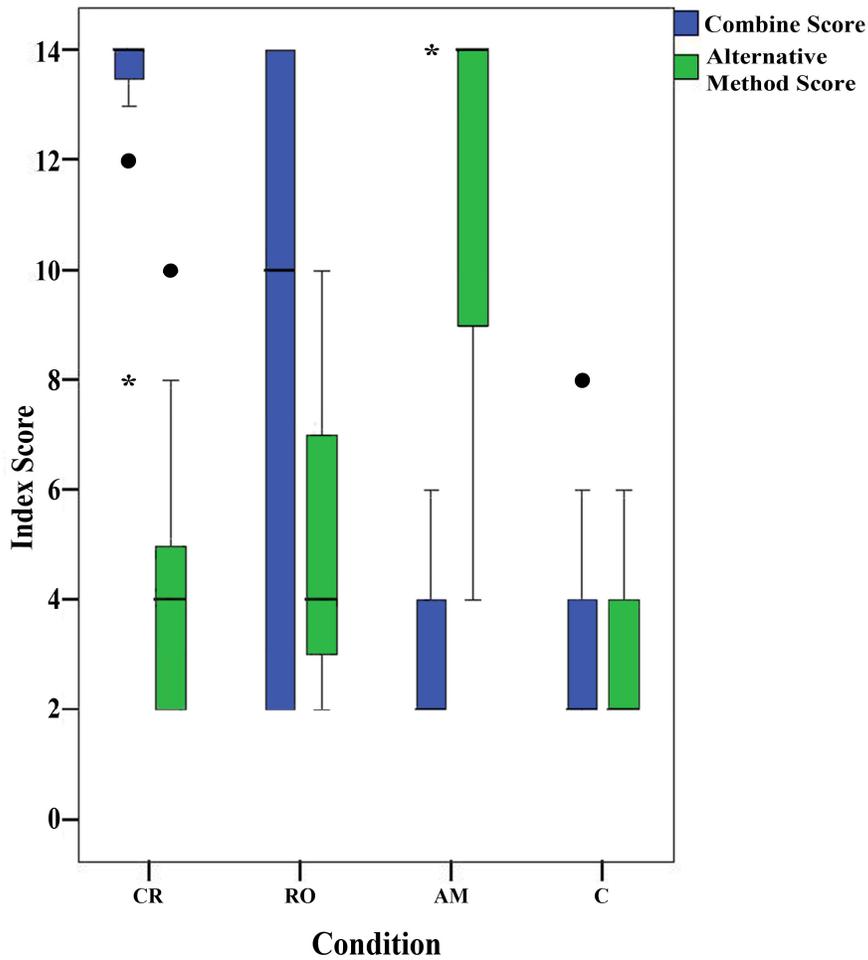
### 3.6. Results

#### 3.6.1. Experimental sessions

As with chimpanzees, the Combine and Alternative Method scores were analysed separately. Overall there were significant differences in the level of combining across groups (Kruskal-Wallis test,  $\chi^2(3) = 22.85$ ,  $p = 0.0001$ ). Participants who saw the Combine-and-Retrieve demonstration scored significantly higher on the combine scale (Median = 14) than those in the Alternative Method (Median = 2; following Siegel & Castellan, 1988), critical value = 14.45; significant at  $p = .05$ ) and Control conditions (Median = 2,  $p = .05$ ) – see Appendix I for a description and alternative analyses). Combine Index scores of those in the Retrieve-Only condition did not differ significantly from those in any other condition (Median = 10,  $p > .05$ ). In the Combine-and Retrieve condition, nine out of the eleven participants successfully combined the two tools, although one of these children was unsuccessful at retrieving the reward. An additional individual attempted to combine the two tools together but was unsuccessful. In the Retrieve-Only condition, five out of the eleven participants successfully combined and retrieved a reward. An additional individual combined, then separated the components and tried to retrieve the reward with the unmodified tool components. One participant combined in the Alternative Method Condition, and none combined in the Control condition. Two children (one from the Combine-and-Retrieve Condition and one from the Retrieve-Only Condition) attempted to retrieve the reward while holding the two tools together (rather than inserting one into the other).

An overall significant difference was also found for the level of using the Alternative method (Kruskal-Wallis test,  $\chi^2(3) = 21.071$ ,  $p = 0.0001$ ). Those in the Alternative Method condition scored higher on the Alternative Method index (Median = 14) than those in the Combine-and Retrieve (Median = 4), Retrieve-Only (Median = 4), and Control conditions (Median = 2; critical value 14.45,  $p < 0.5$ , see Figure 3.2.). Six subjects in the Alternative Method Condition successfully reshaped the tool and retrieved a reward, whereas no participants in any other condition managed to do so. Two participants attempted to modify the tool by twisting and pulling, but were unsuccessful. One additional participant in the Alternative Method condition solved the task using the Combine Method (a female aged 42 months - see Appendix G for participant scores on both indexes).

**Figure 3.2. Scores on the Combine and Alternative Method indexes**



The median scores (represented by black bars) and interquartile ranges (represented by boxes) on the Combine Index (Blue) and the Alternative Method Index (Green) for the Combine-and-Retrieve (CR), Retrieve-Only (RO), Alternative Method (AM), and Control (C) Conditions ( $n = 11$  in each group). Whiskers represent the maximum and minimum values which are not outliers (values between 1.5 and 3 times the interquartile range, marked by circles) or extreme cases (values over 3 times the interquartile range, marked by asterisks).

The overall time spent watching the video demonstrations prior to access to the tool set was only significantly correlated to the Combine Index scores for those in the Retrieve-Only condition ( $r_s = .724$ ,  $n = 11$ ,  $p = 0.006$ , one-tailed). Combine Index scores

for those in the Combine-and-Retrieve condition, and Alternative Method Scores for those in the Alternative Method condition were not significantly correlated with prior time spent watching ( $r_s = .339$ ,  $n = 1$ ,  $p = 0.154$ , one-tailed;  $r_s = 0.096$ ,  $n = 11$ ,  $p = 0.390$ , one-tailed, respectively).

Further analyses were run to determine if there was a relationship between the age of the participants and their scores on the Combine and Alternative Method Indices for those in the Combine-and-Retrieve, Alternative Method, and Retrieve-Only conditions ( $N = 33$ ). Overall, composite scores (the highest achieved score on either Index) were positively correlated with age in months ( $r_s = 0.346$ ,  $n = 44$ ,  $p = 0.011$ , one-tailed). When indexes were analysed individually, only scores on the Alternative Method Index for those in the Alternative Method Condition ( $r_s = 0.549$ ,  $n = 11$ ,  $p = 0.040$ , one-tailed) and scores on the Combine Index for the Retrieve-Only condition ( $r_s = 0.641$ ,  $n = 11$ ,  $p = 0.017$ , one-tailed) were significantly correlated with age. Combine Index Scores and age were not significantly correlated for those in the Combine-and-Retrieve Condition ( $r_s = 0.328$ ,  $n = 11$ ,  $p = 0.162$ , one-tailed).

### 3.6.2. Post-sessions

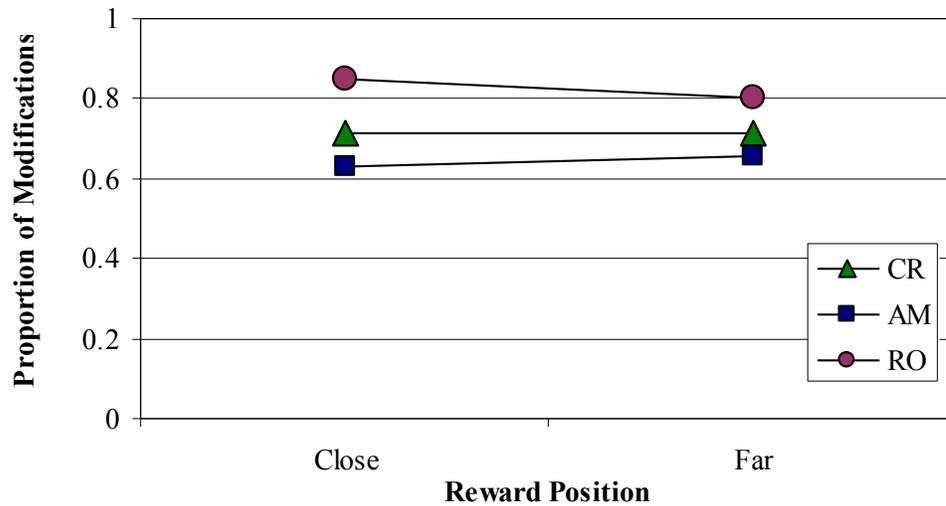
In order to check functional understanding of the tool modification, as well as reliance on social learning versus individual understanding of the problem, those children who successfully solved the task were presented with a post-session two weeks after their initial trial. Unfortunately one participant from the Combine-and-Retrieve condition, and one participant from the Retrieve-Only condition were unavailable for testing, resulting in the following group sizes: Combine-and-Retrieve Condition,  $N = 7$ , Retrieve-Only condition,  $N = 4$ , Alternative Method condition,  $N = 7$  (including the one participant who solved the task using the combine method). None of the children in the Control condition were successful, so did not participate in the post-session.

Participants did not switch between modifying the tools and using the unmodified tool components depending on the placement of the reward in any of the conditions: Combine-and-Retrieve (Close versus Far positions, Wilcoxon test,  $z = 0$ ,  $p = 1.00$ , two-tailed), Alternative Method ( $z = -1.00$ ,  $p = 0.32$ , two-tailed), or Retrieve-Only ( $z = -1.00$ ,  $p = 0.32$ , two-tailed). Rather, participants tended to stick to the method they had used in the initial test, regardless of the reward placement or the amount of information they had

seen in the video (see Figure 3.3.). In all instances, except one, the modification technique used was the demonstrated technique (or in the case of the Retrieve-Only condition, the combine method). The one participant in the Alternative Method condition who used the combine technique, continued to combine in every trial, for both close and far positions (see Table 3.1.)

As with chimpanzees, the copying fidelity of those who saw different amounts of information about the Combine method was compared directly, although the groups were small and the sample sizes unequal (Combine-and-Retrieve:  $N = 7$ , Retrieve-Only:  $N = 4$ ). Unlike chimpanzees, the proportion of children combining in the close position (when the reward could be retrieved without modifying) was not significantly different for those who had seen the full demonstration (Combine-and-Retrieve, proportion median = 1) than those who had only seen the end result of the process (Retrieve-Only, median = 0.9; Mann Whitney  $U = 13$ ,  $p = 0.927$ ).

**Figure 3.3. Proportion of post-session responses**



The proportion of modification responses (rather than using the unmodified tool components) for both Close (N = 5) and Far (N = 5) reward positions. Participants tended to use the demonstrated modification technique (Combine method for Combine-and-Retrieve and Retrieve-Only Conditions, and Alternative Method for Alternative Method Condition participants) regardless of the reward position. CR = Combine-and-Retrieve condition (N = 7), AM = Alternative Method Condition (N=7), RO = Retrieve-Only condition (N = 4).

Table 3.1. Proportion matching in the post-sessions for successful retrievals and first attempts

Condition	Child	Age	Success		1st Attempt	
			Close	Far	Close	Far
CR	1	34	100%	100%	100%	100%
	2	37	0%	0%	0%	0%
	3	38	100%	100%	100%	100%
	4	52	100%	100%	100%	100%
	5	52	100%	100%	100%	100%
	6	45	0%	0%	0%	0%
	7	44	100%	100%	100%	100%
AM	8	41	20%	40%	60%	40%
	9	43	100%	100%	100%	100%
	10	53	100%	100%	100%	100%
	11	49	100%	100%	100%	100%
	*12	*42	*0%	*0%	*0%	*0%
	13	39	20%	20%	0%	0%
	14	41	100%	100%	100%	100%
RO	15	54	100%	100%	100%	100%
	16	47	80%	80%	60%	60%
	17	53	100%	100%	100%	100%
	18	39	60%	40%	60%	40%

Matching is defined as using the Combine modification technique for the CR (Combine-and-Retrieve) and RO (Retrieve-Only) groups, and the Alternative Method modification technique for the AM (Alternative Method) group. First attempts were recorded as the very first instance a tool was put into the raking box in an attempt to reach the reward. Each subject had the opportunity to retrieve 10 times, 5 in the close position, and 5 in the far position. Participant 12 solved the technique using the Combine method. Her percentage using that method was 100% for both Successful and 1<sup>st</sup> attempts in both close and far positions.

### 3.7. Discussion

Children were shown to learn by observation how to obtain a reward either by building a new tool from two separate components, or by reshaping an existing tool, according to the method they had witnessed. This contrasts strikingly with the fact that no

children in the control condition solved the task through individual trial-and-error learning (although one did manage to solve the task using the combine method after seeing the Alternative Method demonstration). Participants typically required complete information in order to learn the tool modification technique; those individuals exposed to information about the end results of the process only (Retrieve-Only condition) did not score significantly differently from those in the Control or Combine-and-Retrieve conditions. There was also a significant correlation between the time spent watching the video demonstrations (prior to access with the tool set) and the scores on the Combine Index only for the Retrieve-Only condition, suggesting it might have required increased evaluation of the material in the video in order to solve the task on the basis of this information. The information thus gained was enough for some to apply a successful technique (45%), but not the majority. This supports previous findings that children have difficulty reproducing the results of actions if they do not see the actions themselves (Bellagamba & Tomasello, 1999; Call et al., 2005; Huang, Heyes, & Charman, 2002).

Although children in the Alternative Method condition were able to socially learn the technique, there is evidence to suggest that this approach was more challenging, as age in months was positively correlated with higher Alternative Method Index scores for those in the Alternative Method condition, which was not the case for Combine Index scores for those in the Combine-and-Retrieve condition. Also, given that one individual solved using the combine method, even after watching video footage of the alternative method, the affordances of the combining process might have been more readily understandable. Children's understanding of the function of combining was not clear, however. Two children tried to hold the tools together in their hands (with the tools overlapping, rather than slotted together) and then retrieve a reward. This reflects that they might have gathered a global, or 'perceptual' idea of the task, although their understanding of the necessary physical relationships between the two tools was inadequate.

As discussed in previous chapters, there is some disagreement in the literature regarding reliance on individual understanding of a problem versus social learning in children. If children are relying heavily on their own individual understanding of the task, then the participants in the control condition should have performed equivalently to those

in the social learning conditions. If the task is too difficult for individual learning abilities (as evidenced from the inability of those in the control condition to discover either method), then none of the children in the experimental conditions should have solved the task. Alternatively, if children are relying completely on the specific actions performed by the model, they should have learned equally well in the two social learning conditions, and no children should have solved the task in the Retrieve-Only condition. The results of the current study, therefore, suggest that children are relying on a combination of, and interaction between, both socially acquired information and individual understanding of a problem.

In the post-sessions, children continued to use the method they had first adopted in their initial session, regardless of the reward position. The majority of children matched very consistently (i.e. used the modification method on 100% of trials) with few individuals switching strategically between modifying and using the unmodified tool components. This was not specific to those who had seen the demonstrator perform the actions involved. Those in the Retrieve-Only condition, who had worked out the actual process of combining for themselves, also persisted in using the combining method, as did the individual who learned the combine method through her individual explorations (from the Alternative Method condition). This suggests that seeing end results only, or learning by emulation, might be sufficient to maintain a particular method in children. Some individuals did not modify the tools at all, despite being sufficiently motivated to retrieve the reward, and having originally solved the task. Although this might be because the social learning effect was not sufficient to sustain their knowledge of the solution after two weeks, it is likely that other cognitive processes, such as memory deficits or motor incompetence, also impeded their performance (Barr, 2002). This might be further confounded by the presentation of the information via video, as there is some evidence to suggest that children have difficulty relating what is perceived in a video as a presentation of something real (Troseth & DeLoache, 1998). Retaining and translating this information two weeks later might have further exacerbated this effect.

### 3.8. Comparison to chimpanzees

As discussed in Chapter 1, reliance on social information over individually acquired information is thought to be a key distinction between humans and chimpanzees, with a propensity to imitate driving human technological success (Call & Carpenter, 2002). The current research supports this claim to some extent. Unlike chimpanzees, children were able to socially learn the Alternative Method of tool modification. This is despite the fact that no children were able to modify the tool in this manner through their own individual explorations, whereas three chimpanzees were able to do so. In order to create the tool using this technique, the internal rod must first be twisted in a specific direction and then extended. This not only involves more precise steps than the combining process, but the mechanism is not as readily observable. This supports existing evidence that a propensity to copy precise actions allows children to learn the often subtle and causally opaque features common to human technologies (Gergely & Csibra, 2005).

This does not necessarily implicate a greater reliance on social information in children, however, for a number of reasons. For one, these studies also found evidence contrary to the common conclusion that children rely more heavily on the details and actions of the task and chimpanzees on the end results. Prior research suggests that chimpanzees outperform children when confronted with end results only (Call et al., 2005; Nagell et al., 1993). For example, Call, Carpenter and Tomasello (2005) presented children and chimpanzees with a novel task which involved breaking a tube open to obtain a reward. They found that chimpanzees performed equally well when presented with end results or specific actions, whereas children performed better after seeing the full demonstration. The authors thus concluded that chimpanzees were emulators and children imitators. Nagell et al. (1993) came to a similar conclusion when chimpanzees, but not children, flipped over a rake to a more effective position, even when they had not seen a prior demonstration.

In the current study, both children and chimpanzees performed best when provided with a full demonstration of the actions involved. In both species, some individuals (3 out of 10 chimpanzees and 5 out of 11 children) were able to solve the task and retrieve a reward with end results only (one additional chimpanzee and child learned

to combine but did not retrieve a reward), but overall participants in these groups did not score significantly higher than those in control conditions. Furthermore, chimpanzees, like children, persisted in using the socially learned method in the post-sessions, even when the reward was easily obtainable with either unmodified tool component. This discrepancy with previous research might be a product of the difficulty of the task. In the Call et al. (2005) study, chimpanzees might have found breaking a tube open simpler than the 2-year old subjects did, and indeed the majority of chimpanzees opened the tube successfully in the baseline condition (before receiving any information). Once they had learned themselves, they had little reason to adopt a new technique to solve the task. The tool construction task used in the current study is more complicated, both in terms of manual coordination and causal understanding. Although two chimpanzees and one child were able to solve the task using the combine method without any prior information about combining, it remained a difficult task for the majority. Chimpanzees and children might therefore be relying on social information because the causal features of the task were not readily obvious, as has been found in previous studies (Horner & Whiten, 2005).

Secondly, although both children and chimpanzees required information about the precise process involved to score significantly higher than the control conditions, it is less clear if either were imitating the actions of the demonstrator. Seeing the precise details involved might have facilitated subjects to interact with certain parts of the devices, and as a result they were more likely to come to the solution with their subsequent manipulations. Alternatively, in the case of chimpanzees, the process of combining might have existed in their repertoire and thus been more readily primed by seeing the demonstration (Byrne & Russon, 1998). If no such innate propensity exists for twisting and extending objects, this would explain why they were unable to learn in the Alternative Method condition.

If subjects were emulating, it is also difficult to pinpoint what form this took. As previously discussed, the term emulation is used to describe a range of learning processes (Byrne, 2002b) and can imply learning about the affordances of object movements only (Tomasello, 1990, 1996, 1998), to understanding and replicating perceived goals (Whiten & Cusance, 1996). Cusance et al. (1999) break emulation down into four processes:

affordance learning (learning about the consequences of the movement involved), object movement re-enactment (replicating the movement of the perceived objects, not the action of the demonstrator), end state emulation (attempting to replicate the result of the action), and goal emulation (attributing and replicating a perceived goal). It is unlikely that children or chimpanzees were learning by end state emulation, since information about the end state only was not sufficient to score significantly higher than those in the control conditions. However, by seeing the full details, chimpanzees and children could still have been replicating the movement of the objects, or learning about the affordances involved in combining. This might explain the difference between children and chimpanzees in the Alternative Method condition. The movements involved in the combining method are more obvious than those involved in the alternative method. For example, it might be more difficult to perceive the essential twisting movement required to unlock the mechanism if you are attending to the movement of the device rather than the action of the person twisting it. If children are attending to the actions of the demonstrator, this might explain their advantage. In order to test for this possibility directly, it would be necessary to include a video ghost control condition, where the objects move in the absence of an active model. If chimpanzees are attending to object movements more, they would be expected to perform equally well in both conditions, unlike children.

Lastly, there is some evidence of emulation in children not present in chimpanzees. If imitation is necessary to support conformity to a particular technique, and imitation is defined as learning by copying specific actions, then only those in the Combine-and-Retrieve method should continue to perform the behaviour when it is no longer necessary (i.e. the reward is within reach). Chimpanzees followed this trend, with those who had learned individually or via emulation (end-results only) only combining when required, unlike those who had seen full social information. Children did not differ in their approach during the post-sessions, continuing to modify the tools regardless of how much information they had seen in the demonstration. Thus end results only were sufficient to sustain the behaviour even when unnecessary in children, but not in chimpanzees. One potential explanation of this difference is that children in the Retrieve-Only condition, despite not seeing the actual details, might nonetheless have perceived

the goal as combining the tools together. In this sense, the assumed actions of the model might be encoded in a similar fashion to actually perceived actions – resulting in the same conformity to a specific method.

It must also be acknowledged that children might have had an advantage by being more accustomed to video technology than chimpanzees. Although chimpanzees performed equivalently, perhaps slightly better, from video demonstrations, than live models, subtle precise actions might have been more difficult for them to decipher from this medium, than the broad actions involved in combining. Children might have also been more motivated to reach a solution, which would be advantageous in the more difficult alternative method. The potential confound of social engagement is discussed more thoroughly in Chapter 5.

### 3.9. Conclusion

In the preceding studies, I have highlighted important differences and similarities in the learning processes underlying the acquisition of tool modification in chimpanzees and children. To a degree, the research supports prior claims, with enhanced social learning abilities in children under some conditions, which might drive the human ability to learn particularly complex technological additions. However, they have also revealed striking similarities which are contrary to certain prior expectations. First, chimpanzees and children were comparable in their reliance on the details involved in the solution over end results only. Second, both chimpanzees and children showed a marked tendency to use the socially learned combine method, even after a delay of two weeks, and at the cost of efficiency (hitherto thought to be a particularly human propensity). Finally, whether or not they perceived the goal of the demonstrator, or solved the task through their own explorations, emulation was sufficient to create a conformity effect in children (although seeing end results only was not sufficient for a majority to learn in the first place). This lends support to the possibility that imitation might not be the only learning process crucial to human cultural learning (Caldwell and Millen, 2008). Video demonstration technology can help to further isolate the learning mechanisms at work, as discussed in Chapter 5.

**CHAPTER 4. EXPLORING VIDEO  
DEMONSTRATIONS WITH RAVENS**

#### 4.1. Introduction

As previously discussed, primates are obvious subjects for tests of higher level cognitive processing, particularly when attempting to understand human cognition as the result of evolutionary processes. Many of the challenges thought to drive intelligence in primates are shared with other animals, however, and there is some evidence to suggest convergent evolution in relation to mental processes (Emery & Clayton, 2004b; Seed, Emery, & Clayton, 2009). Corvids, for example, inhabit diverse, often harsh terrain, frequently live in complex societies, forage opportunistically, and have long developmental periods (Emery & Clayton, 2004a; Emery & Clayton, 2004b). In addition, they have the largest brains of any avian species, the same in relative size as the chimpanzee (controlling for the effects of body weight - Emery, 2006; Jerison, 1973).

Despite having very different neurological structures, recent research has found that many of the cognitive capabilities previously thought restricted to apes, are exhibited by corvids (for a recent review see Seed et al., 2009). For example, one corvid species, the New Caledonian crow displays some of the most complex tool use seen in any species. New Caledonian crows use different tools selectively for different functions (Chappell & Kacelnik, 2002; Chappell & Kacelnik, 2004; Hunt, 1996; Hunt & Gray, 2004), modify tools to solve novel problems (Weir & Kacelnik, 2006; Weir, Chappell, & Kacelnik, 2002), use tools sequentially (Wimpenny et al., 2009), and there is evidence to suggest that their tool use is supported by social learning and possibly even cumulative culture (Hunt, 2000; Hunt & Gray, 2003; Kenward, Rutz, Weir, & Kacelnik, 2006; Weir et al., 2002). Many corvids who do not exhibit tool use in the wild demonstrate sophisticated cognitive abilities in both the social and physical domains (for example: insightful tool use and modification, *Corvus frugilegus*, Bird & Emery, 2009a; Bird & Emery, 2009b; social learning of novel foraging techniques, *Aphelocoma coerulescens*, Midford, Hailman, & Woolfenden, 2000; deception during caching, *Corvus corax*, Bugnyar & Kotrschal, 2002; Bugnyar & Kotrschal, 2004; cooperative problem solving, *Corvus frugilegus*, Seed, Clayton, & Emery, 2008; and episodic-like memory, *Aphelocoma coerulescens*, Clayton & Dickinson, 1998). Despite this, the interaction between social and individual learning strategies is rarely explored experimentally in corvid species.

Of the corvids, ravens make ideal candidates for such studies. Young birds join non-breeder groups at the end of their first summer and live in fission-fusion societies until pair formation, for a period of between three to 10 years (Heinrich, 1999). Recent analyses suggest they have similarly complex social relationships to chimpanzees (Fraser & Bugnyar, 2010b – replicating a principal components analysis completed with chimpanzees – see Fraser, Schino, & Aureli, 2008) and even exhibit possible post-conflict consolation with closely affiliated individuals (Fraser & Bugnyar, 2010a). Ravens also congregate in large numbers at feeding sites and individuals will actively recruit others to compete with mated pairs (Bugnyar, Kijne, & Kotrschal, 2001; Dall & Wright, 2009). In addition, as a food-caching species, they face the challenge of food pilfering and there is evidence that ravens have some knowledge about other individuals' mental states when protecting or pilfering cache sites (Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Heinrich & Pepper, 1998) and possibly even employ tactical deception during caching (Bugnyar & Kotrschal, 2004).

As such, there is environmental pressure for the development of both individual problem-solving abilities and social cognition, and captive studies have found evidence of both causal understanding and social learning in ravens. When presented with food dangling at the bottom of a string, ravens quickly learned the solution of pulling up bits of string at a time, stepping on the string to hold it in place before continuing to pull. When the string was first looped over a point above the perch, so that it went up and then hung down, they also learned a less intuitive solution of pulling down on the string to gain access to the meat. This suggests that they have some understanding of the physical relationships between the string, their foot, and the food (Heinrich, 1995; Heinrich & Bugnyar, 2005, although see Taylor, Medina, Holzhaider, et al. 2010 for the alternative explanation of operant conditioning in New Caledonian crows).

Ravens are a very neophobic species (Heinrich, 1988; Kijne & Kotrschal, 2002) and can be facilitated to interact with new objects by watching other ravens, particularly siblings (Schwab, Bugnyar, Schloegl, & Kotrschal, 2008; Stöwe et al., 2006). In addition, ravens exposed to a conspecific using a particular method to open a box, were more likely to approach the box, and also more likely to use the same opening method than those who had not previously seen the demonstration (Fritz & Kotrschal, 1999).

Social learning of more complex tasks has yet to be investigated in ravens. For example, it is unclear if ravens would imitate the actions of others, or if they would be more likely to learn by stimulus enhancement or emulation, relying more heavily on their own methods to solve a task. Further, it is uncertain if these processes might be affected by the amount of information available in a demonstration as seems to be the case in chimpanzees. Just as video footage playback has proved a useful tool to manipulate the amount of information in a demonstration with chimpanzees and children, so might it be with ravens. Videos have been used to successfully influence behaviour in birds before, and studies have shown that if the flicker-fusion rate is adjusted for by using Liquid Crystal Displays (LCD) (since birds have evolved the ability to process visual images faster than mammals - Hart, 2001; Lythgoe, 1979) birds respond similarly to video footage as they would to live conspecifics (see Cuthill et al., 2000; D'eath, 1998; and Fleishman et al., 1998 for reviews). The majority of these studies aim to gauge behavioural reactions to video stimuli. For example, both male and female pigeons (*Columba livia*) perform courtship behaviours to video footage of opposite sex conspecifics (Partan, Yelda, Price, & Shimizu, 2005; Shimizu, 1998). In addition, male Zebra (*Taeniopygia guttata*) and Bengalese finches (*Lonchura striata domestica*) and female budgerigars (*Melopsittacus undulatus*) respond with similar displays to video footage of opposite-sex conspecifics as they do to actual conspecifics (Ikebuchi & Okanoya, 1999; Moravec, Striedter, & Burley, 2010), and female Japanese quail (*Coturnix japonica*) affiliate with males more often after seeing video footage of them mating (Ophir & Galef, 2003).

This methodology has only been applied to corvids in one case, to the best of my knowledge. Rooks presented with visual access to a live conspecific, a stuffed conspecific, a still image, or a video of a conspecific, preferred all four stimuli over an empty compartment. Furthermore, rooks preferred looking at affiliates rather than nonaffiliate conspecifics in videos, but not in static images, suggesting that they were able to identify individuals from the video footage (Bird & Emery, 2008). The feasibility of using video playback for social learning studies has been addressed in the previous chapters, and has been successful with birds (Mottley & Heyes, 2003; Richards et al., 2009).

Behavioural reactions to video stimuli have yet to be tested in ravens. Scheid, Range and Bugnyar (2007) tested preferences for different types of live conspecifics by presenting ravens with two circular holes through which they could see either affiliates or non-affiliates engaging in foraging and object manipulation. By analysing the frequency and duration of looking times, they were able to ascertain that ravens preferred watching affiliates over non-affiliates. Viewing holes have been used to measure attention in other bird species, and are particularly useful given the wide visual field of birds (Dawkins, 2002). The present chapter describes a series of studies attempting to assess the use of video stimuli with ravens as a precursor to future tests investigating individual versus social learning strategies (as previously done with chimpanzees and children), using a similar “viewing hole” procedure. Ravens are highly neophobic, so first a brief pilot study was completed at the Edinburgh Zoo to assess the feasibility of the experimental protocol. Study 1 presents a more thorough examination of behavioural reactions to varying types of video footage with a larger sample of ravens. If ravens can successfully identify another raven in the video footage, subjects were expected to exhibit more social behaviours and vocalisations following clips of other ravens than of different species of birds. Finally, Study 2 investigates social learning from video demonstration on a two-step proto-tool-using task.

## 4.2. Pilot Study

### 4.2.1. Subjects

One male (age 5, captive born) and one female (estimated age 18, wild born) ravens acted as subjects. Subjects had been residing in Edinburgh Zoo as a mated pair for approximately one year at the time of testing. Ravens were housed in an aviary with 112 m<sup>2</sup> of ground space, and 5m vertical space, consisting of natural substrate, trees, perches and a small pond. Subjects were fed twice a day on a diet of meat, fruit, and vegetables. All tests were approved by the Royal Zoological Society of Scotland (RZSS).

### 4.2.2. Method

#### *a. Apparatus*

A 1m by 1m by .5m wooden cabinet was constructed outside the raven enclosure, placed flush with a clear window. An external 19” screen LCD monitor attached to a

laptop was placed inside the cabinet so that it was approximately 15 cm back from the glass. The monitor could be seen through a circular hole (13cm in diameter) which was covered by a wooden door when not in use. At the start of the trials, the door was swung up on a hinge and a white opaque flap was put in front to block the view of the ravens during the pre-testing session. Ravens had access to the viewing window from a 60 cm by 50cm platform. The centre of the viewing window was roughly 32 cm above the platform, or about head height for an adult raven.

*b. Video footage*

Video footage of three unfamiliar ravens (adult female, adult male, and juvenile, housed at the Konrad Lorenz Research Station, Grunau Austria – footage obtained from T. Bugnyar) was edited to show them engaging in three instances of each of three different behaviours (preening, vocalizing, and resting) resulting in 9 clips in total, each 1 minute long.

*c. Procedure*

Subjects were given several weeks to habituate to the experimental set-up. Once they were comfortable sitting on the viewing platform, sessions started. Twelve experimental sessions were run, two daily (one in the morning and one in the afternoon, three hours apart). At the beginning of each session, the wooden door was moved, and the white flap put in place to signal the start. Sessions commenced with a 3-minute period, during which baseline behaviours were recorded. The white flap was then removed to signal the start of the first clip. During each session, three 1-minute clips were played, each followed by a 2-minute pause. The white flap was then put back in place, and behavioural data scored for an additional 3 minutes, so that each session totalled 15 minutes. Each of the nine clips was played a total of four times across sessions, and the order of the clips was randomised.

*d. Data coding*

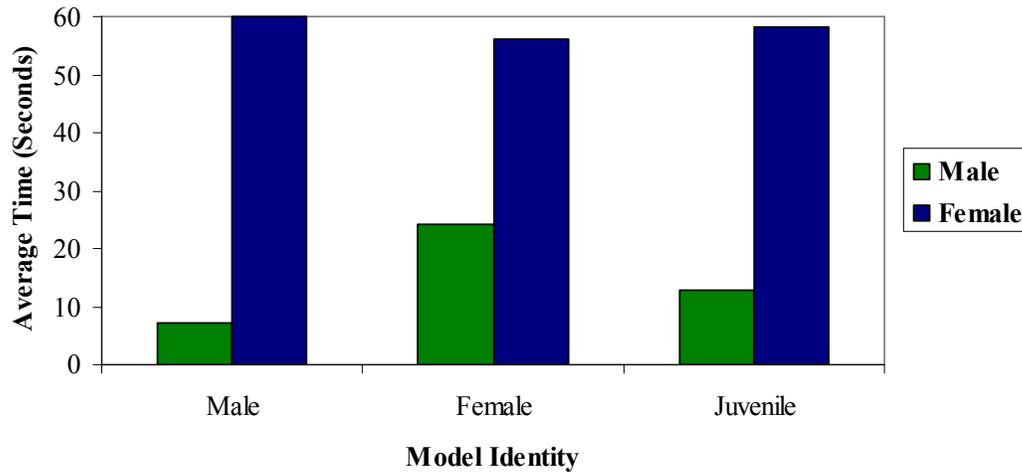
Duration and frequency of behaviours were coded for both subjects for each segment of the sessions: the baseline period (3 minutes), the periods during video clips (each 1 minute), the following post-clip periods (each 2 minutes), and the post-session period (3 minutes). Proximity to the viewing platform was measured in seconds, and coded as follows: Proximate (directly in front of the screen on the platform), within 3 m

(within a 3 m radius of the screen, so that the video could still be seen), and distant visual (within 5m – including two different perches, one above the video, and one directly in front of the video, both approximately 4m away). Duration of preening bouts was measured in seconds. Frequency behaviours included vocalisations, Social Affiliative (preen solicit, approach) and Agonistic behaviours (displace, contact aggression – see Study 1 for a description). All behaviour was video-taped and coded later by E. Price.

#### 4.2.3. Results

Overall, the female subject spent more time than the male watching the videos (defined as within 3 meters of and oriented towards the viewing window, mean = 59.08 seconds, versus 37.69 seconds, out of a total of 60 seconds). The male was much more wary of the viewing window when the videos were playing, and watched from farther away, whereas the female spent all her time watching from the viewing platform. The female tended to watch all clips, regardless of the model type (Male, Female, or Juvenile), whereas the male subject tended to watch the female clips longer, and also to stay in proximity to the viewing window after the female clips longer than the other clips (see Figures 4.1 and 4.2).

**Figure 4.1. Average time spent watching video clips**



There were three different types of clips for each Model Identity (e.g. Female Inactive, Female Preen, Female Vocal) and each clip was seen a total of 4 times, so that subjects saw 12 clips each of Male, Female, and Juvenile ravens. Figure 4.1 shows the average amount of time the subjects spent watching during the 60 seconds each clip played. Time spent watching was defined as being within three metres of and oriented towards the viewing window. The female spent the majority of the time on the platform, immediately in front of the window, and the male spent the majority of the time 2m away on a perch.

Overall, the levels of preening were very low for both subjects, and only the male subject preened more during Preening clips (mean Preen clips: 7.42, mean vocal clips: 3.25, mean inactive: 2.92). Levels of preening were also higher during the 3 minute post-session than they were during the 3-minute baseline session for both the male and female subject (male: 9.5 versus 18 seconds, female: 1.17 versus 2.5 seconds, see Figure 4.2.). The subjects vocalised more during and directly following vocal clips (mean number of vocalisations: 4.54) over those clips involving Preening (mean: 1.25) or Inactive ravens (mean: 1.79, see Figure 4.2.). Social behaviours (both affiliative and agonistic) were relatively infrequent (only a total of 5 female initiated behaviours and 12 male initiated behaviours) and were spread out evenly throughout the clips, thus were not explored further.

**Figure 4.2. Average duration of preening bouts**

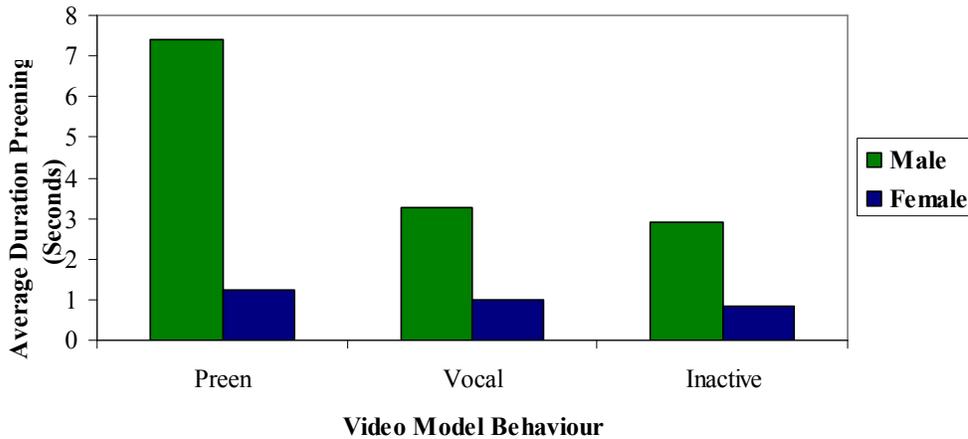
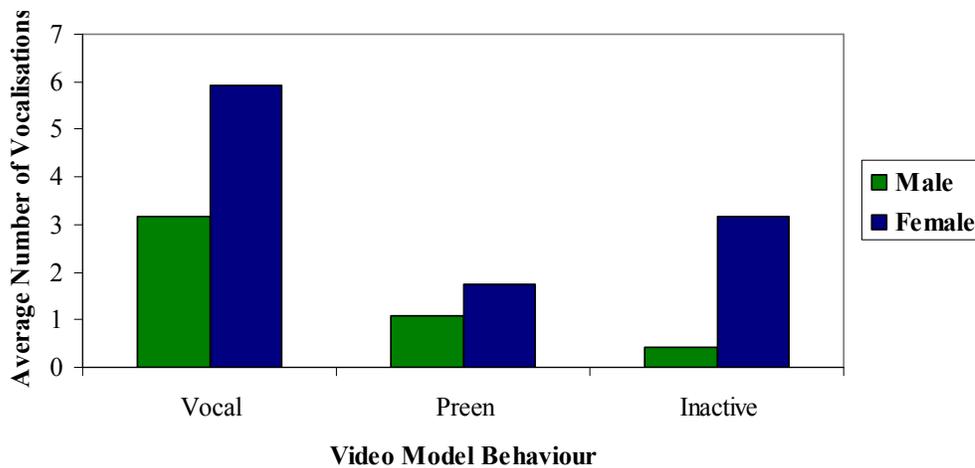


Figure 4.2 shows the average amount of time subjects spent preening and Figure 4.3 shows the average number of vocalisations during the 60s video clip and the following 120s post-clip session (out of a total of 180s)

**Figure 4.3. Average number of vocalisations**



#### 4.2.4. Preliminary conclusions

Given the small sample size, only very preliminary conclusions can be drawn from the pilot study. Both ravens did tend to vocalize more during and after the vocalizing clips. There was also slight evidence that the preening clips might have influenced preening behaviour in the male raven. The primary purpose of the pilot study

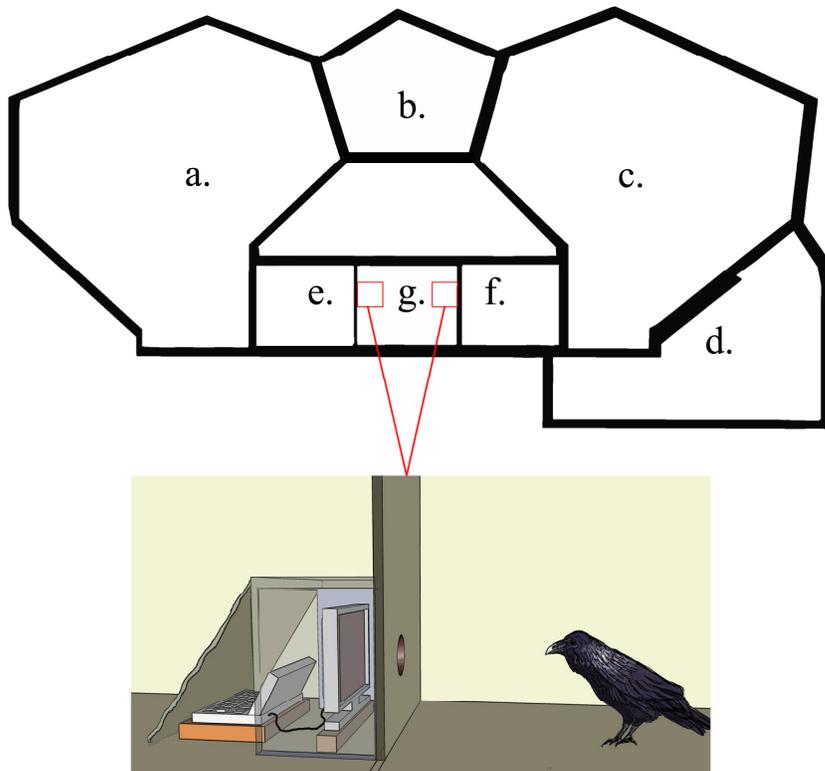
was to test the feasibility of the experimental set-up. First, although the female raven exhibited very low levels of neophobia, she was accustomed to extensive human interaction. The male raven was much more cautious, and was very wary to approach the video, even with his mate's high levels of interest. This demonstrated the need to design the task in such a way as to gradually introduce the ravens to the process. Second, the overall length of the sessions, and specifically of the clip and post-clip periods, was deemed appropriate, giving the ravens enough time to watch the videos without losing interest.

### 4.3. Study 1 – Behavioural reactions to video stimuli in ravens

#### 4.3.1. Subjects and housing

Both juvenile (N = 4) and adult ravens (N = 6) were tested. Juveniles and 4 of the adults were housed at the Konrad Lorenz Research Station (KLRS) and the Cumberland Wildlife Park in Grünau im Amtal, Austria. Five ravens were housed in the main aviary comprised of two outdoor aviaries measuring 10 m in diameter and 7 m in height at the highest point, joined by two testing rooms (5m x 4m and 3.5m high) and an observation room in the back. Parts of the two main aviaries could be locked off, allowing animals to be shifted between different parts of the enclosure (see Figure 4.4.). Three of the adults at the KLRS were housed in separate aviaries: two as a mated pair in an aviary measuring 12 x 10 m, and one female in an aviary measuring 9 x 11 m. An additional two subjects were housed together at the Wels Zoo (Wels, Austria) in an aviary measuring approximately 3 x 5 m. Subjects were fed twice daily, and had ad libitum access to water. All ravens had been used in previous studies, and all research was approved by the KLRS, the Cumberland Wildlife Park, and the Wels Zoo. All subjects were already marked with coloured leg tags for identification purposes (See Appendix I for subject information).

**Figure 4.4. The Main aviary and experimental set-up**



Subjects housed in the main aviary consisted of a mated pair (a) and a group of 4 juveniles (c). The video monitor was set-up in the middle chamber (g) and was moved so that it rested up against the doors of the two testing rooms (e and f). Video footage could be viewed through a small viewing window as seen in the bottom illustration. The adults were isolated by moving one individual into the front chamber (b), allowing the test subject to have access to the testing room (e) and the main aviary (a). Juveniles were shifted to the back holding section (d), allowing the test subject access to both the main aviary (c) and the testing chamber (f).

#### 4.3.2. Method

##### *a. Apparatus*

All videos were played on an external 19” LCD monitor viewed initially through a 13 cm diameter circular hole in a wooden viewing box measuring 1 m by .5m, made from wood on three sides and a back covered by a large opaque flap (the viewing hole was decreased in size to 5cm in diameter once ravens were comfortable approaching the viewing window). As before, the monitor was attached to a laptop (see Figure 4.4).

##### *b. Video demonstration footage*

Video footage was captured of unfamiliar ravens (the male and female housed at Edinburgh Zoo), jackdaws (*Corvus monedula*), and geese (*Anser anser*). Both jackdaws and geese were housed at the KLRS. Footage was then edited to show one minute clips of each model type either preening or resting (standing inactive), resulting in a total of 8 clips (see Figure 4.5. for demonstration still examples). All videos were taken using a Sony Handicam (DCR HC35E) and footage was edited using Adobe Premier Pro 2.0.

**Figure 4.5. Stills taken from video footage clips**



Example stills taken from the video playback footage, including Male Raven Inactive (upper left), Female Raven Preen (upper right), Goose Preen (lower left) and Jackdaw Inactive (lower right).

### *c. Habituation period*

Because ravens are highly cautious in relation to changes in their enclosures, they were first given a period to habituate to the experimental set-up. For those 6 individuals tested in the main aviary, the monitor box was put in place in the centre room between the two testing chambers behind the door. A circular hole was cut in an opaque flap covering the mesh door, which could be removed during testing. The position of the box was alternated between the two testing rooms so that both groups of ravens could acclimate to its placement (see Figure 4.4.). For those in the other aviaries, the viewing boxes were put up directly against the mesh of their enclosures. Ravens were given between three to six weeks to habituate to the new changes with an opaque cover in front of the viewing window. Next, the cover was removed for a few minutes at a time, displaying a still image of a goose, jackdaw, or raven, randomized across several days. Once all ravens were comfortable approaching the viewing window to within 3 meters, the experimental sessions started. During this time period, ravens were fed daily by the experimenter (E. Price) so that all were comfortable with her presence in and out of the aviaries.

### *d. Procedure*

Each subject participated in 8 sessions, during which they saw 4 randomly selected clips (for example: Male Preen, Female Inactive, Jackdaw Inactive, Goose Preen). Each clip played 4 times, for a total of 32 clip presentations. Ravens in the main aviary were tested singly in the testing chambers. All ravens were habituated to shifting to different parts of the aviary, and to being isolated from the rest of the group. Other ravens in these groups (4 juveniles, and one mated pair) were put into either the front enclosure (in the case of the mated pair) or the back enclosure (for the 4 juveniles – see Figure 4.4.) in order to isolate the target individual. Demonstration clips were played in the testing chamber, so that the subject could choose to enter to watch, or remain in the main aviary. Each session started with a 3-minute baseline period once the individual had been isolated. The flap covering the viewing window was then removed, accompanied by a vocal cue (clicking), and the first clip started. Each clip lasted one minute, and was followed by a 2-minute break with nothing on the screen. Once all clips had played, the

flap was put back in place, covering the viewing window, and behaviour recorded for an additional period of three minutes. Subjects were then reintroduced to their groups/mates. One adult male (his mate did not participate) and four juveniles (two females and two males) were tested in this way.

Those individuals not in the main aviary could not be isolated, and were tested in pairs, with the exception of one female, whose mate was removed during testing<sup>1</sup>. The procedure was the same and social interactions between the subjects were also recorded.

*e. Scoring of behaviours*

All sessions were video-taped and analysed later. Data scoring was broken down into segments as before, including the 3-minute baseline session, each 1-minute video clip, the 2-minute post-clip periods, and the 3-minute post-session. Preening bouts were measured in seconds. Frequency behaviours included vocalisations and startle responses (jumping in the air - Heinrich, 1989). Ravens have a large repertoire of calls (Boarman & Heinrich, 1999), thought to be supported by cultural transmission (Enggist-Dueblin & Pfister, 2002), so there is considerable variation between individual calling repertoires. For this reason, only the most well-defined calls were recorded, including territory calls (loud, repetitive, staccato “raps”), and social courtship and dominance calls accompanied by characteristic body displays (Self-Assertive-Display and bowing display). Self-assertive displays (SAD) are used by both males and females. In males, they typically consist of a “chiguck” vocalisation accompanied by a display with erected head and throat feathers, slightly extended wings, and swallowing motions. In females SADs are accompanied by similarly erect feathers, but typically include a repetitive purr or knocking vocalisation (Heinrich, 1989). Bowing displays here are defined as repeatedly lowering the head in a bowing movement and uttering a soft, low call. These are sometimes exhibited with SADs, but are also seen in isolation. Both behaviours are associated with courtship and dominance displays, although it has also been suggested that the bowing display is used more often to denote aggression than sexual interest (Heinrich, 1989, 1999).

Those animals tested while in pairs were also scored on the following social behaviours measured by duration: “allopreening” (preening his or her mate) and

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<sup>1</sup> During testing, this subject’s mate was injured and had to be removed from the aviary.

“contact” (initiating physical contact with his or her mate), and measured by frequency: “approach” (moving into closer proximity with his or her mate – in order to be scored the subject had to move from a distance greater than 1 m to within one body length of the other individual, but not contact), “preen solicit” (offering part of the body to the mate – typically bending the head down in his or her direction - and resulting in a preen bout), “contact aggression” (included pecking or kicking of mate), and “displace” (approaching the mate and resulting in that individual moving away). Social behaviours were scored only for the initiating subject.

#### 4.3.3. Results

Given the small sample size, all tests were nonparametric and two-tailed. Reported medians are for the averages per session (for either the 60 seconds during the clip, or the total clip and post-clip period - 180s, as reported), rather than total frequency or duration of the given behaviour, unless otherwise stated. In order to cut down on the overall number of tests, and thus avoid a Type I error (Mundry & Fischer, 1998; Siegel & Castellan, 1988), comparisons were made between conspecific video identities (combined raven male and female) versus heterospecific (combined jackdaw and goose), rather than across all demonstrator types, where appropriate.

##### *a. Preference for model type*

Subjects spent more time within 3 meters of the viewing window during raven clips (male and female clips, median = 14.86) than non-raven clips (goose and jackdaw clips, median = 9.82; Wilcoxon signed-ranks test,  $z = -2.09$ ,  $p = 0.037$ ).

##### *b. Behavioural reactions to model identity*

##### Vocalizations

Juvenile ravens did not call very often (average number of vocalizations per session: 0.88), unlike adults (17.89). Although adult subjects tended to call more during and after male clips (median per session = 22.88) than they did for female (median = 19.38), jackdaw (median = 11.81) or goose clips (median = 17.88), the overall effect of model identity was not significant (Friedman test,  $\chi^2 = 5.00$ ,  $df = 3$ ,  $p = 0.172$ ).

Subjects were housed in an area with a large population of wild ravens, and wild ravens frequently flew over the aviaries during testing. As a result, it is difficult to say whether territory calls were directed at free-ranging ravens or at the videos. For this

reason, courtship and dominance calls and displays were analysed separately in adult subjects (N = 6; juveniles were too young to produce these calls). These calls are much quieter and include body posturing, so might be more relevant to individuals at close proximity rather than flying overhead. When raven and non-raven clips were compared directly, SADs and bowing displays were made more frequently during and after raven clips (median: 5.25 displays) than non-raven clips (1.25 displays;  $z = -2.023$ ,  $p = 0.043$ ). Males used these displays more often than females overall (a total of 142 versus 38 times across sessions). There was some evidence to suggest that male and female ravens tended to use different displays (either bowing or SAD) to Male and Female Raven clips. Unfortunately, the small sample size makes this difficult to test, as one male did not produce any SAD or bowing calls, and *only* one female out of the three produced the bowing display. Of these individuals, both males (N = 2) and females (N = 3) produced the SAD more often during and following opposite sex clips (Male Subject – Female Clip: 66.32% of displays to Raven clips, or 189 out of 285 calls; Female Subject – Male Clip: 60.29%, or 41 out of 68) than they did after same sex clips (Male Subject – Male Clip: 33.78%, or 96 out of 285; Female Subject – Female Clip: 39.71%, or 27 out of 68). Of those who produced the bowing display (1 female and 2 males), this display was used more often after same-sex clips (Male Subject – Male Clip: 70.21%, or 99 out of 141; Female Subject- Female Clip: 95.65%, or 44 out of 46) than it was after opposite sex clips (Male Subject – Male Clip: 29.79%, or 42 out of 141; Female Subject – Female Clip: 4.35%, or 2 out of 46).

#### Startle responses

Startle responses during video clips were analysed to see if subjects responded differentially to the different identities in the videos. It was anticipated that overall startles would be high, given the novel nature of the stimuli. There was not a significant difference across demonstrator type for the number of startle responses ( $\chi^2 = 4.692$ ,  $p = 0.196$ ). When raven versus non-raven clips were compared, however, ravens startled more during clips of male and female ravens than of the jackdaws or geese ( $z = -2.136$ ,  $p = 0.033$ ).

*c. Behavioural reactions to demonstrator behaviour*

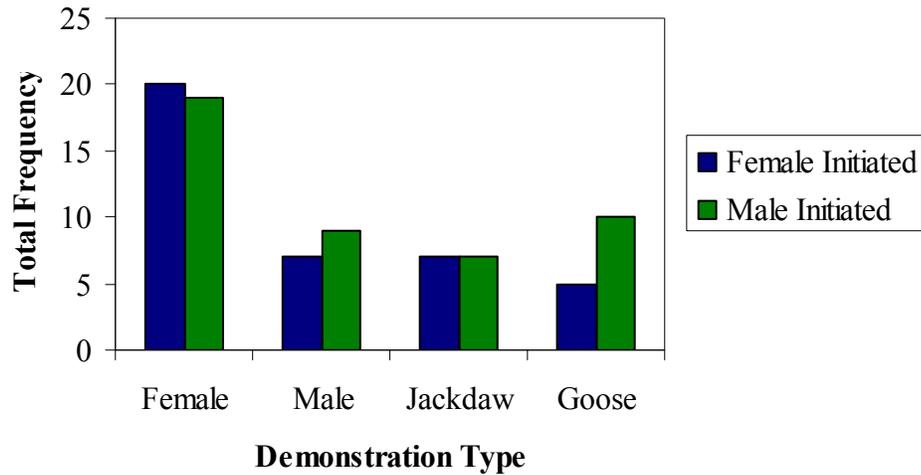
Overall levels of preening were low, and subjects did not preen more during and immediately following preening clips (Median = 2.38), than they did during or immediately following inactive clips (Median = 1.25), although this was approaching significance ( $z = -1.82$ ,  $p = 0.079$ ). Subjects also did not preen more after clips of ravens preening (Male and Female – median: 0.81) than they did non-raven preening clips (Goose and Jackdaw – median: 0.13;  $z = -.280$ ,  $p = .779$ ).

For the 4 subjects tested in pairs, the overall level of allopreening (only scored for the subject who initiated the bout) was not significantly different after preening clips (median: 6.44) than it was inactive clips (median: 3.94;  $z = 0$ ,  $p = 1.00$ ), or after raven preening clips (median: 0.625) versus non-raven preening clips (median: 2.94;  $z = -.447$ ,  $p = 0.655$ ).

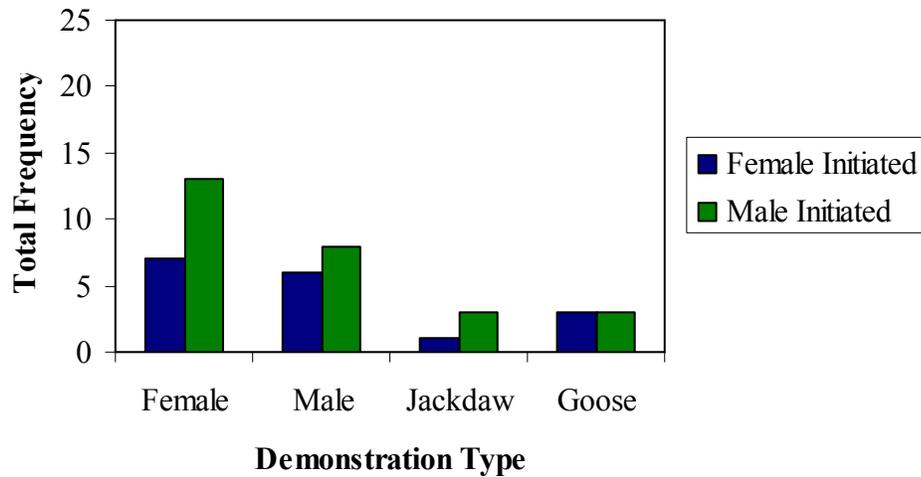
*d. Social interactions and model identity*

The following analyses were completed only with those individuals who were socially housed during testing ( $N = 4$ ). Duration of social behaviours (allopreening and contact) during and after clips did not vary significantly across all four demonstrator types (Friedman test,  $\chi^2 = 1.971$ ,  $df = 3$ ,  $p = 0.578$ ), or between raven clips and non-raven clips ( $z = -1.461$ ,  $p = 0.144$ ). Overall there were more frequency social interactions during and immediately after raven clips (median of total frequency: 9.5) than non-raven clips, although this trend was only approaching significance (median: 5;  $z = -1.826$ ,  $p = 0.068$ ), see Figures 4.6 and 4.7.

**Figure 4.6. Frequency of affiliative social behaviours in socially housed subjects**



**Figure 4.7. Frequency of agonistic social behaviours in socially housed subjects**



Figures 4.6 and 4.7 show the total frequencies of affiliative (preen solicit, approach) and agonistic social interactions (contact aggression, displace). Levels were higher during and after Female and Male Raven clips than during Jackdaw and Goose clips, although this trend was only approaching significance.

#### 4.3.4. Discussion

Study 1 represents the first analysis of video playback stimuli with ravens. Although subjects did not respond to the behaviour of the individual in the video clip (they did not preen longer during or following preening clips), overall, there was some evidence that ravens reacted differently to video footage of ravens versus other species of birds, including another corvid species. This was evidenced by increased interest during raven clips than non-raven clips. In addition, adult ravens performed more displays during and immediately following raven clips as compared to non-raven clips. It seems likely that ravens were therefore responding to the video clips, which is consistent with previous research in other avian species.

There was some evidence that adult ravens reacted differently to male and female raven clips. Self-Assertive-Displays and bowing displays are used for both courtship and dominance displays; however, Heinrich (1989) suggests that the bowing display might be used more frequently in aggressive encounters than in courtship displays. In the current study, males performed more of these displays during male raven clips than they did female raven clips. A similar trend was found for the one female who produced the calls (with all but two of her displays during the female clips). Conversely, both male and female subjects produced the SAD more often during opposite-sex raven clips than they did during same-sex raven clips. If, as Heinrich suggests, the bowing display is used in more aggressive contexts, it makes sense that mated pairs would perform the display to potential challengers. The responses were therefore suggestive that ravens might be able to detect the sex of the raven in the video, although unfortunately, the current sample sizes were very small, and the trends not significant.

This might be further confounded by differences in colour perception between birds and mammals. Video playback equipment is designed with the visual system of humans in mind, and avian species might perceive colour on a video screen very differently than it appears in the real world (Fleishman et al., 1998). Many species can perceive shorter wavelengths than humans can (Ultraviolet or UV light), and there is even evidence to suggest that this information influences mate selection. For example, removal of UV information significantly altered mate preferences in starlings and finches (Bennett, Cuthill, Partridge, & Lunau, 1997; Bennett, Cuthill, Partridge, & Maier, 1996).

Raven feathers have UV reflectance (Burkhardt, 1989; Burkhardt & Finger, 1991), and this likely influences how they identify other ravens.

It is difficult therefore to determine what cues ravens were attending to in the video clips. Further, subjects were housed in aviaries with visual and acoustic access to the abundant free-ranging ravens in the area. The presence of live competitors might have had a diluting effect on the video stimuli. The current study aimed to assess basic behavioural reactions to video playback in a way that would reduce the stress involved in using a new method. For that reason, ravens were tested in as unobtrusive a way as possible, and could choose whether or not to enter the testing chamber, making it impossible to visually isolate them from their surroundings. They were also presented with non-threatening clips so they were not overly intimidated by the videos. It would be useful in future studies to further manipulate the behaviour of the raven in the clip (i.e. exhibiting dominance or courtship displays) as has been done with other bird species. Finally, the quality of the visual information was key to the current study, so auditory information was not included; manipulating auditory and visual stimuli in the future would also prove instructive.

#### 4.4. Study 2 – Social learning from video demonstrations in ravens

Study 1 demonstrated that ravens were willing to approach the video clips, and further there was some evidence that they could differentiate between raven and non-raven clips. Study 2 set out to test if ravens could socially learn a novel task from a video demonstration. Retrieval of out of reach food has been used to ascertain cause-effect comprehension in many species (Köhler 1925; Piaget, 1954; Povinelli, 2000). While this typically involves a tool or rake of some kind in primate studies as reviewed in previous sections, string-pulling is often referred to as a “proto-tool” behaviour and is used to assess this ability in birds (for example: Pepperberg, 2004; Vince, 1956, 1958, 1961; Werdenich & Huber, 2006). Ravens learn quickly on string-pulling tasks, even those involving multiple steps (Heinrich, 1995; Heinrich & Bugnyar, 2005), as described in the introductory section of this chapter. The social learning task used in Study 2 was designed to build off this, by adding an extra step. A similar design was used successfully to test for social learning in marmosets. Marmosets presented with video footage of a

two-step string-pulling task solved the task significantly more than those in a control condition (Burkhart, Strasser, & Foglia, 2009). Here, access to the string was blocked by a clear door, which must first be moved out of the way. The door was clear rather than opaque to ensure that subjects could see the string behind the door and were sufficiently motivated to retrieve the reward. If ravens can perceive a conspecific interacting with the door in the video, they should be facilitated to interact with the device more than those in the control condition (who did not see a demonstration). Further, if they socially learn the task, they should match the method used by the demonstrator in the video, rather than employ their own technique to access the string.

#### 4.4.1. Subjects

A female raven housed at the Edinburgh Zoo acted as the demonstrator in the video footage. The four juveniles and one of the males from Study 1, plus an additional female (housed in the main aviary at the KLRs) and one additional male (housed at the Edinburgh Zoo) were tested.

#### 4.4.2 Method

##### *a. Apparatus*

The device consisted of a clear plastic door (12 cm in length by 8cm high) with two side handles, blocking access to a 20 cm string which could be pulled in to retrieve a reward. The reward was placed atop a small blue platform (4 cm<sup>2</sup>) attached to the end of the string. The string and platform were placed atop a piece of clear Perspex measuring 25.5 cm long by 13.5 cm wide, which could be placed on different surfaces to ensure the platform slid smoothly (string platform). The door was attached to the mesh of the aviaries using a small clear frame and could be lifted up and swung to the side on a hinge, exposing the string (see Figure 4.8. for demonstration stills).

##### *b. Video demonstrations*

The female raven housed at the Edinburgh Zoo (who had participated in the earlier pilot study) was used as a model for the demonstration footage. Video footage was captured in the summer of 2008. She was first allowed to pull the string through the frame, without the door attached. Next, the door was put in place and the female was trained to open the door using the handle on her right through positive reinforcement. The female raven was trained to lift the door by grabbing the handle on her right side and

lifting it up and over. She then pulled on the string and ate a small piece of cheese. Once she did this consistently, video footage was captured of her solving the task: opening the door, pulling in the string, and eating the food (see Figure 4.8). The string was then pulled back and the door reset by the experimenter (E. Price). During training sessions and video footage capture, the male raven was distracted with food at the other side of the aviary by a keeper. Video footage was then edited using Adobe Premier Pro 2.0, resulting in a total of 14 clips, each of which lasted approximately 25 seconds for a total demonstration period of 6 minutes.

**Figure 4.8. Stills taken from the demonstration footage**



Stills show the female grabbing the right handle (upper left) and lifting the door up and over (upper right). Next she grabs and pulls the string (lower left) and eats the reward (lower right).

*c. Baseline habituation period*

The clear frame of the door was attached to enclosures at ground level to allow the subjects to habituate to the new device. The device was attached inside each testing chamber for the 6 ravens housed in the main aviaries, approximately 1.5 meters away from the viewing window for the demonstration footage (see Figure 4.4). For the subject tested at Edinburgh Zoo, the device was attached approximately 1 meter beneath the viewing window directly in front of a perch.

Again, owing to the highly neophobic nature of ravens, subjects were first given a habituation period, during which they were encouraged to eat a piece of cheese placed inside the door frame (without the door in place). The reward was then placed on the small blue platform attached to the 20cm long string. The end of the string was placed between the door and frame protruding approximately 2 cm inside the enclosure, and placed atop the clear piece of plastic so that it could be pulled in easily. Once ravens were habituated enough to the device to pull in the string and retrieve the reward from the platform, sessions started. An additional four individuals were presented with this baseline test, but only those ravens that passed this baseline were used, resulting in 7 subjects, as described above. During the habituation period, the door was never in place, so subjects did not have a chance to interact with it prior to testing sessions.

*d. Testing sessions*

Subjects were randomly divided into two conditions: Video condition (N = 3, one male adult, and one male and one female juvenile) and Control condition (N = 4, one male and one female adult and one male and one female juvenile). All subjects in the main aviary were isolated from their groups, following the same protocol used in Study 1. The male housed at Edinburgh Zoo had free access to his aviary, while the female was isolated in a smaller section of the aviary. Those in the Video Condition were first presented with a video demonstration period lasting 6 minutes. As before, the start of the demonstrations was signalled visually (removing the flap covering the viewing hole) and acoustically (by a clicking sound). A total of 14 demonstrations were played, each lasting approximately 25 seconds, for a total of 6 minutes. Subjects could choose to watch as before, by entering the testing chamber. Once the video demonstrations ended, the door to the testing chamber was closed, thus not allowing ravens access while the device was

set up. The viewing window was closed, the door was attached to the door frame, and the string and platform put in place. Subjects were then given access to the complete device for up to 15 minutes. Video demonstrations were not played during this period in order to make the testing environment as similar as possible to the Control condition. For the subject at Edinburgh Zoo, the process was the same, with video footage played in the viewing box as described in the Pilot Study.

Subjects in the control conditions were allowed access to the chamber for a period of 6 minutes during which only the door frame was in place. During this time, no videos were played and the viewing window remained closed. As with those in the Video condition, they were then briefly locked out of the testing chamber while the door and string were put in place (this took roughly 2 minutes). Subjects in both conditions were given an auditory cue at the start of the 15 minute trial period and were shown the food reward (a small piece of cheese) as it was put in place. All subjects were given up to four testing sessions to solve the task. If a reward was successfully retrieved, the device was re-set and the subject was given the opportunity to solve the task again two times. Once a reward was achieved during a session, no subsequent sessions were conducted for that subject.

*e. Coding and reliability*

All interactions with the device were recorded and analysed from video later. Proximity to the device was coded as follows: proximate (within 15 cm), within 0.5 m, 1 m, 2 m, or 3 m. All interactions with the door and frame were recorded and scored as followed: touches to the door – which did not result in moving the door (right handle, left handle, or anywhere else), open attempts – resulting in moving the door, but not opening it completely (using the right handle, left handle, or lifting from the bottom), open successes – completely opening the door and retrieving the food from the string (using the right handle, left handle, or lifting from the bottom). All data was coded by E. Price. Coding of solutions and attempts were unambiguous, therefore only one coder was required.

4.4.3. Results

Those ravens in the video condition were significantly more likely to attempt to open the door than those in the control condition (100% or 3 out of 3, versus 0% or 0 out

of 4 - Fisher's exact test,  $p = 0.0286$ , two-tailed), however they were not significantly more successful at getting the reward (Fisher's exact test,  $p = 0.1429$ ). Of the three subjects who saw the video, two successfully opened the door, pulled the string, and retrieved a reward, and one made several attempts at opening the door. None of the four control subjects touched the device.

*a. Matching the technique used*

One of the video condition subjects solved the task within one minute, using the same technique that had been demonstrated in the video (opened the door by grabbing the right handle with the beak and pulling to the side – see Figure 4.9). After the door was re-set, he again used the demonstrated method, however on his third attempt, he levered his beak under the door to lift it. The other subject who successfully retrieved a reward first attempted to open the door during his second session by trying to lift it from the bottom (where the end of the string was visible through the door). During his fourth session, he attempted to move the door using the handle on the left (the same technique demonstrated in the video, but using the opposite handle). First he pecked at it 35 times, and then was successful at moving the door slightly a total of 6 times using this method. Finally, he successfully opened the door by levering his beak under the bottom and moving it aside that way. When the door was re-set, he again attempted to lift it several times using the left handle, and finally lifted it by levering it up from the bottom. Unfortunately, he was distracted during his third opportunity, and did not make any further attempts. The female juvenile who was unsuccessful at retrieving a reward, nonetheless made several attempts. Within the first 30 seconds of her first session, she made an attempt to open the door using the left handle. During her 4 sessions, she made a total of 7 attempts to open the door using the demonstrated method (matching the right handle) and additionally pecked the door on the other handle (3 times) and at the bottom of the door (10 times).

**Figure 4.9. Video subject matches the demonstrated technique**

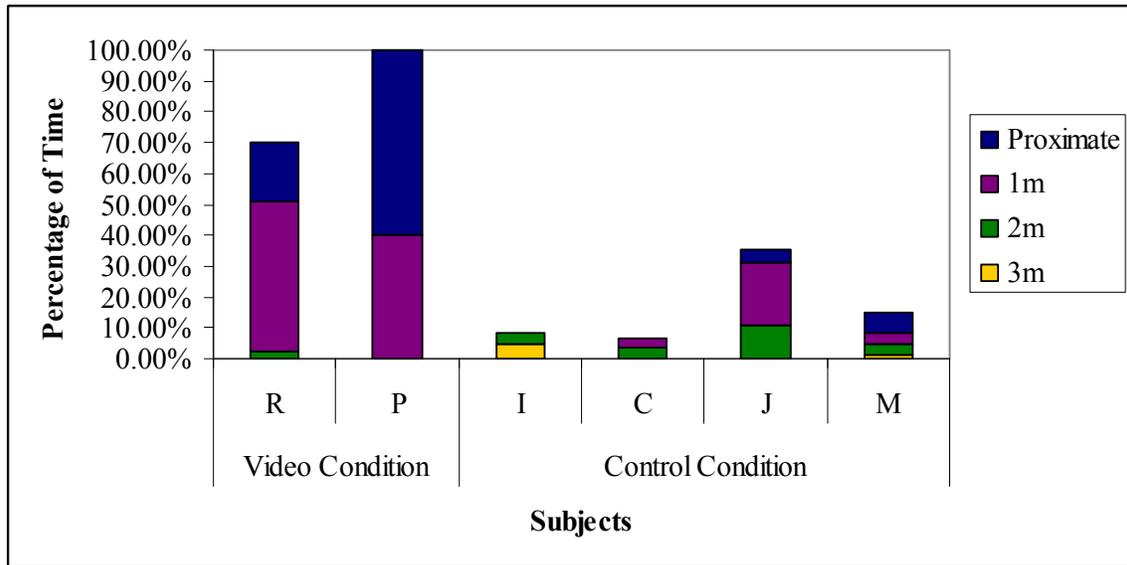


Subject “H” solves the task using the same technique that had been demonstrated in the video (grabbing the right handle and lifting up and over).

*b. Proximity to the device*

None of the subjects in the Control condition touched the device. Overall there was a tendency for those who had seen the video to spend more time in closer proximity to the device than those who had not seen it (see Figure 4.10). The proportion of time spent within one meter of the device in relation to the total available time was compared between groups, with those in Video condition spending more time within one meter (median = 1.0, or 100% of the time) than those in the Control condition (median = 0.1, the trend was approaching significance: Mann Whitney  $U = 0$  ,  $p = 0.057$  two-tailed).

**Figure 4.10 Percentage of overall time spent in proximity to the device**



Duration spent in each distance zone was measured in seconds. Percentages were calculated out of the total amount of time subjects had to interact with the complete device. Since the subjects' sessions ended after they solved the task, subject "R" had a slightly different total amount of time. Subjects "P" from the Video Condition and all subjects from the Control Condition had four 15- minute sessions (or 3,600 total seconds). Subject "R" had three 15-minute sessions, and one 8-minute session (for a total of 3,120 seconds). Subject "H" (video condition) solved the task during the first 60 seconds of the first session, and therefore was not included.

#### 4.4.4. Discussion

Only those subjects that had first seen video footage of another raven solving the task interacted with the device. Of these, two successfully opened the door and retrieved a reward, and one made several attempts. To the best of my knowledge, this supplies the first evidence of social learning from a video demonstration in ravens.

Although ravens were facilitated in some way to interact with the door in the Video condition, it remains unclear what features of the demonstration influenced task acquisition. Seeing a conspecific interact with the door might have merely reduced neophobia, resulting in an increased likelihood of contact with the device and thus of

reaching a solution. Ravens will interact with objects more frequently after they have seen other ravens do so (Schwab et al., 2008; Stöwe et al., 2006), and there is evidence to suggest that ravens are facilitated to interact with particular parts of a device after seeing a live demonstration. In the latter example, ravens tended to use the demonstrated method of opening a box, rather than the simpler method adopted by those in the control condition (Fritz & Kotrschal, 1999). In the current study, none of the Control subjects touched the device, therefore a comparison between opening attempts is not possible. However, there is some evidence of matching the demonstrated method in all three Video condition subjects. One subject (“H”) solved the task very quickly (within 60 seconds) and used demonstrated technique, including the same handle, to open the door. Many parts of the device might have drawn his attention - both handles were identical, and the end of the string was clearly visible at the bottom of the clear door. Furthermore, if he was replicating the action of the door, or object movement re-enactment (OMR), he could have moved the door in a number of ways. The unsuccessful subject’s (“P”) very first interaction with the device was a touch to the opposite handle within 30 seconds of her first trial, and she and the other video condition subject (“R”) repeatedly attempted to open the door using the demonstrated handle method, although not always matching the handle on the same side. This suggests stimulus or local enhancement was most likely influencing the subjects. Even though they did not always match the correct side, they might have generalised from the video, since both handles were identical.

Whether subjects were facilitated by a combination of stimulus enhancement and OMR, or by the actions of the demonstrator, the effect was short-lived. Subject “H” continued to use the demonstrated method on his second attempt, but on his third attempt, he opened the door by sticking his beak under the bottom and lifting (“bottom-lift”). The “bottom-lift” method might have been more intuitive, since the string was clearly visible behind the glass at the bottom of the door. The other successful subject “R” first attempted to open the door using this same “bottom-lift” method. He nonetheless persisted in several unsuccessful attempts at opening the door using the handle across subsequent sessions, finally successfully opening the door using the “bottom-lift” method. This suggests that the handle opening method might have been more difficult for the subjects. Lifting the door using the “bottom-lift” method involved sticking the beak

under the bottom of the door and flipping it up, whereas the demonstrated method involved pulling the door both up and over to the side.

The success of subject “H” might be related to the fact that the demonstrator in the video footage was his mate. He showed the greatest interest in the video demonstration of the three subjects, even pecking at the screen several times while it was playing. As previously discussed, there is evidence to suggest that ravens are more easily facilitated to explore novel objects by closely related affiliates than non-affiliates (Schwab et al., 2008; Stöwe et al., 2006) and when offered the opportunity to watch affiliates or nonaffiliates, they watch affiliates longer (Scheid, Range, & Bugnyar, 2007). This might explain his fast success in comparison to the other subjects. Arguably, he could have learned from watching the female during taping of the demonstration clips. During filming, the subject was distracted on the opposite end of the aviary, and every effort was made to visually isolate him, yet it is difficult to be certain he did not see any of the demonstrator’s manipulations with the device. However, given that taping of the demonstrations was completed over a year (16 months) prior to the time he was tested, it seems most likely that his advantage stems from the fact that he was familiar with the demonstrator, rather than affordances of the device itself.

The current study aimed to assess the feasibility of video demonstrations with ravens, and although limited in its scope, has shown that the methodology is possible. Future studies should further assess what learning mechanisms are in play. First, as was done with chimpanzees and children, the amount of information available in the video demonstration and the complexity of the given task should be manipulated. It is anticipated that if a solution can be discovered easily through individual exploration, individual learning might corrupt social learning effects on simpler tasks. More complex tasks might be more likely to produce stronger copying fidelity, as has been seen with chimpanzees (Price, Lambeth, Schapiro, & Whiten, 2009 and reported in Chapter 2). This interaction between individual understanding and social learning has yet to be explored in ravens, and the current studies have shown that video demonstrations would provide a promising method with which to dissect these learning processes.

#### 4.5. Conclusion

As discussed, recent work with corvids suggests that they share many of the same cognitive capacities as the great apes. In the thriving field of cultural cognition, much work has been done to analyse potential differences between humans and their closest living relatives on tasks of social learning. The majority of these focus on copying fidelity and reliance on individual learning versus social learning on novel tasks. Recent research with ravens suggests that they make good candidates for such study. As shown previously, video demonstrations offer much scope to dissect the interaction between learning processes. The studies discussed in this chapter provide the first analysis of video stimuli in ravens and provide two useful conclusions. First, that ravens can distinguish between ravens and other birds in video footage. Second, that task acquisition can be socially facilitated by video demonstrations in ravens. Although subjects tended to match the demonstrated method, this effect may be ephemeral when a simpler method is discovered. Future work should include conditions which vary the both the amount of information available in the video demonstration, and the complexity of the task.

## **CHAPTER 5. GENERAL DISCUSSION**

## 5.1. Introduction

The studies outlined in this thesis offer new insight into similarities and differences between how children and chimpanzees learn and retain information about tool modification. This in turn has implications for cumulative culture and tool technology in humans and wild chimpanzees. This work also provides the first evidence of social learning from video demonstrations in chimpanzees and ravens, and supports the use of this medium to dissect social learning mechanisms in a range of species. This final chapter analyses the findings of the previous chapters in the context of the larger body of work in the area and suggests future directions. As the primary focus of the tests examined children and chimpanzees on the tool modification task, the following discussion focuses primarily on the implications of those outcomes. The studies outlined in Chapter 4 were exploratory in nature, thus firm conclusions cannot be drawn. However, as discussed in the previous chapter, given the ability of ravens to socially learn and solve causal tasks, they make particularly good candidates for further study.

## 5.2. Children and chimpanzees – Opportunities and motivation for social learning

The studies outlined in this thesis differed from previous comparative research in several ways. Studies comparing children and chimpanzees typically attempt to use novel actions or arbitrary sequences of behaviour. This is useful when attempting to distinguish between different learning mechanisms as outlined in Chapter 1, but the key to cumulative culture with regard to human technology involves learning functionally useful techniques. At the most basic level, a given species must be able to innovate and socially learn an effective modification to an existing tool. The task used in these studies was designed from this perspective, and sought to examine if chimpanzees and young children possessed this key ability, and if so, how much information they required to learn it. This is somewhat analogous to “ratcheting-up” to a more effective technique, but in this case, rather than increasing the benefit of an existing tool behaviour (Marshall-Pescini & Whiten, 2008) the tool modification was essential in order to retrieve the reward. All chimpanzees and children were first assessed on their ability to retrieve a reward with a simple tool. They were then presented with the problem of an ineffective tool and an out of reach reward. In order to retrieve the reward in this context, they had to

build a more efficient tool. The method of modification was manipulated to include a more perceptually obvious means – combining two tools – contrasting with one that was more subtle and precise. The use of video demonstrations allowed for conspecific models to be used in both cases, while still maintaining precise control over the details in the task. Rather than attempting to rule out different types of learning, these demonstrations were set up to manipulate the amount of information available in the demonstration in a way that might be more consistent with what is encountered in a natural environment. In this sense, subjects were presented with the raw materials (which might be akin to left over tools), and access to either full details of the process, or some information about a conspecific interacting with the tools, but not precise details of the actions involved.

Finally, the interaction between functional understanding and social learning was directly assessed by manipulating the necessity of building the tool after a substantial delay. This allowed for the effects of the initial learning environment (i.e. social learning with full information, partial information, or individual learning) to be analysed with respect to copying fidelity both over time and with respect to necessity. Taken together the results of these studies increase our understanding of differences in the way chimpanzees and children learn about tool modification, and subsequently might help explain differences in the complexity of tool use between the species.

#### 5.2.1. Enhanced social learning in children

The dichotomous view of children as imitators and chimpanzees as emulators has shifted somewhat in recent years with the advent of studies manipulating the quality and quantity of causal information. Both children and chimpanzees seem to build up a “portfolio” of learning strategies which are employed depending on how well they understand the problem at hand (Whiten et al., 2009). If the task is sufficiently easy, or causal information readily available, both chimpanzees and young children tend to focus on the outcomes of the behaviour, using their own actions to solve the problem. Nonetheless there is some evidence to suggest a shift in children as they get older towards copying precise actions, even to the point of copying irrelevant, or inefficient actions (“overimitation”: Lyons & Young, 2007; Nielsen et al., 2008). This focus on precise actions may be what allows humans to acquire information about complex tool-using skills (Nielsen & Tomaselli, 2010). The comparison between children and

chimpanzees in these studies found that children aged 2.5 to 4.5 years were able to socially learn a tool modification technique that chimpanzees could not. This is despite the fact that no single individual could solve it on their own (whereas three chimpanzees did spontaneously innovate the technique). Thus children were able to learn a technique that was potentially out of the reach of their physical understanding. If chimpanzees are limited to learning tasks that only individuals can solve on their own, this could explain the species differences in social learning of the alternative method. However, some chimpanzees were able to spontaneously work out how to use the combine *and* the alternative methods, yet only failed to socially learn the alternative method. As discussed in Chapter 3, this might be demonstrative of a focus on copying specific actions in children but not chimpanzees, which would make the combine method easier to learn than the alternative method given the more obvious object movements involved.

Alternatively, children might have been more socially motivated to solve the task. Most evidence of over-imitation in children emerges between the ages of two and four, and it has been suggested that this might coincide with the development of theory of mind (McGuigan, Whiten, Flynn, & Horner, 2007a; Tomasello, Carpenter, Call, Behne, & Moll, 2005). The fact that in the present study the children's age in months was significantly positively correlated with their scores on the Alternative Method index lends support to this. Imitation as a means to engage with others or encourage interaction is well documented in children (Eckerman, Davis, & Didow, 1989; Nadel, Guerini, Peze, & Rivet, 1999; Nielsen & Dissanayake, 2004; Uzgiris, 1981, 1991). Social motivation to copy others has been experimentally manipulated in past experiments, with results suggesting that children are more likely to copy the actions of socially interactive, responsive models, than aloof ones (Nielsen, 2006). This has even been tested directly regarding the use of televised models: children exposed to a "traditional" pre-recorded video demonstration did not copy as faithfully as those exposed to video playback of a socially interactive model (Nielsen et al., 2008). Video demonstrations thus offer the potential to control for the effects of social engagement. However, in these studies, I did not find the "video deficit effect" which has occasionally been found in other studies (whereby social learning is reduced following a video demonstration versus a live demonstration - Barr, Muentener, & Garcia, 2007; Flynn & Whiten, 2008), with children

in my study copying at high levels. Thus children might have still been socially motivated to engage with the model in the video. It also seems impossible to rule out the effects of my presence during testing as I was unable to leave the children unattended in the testing rooms. Although I was unresponsive to requests for help, I was initially engaging to put the children at ease. For example, it was necessary to say “Would you like to come and play a game with me?” in order to create a comfortable environment for the child. Therefore, my presence might have been sufficient to increase motivation to persist in attempts until a solution was reached. In this case, children might have had an advantage by having a conspecific experimenter in the room, unlike chimpanzees. Perhaps only the most exploratory chimpanzees were able to solve the task, but the majority lacked sufficient social motivation to persist in attempting to solve the task using the more subtle and precise technique of unlocking the mechanism. This may be further confounded by potential biases inherent to the experimental methodologies typically employed by child-chimpanzee comparisons, as outlined in Section 5.4.

#### 5.2.2. A Potent effect of social learning in chimpanzees and children

Despite the above evidence of enhanced social learning in children, there were several important departures from this trend. First, chimpanzees and children performed equivalently when presented with end results only, versus complete information about the modification technique. In addition, both chimpanzees and children who had seen a complete demonstration continued to use the technique two weeks later, even when it was no longer necessary. This is particularly suggestive of a potent effect of social learning, as the more efficient solution would be to only combine when the reward was out of reach. The combining process was time consuming and even made retrieval of the reward in the close position more difficult than it would have been with one of the unmodified tool components, as it was awkward to manoeuvre the longer tool between the bars. Furthermore, in chimpanzees, this effect was contingent on whether or not they had seen a conspecific combine the tools. Depending on how they learned the process, this behaviour is suggestive of “over-imitation” or at least “over-copying”, because subjects were performing an unnecessary action (Lyons et al., 2007). In fact behaviour labeled as overimitation in Lyons et al.’s (2007) study can actually be explained in terms of emulation, as there was little evidence to suggest definitively that children were copying

specific actions (Whiten et al., 2009). Likewise, since children in the present study who learned by seeing end results only tended to continue combining, even when unnecessary, it seems likely that emulation in some form is sufficient to maintain a new behaviour in children.

### 5.2.3. Complexity in free-ranging chimpanzee tool-use

The ability of chimpanzees to innovate and socially learn to construct a tool from two parts in these studies might help understand chimpanzee tool using complexity in the wild. As discussed in Chapters 1 and 2, chimpanzees are distinguished from other species by the breadth and complexity of their tool use. They routinely manufacture tools, use different tools for different functions in sequence, and use more than one tool in combination in the form of tool composites. There is even some evidence that they combine more than one element together to form a “single working unit” or compound tool, or that they use one tool to render another more effective (metatool or secondary tool - McGrew, 2010). Instances of these behaviours are very rare, however, unlike simpler tool using behaviours (Biro, Carvalho, & Matsuzawa, 2010).

The combining method in the current studies creates a compound tool, and further it is an addition to an existing form of tool use (in this case raking in a reward). The potent effect of social learning found in these experiments suggests that this type of behaviour is not being limited in the wild by a cognitive inability to learn from others. As chapter 2 discusses, this could be the result of a disparity between the development of physical cognition and the availability of socially tolerant demonstrators. However, it might also be the result of a trade-off between the effort involved in social learning and the benefits. Those few examples of secondary tool use in wild chimpanzees (i.e. anvil prop for a more balanced surface or push-pull stick attached to a leaf sponge to reach for water) might not convey enough of a benefit to warrant social learning. Chimpanzees in the captive experiment were also provided with the appropriate materials and a situation that necessitated modification in order to retrieve the reward, making it much less costly than it might be in the wild. Thus, the lack of a “ratchet effect” in wild chimpanzees may not be the result of limited social learning abilities; instead chimpanzees could be limited by their ability to innovate techniques useful enough to warrant social learning.

Humans are the only animals (to the best of our current knowledge) to make machines, here defined as complex objects with multiple interacting parts (Aunger, 2010). In each example of compound or secondary tool use in chimpanzees, although the tool might not be directed toward the immediate goal, it is still being used for an immediate purpose. Much of human technology involves making objects into tools for no immediate purpose (Hansell, 2005). For example, a bow-and-arrow consists of two interacting parts, each of which is comprised of at least two different materials. This necessitates construction of a tool from several parts (the bow) which then must be set aside, as it is only functional when used with an arrow, which requires its own constructive sequence. This hierarchically organized construction has been called “second-order instrumentality” and requires executive control and planning (Jackson, Jackson, & Roberts, 1999). There is some evidence to suggest that this kind of executive control is of recent evolutionary origin (Streidter, 2005) and it is one of the latest abilities to develop in the brain on an individual level (Luciana, Conklin, Hooper, & Yarger, 2005).

Those additions that might confer enough benefit to warrant social learning, might necessitate this level of executive control to innovate. It is unclear if chimpanzees possess even the most fundamental ability to plan in this way. Although chimpanzees have been seen on occasion to transport tools (Boesch & Boesch, 1984; Sanz et al., 2004), examples of tool use that might require this level of planning and combination are thus far absent in wild chimpanzees. In addition, although there is some experimental evidence of future planning (in this case selecting and retaining the appropriate tool for a particular task in advance) in captive chimpanzees, orangutans and bonobos (Dufour & Sterck, 2008; Mulcahy & Call, 2006a; Osvath & Osvath, 2008), others argue that these experiments have not controlled for associative learning well enough (Suddendorf & Corballis, 2008). Even if chimpanzees are able to use this form of reasoning, the ability might develop later on, as it does in humans. If there is an important interaction between social and physical cognition, as has become increasingly evident in recent years (Byrne & Bates, 2010; Matsuzawa, 2009) and as suggested in Chapter 2, then chimpanzees’ lack of access to sufficiently tolerant demonstrators as adults might further impede learning.

It is important to note that we might not have watched chimpanzees long enough to see any real changes in their tool technology (McGrew, 1992a). It might be that cumulative culture exists in chimpanzees and other animals, but that the process is slower and that a unique combination of pedagogy coupled with communication, social tolerance and co-operation, work together to increase the rapidity of the cumulative effect in humans (Gergely & Csibra, 2005).

### 5.3. Drawbacks of the chimpanzee – child comparison

The experiments outlined in chapters 2 and 3 were designed to be comparable to previous studies and thus used young children in comparison to chimpanzees. While this is instructive, especially given the differences found in these studies as compared to previous work, there are other factors which are rarely considered and which undoubtedly affect results. Without a careful analysis of the effects of the experimental methodology and process, it is unwise to make sweeping conclusions regarding the nature of learning in the two species, especially when one of the species under study is in charge of designing the experiments. Outlined below is an overview of potential problems associated with such comparisons, and considerations for future research designs.

#### 5.3.1. Captive chimpanzees and “free-ranging” humans

What is often lumped together as “chimpanzee and human social learning” (Tennie et al 2009, p. 2407), is in fact comparing human children of a very specific age to captive chimpanzees of vastly different rearing histories and ages. Comparative research has been criticized because captive chimpanzees have the obvious disadvantage of captivity – they are tested in human environments, quite often by human demonstrators, and are frequently isolated from their social groups (Boesch, 2007, 2008; de Waal et al., 2008). The performance of such animals might therefore not be representative of their cognitive abilities. In addition, rearing history may affect the performance of chimpanzees on cognitive tasks. Some of the best examples of imitative behavior are from enculturated chimpanzees (here defined as being raised in a human environment), and there is evidence that enculturated individuals perform better than mother-reared chimpanzees on both social learning and physical cognition tasks (Bering, Bjorklund, & Ragan, 2000; Buttelmann et al., 2007; Furlong, Boose, & Boysen, 2008; Tomasello,

Savage-Rumbaugh, & Kruger, 1993). A human oriented environment might allow them to perform better because they have had access to a “socialization of attention” or active engagement and encouragement. Alternatively, because they have been raised in a human environment, they are more likely to perform better on tasks designed by humans. It is difficult to be sure that comparative tasks designed from a human perspective are not inadvertently biased towards a human advantage. In addition, adult chimpanzees presented with the same task performed very differently depending on the types of object interactions they had access to when developing. Those who had been exposed to various objects while infants showed a better functional understanding of tool tasks (Bania et al., 2009 replication of Povinelli, 2000). There is also some evidence that wild born individuals are better at solving tool use problems than are captive born chimpanzees (Morimura & Mori, 2010). Whether enhanced, or inhibited, cognitive abilities in captive tests might not be representative of natural behavior in the wild; we might know more about what they can do, but not what they have evolved to do in a natural environment.

#### 5.3.2. Developing humans and adult chimpanzees

In addition, just as there might be a cognitive shift in children, so there might be in chimpanzees. There is some evidence for a critical learning period in free-ranging chimpanzees for some types of tool use between the ages of three and five. Individuals who do not learn the challenging skill of nut-cracking during this period, do not become proficient later in life (Matsuzawa, 2001a). Unfortunately the majority of captive chimpanzees tested are adults, and comparing a wide range of ages in chimpanzees to very specific ages in children can cloud results. Adult chimpanzees might apply very different strategies than young, developing chimpanzees, and research on cognitive development in captive chimpanzees is needed to look for changing patterns across ontogeny (Matsuzawa, 2006). In addition, young children might not be as well equipped as adult chimpanzees at dealing with problems involving physical objects. If this understanding plays a role in their social learning strategies, this could affect results.

Along the same lines, very few studies apply these same techniques to look at adult human cognition. It might be that children are disposed to imitate because they have an abundance of new things to learn, and adults might perform differently. Although there is some evidence to suggest that adults imitate actions very precisely in some

circumstances (Custance, Prato-Previde, Spiezio, & Rigamonti, 2006), there is also evidence to suggest that emulation alone might be sufficient for the spread and maintenance of artificially generated “cultures” in adults (as discussed in Chapter 1 – Caldwell & Millen, 2009).

### 5.3.3. Experimental designs

The way in which chimpanzees and children are tested might also affect results. Despite a shift toward the use of conspecific models in recent years, much of the compiled evidence in the comparative literature is based on studies using human demonstrators for both children and chimpanzees. For example, a recent article claiming the evolution of specialized social cognition skills in humans used human demonstrators for all species, including chimpanzees and orangutans (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). Nonhuman apes’ motivations for copying a human demonstrator might be very different than learning from a conspecific, and this is particularly important when measuring aspects of social cognition (de Waal et al 2008)

In addition, the typical experimental paradigm used for comparative studies may be constructed in a way that fundamentally changes the motivation for chimpanzees and children. Typically (perhaps because of difficulties in using food rewards with human participants) chimpanzees are rewarded with food, and children with a sticker, or a toy. Food is an actual, immediate reward, with a biological benefit, whereas a sticker must be rewarding in quite a different way. This problem is applicable to the current studies. Chimpanzees are not typically given grapes as part of their daily diet (this is the case with the subjects in these studies, and is perhaps frequently the case in captive environments because of their high sugar content), and the drive to acquire them is very high. Chimpanzees might therefore be expected to use the most direct method to retrieve them, rather than focusing on copying the precise actions of a demonstrator. Children often receive stickers when they have achieved something from teachers or other approving adults. This might place the onus of the task on pleasing the human demonstrator, rather than retrieving the reward. Children placed in a more restrictive environment working for high-preference food might behave very differently. Thus experiments might be fundamentally constructed in a way that sets children up to be more socially motivated than chimpanzees.

#### 5.4. Future directions

The interaction between social learning and individual understanding, as well as how these learning processes affect tool use and cumulative culture is still very much open to debate. For example, it is unclear if imitation is essential, or if other learning processes can support cultural variation. It is further unclear if imitation is a cognitively advanced process, relying on shared intentionality (Tomasello et al., 2005) or if it can be explained by simpler mechanisms (Byrne, 1999; Leighton, Bird, & Heyes, 2010). Along the same lines, it is unclear if tool use relies on cognitive processes shared with non-tool users, or if it is specialised, relying on domain-specific cognitive specialisations unique to tool-users (Santos et al., 2006). The methodology developed in these studies can provide a useful springboard for further tests exploring these questions in the laboratory. In addition, the combination of increasing ecological validity in laboratory studies, and continued observation in the field will continue to further our understanding, as discussed below.

##### 5.4.1. Testing in captivity

The use of a tool modification task, coupled with manipulating the amount of available information in a demonstration and testing functional understanding after a delay, has produced useful results. This methodology can be expanded in several ways, to help address related questions. Next steps could involve additional video demonstrations, further manipulating the amount of available information. For example, in order to determine how observers were encoding the information in the Retrieve-Only condition, it would be useful to have a condition in which the demonstrator picks up an already completed tool and uses it. The viewer would thus not see the demonstrator pick up both pieces, and end up with a complete tool. This information might have played a crucial role in helping some children and chimpanzees solve the task; it might also explain the lack of difference during the Post-sessions between children in this condition and those who had complete information. Conditions involving actions only would also provide a useful comparison. Further, these tests should be adapted for other tool-using species, like capuchin monkeys, and for non-tool users both closely related to humans (e.g. gorillas) and distantly related (e.g. ravens).

Additionally, it would be useful to measure the ability of chimpanzees and other animals to locate and extract the necessary materials required to solve tasks. Although both chimpanzees and humans probably rely on left over tools and materials to some degree, the ability to observe a task and then find the requisite materials needed is understudied, and would provide insight not only into innovative abilities, but also into possible impediments to social learning. Demonstrations could thus include information about extracting the correct materials from a natural substrate, modifying them, and using them for a given task. The raw materials could then be provided to the subjects, perhaps even in a location spatially distant from the provided task, to see if chimpanzees and other species can apply this knowledge. Studies introducing models using actual processes and materials found in the wild would also provide a useful counterpart to field studies (Hirata, Morimura, & Houki, 2009).

In addition, there is arguably an over-emphasis on studies involving food extraction or retrieval in social learning studies. Many of the behaviour patterns that distinguish humans culturally are arbitrary social customs, and this is also the case for several behavioural traditions in chimpanzees and other primates in the wild as discussed in Chapter 1. It would therefore be helpful to examine such behaviour in an experimental setting (Watson & Caldwell, 2009). One could also use social motivation as a reward. Recent innovative tests have found that capuchin monkeys will copy behaviour even in the absence of a reward (Bonnie & de Waal, 2007), and that they affiliate more with humans who copy their actions (Paukner, Suomi, Visalberghi, & Ferrari, 2009).

Despite the inherent artificiality of the stimulus, video demonstrations help allow for conspecific demonstrators and can also be used to manipulate available information in order to dissect social learning mechanisms in ways that might be more intuitive than the more typically used methods like ghost conditions. Video demonstrations can go beyond the current study, by digitally altering demonstrations, or even using computer generated models, which might be particularly useful when attempting to create arbitrary actions (Moravec et al., 2010; Watanabe & Troje, 2006). The current studies have shown that chimpanzees react to videos much as they do to live demonstrations, and further that they might even have the potential to enhance learning by providing a clear and repetitive demonstration. The fact that animals can learn from video on manipulative tasks (rather

than just reacting behaviourally) is itself remarkable; it involves taking 2D information and translating this into useable information in a 3D environment, so there is still much scope to explore the underlying cognitive mechanisms involved (Troseth & DeLoache, 1998).

Finally, as discussed in the above section, it is important to be aware of the effect of the testing environment. In addition, tests focusing specifically on developing children and adult chimpanzees might be misleading. Comparisons between infant chimpanzees and children are warranted, as are those addressing learning differences between adult humans and adult chimpanzees (Matsuzawa, 2009; Matsuzawa, Tomonaga, & Tanaka, 2006).

#### 5.4.2. Tracing behaviours in wild chimpanzees

As discussed in Chapter 1, opportunities to trace the spread of new behaviours have arisen in recent years, allowing researchers to document the possibility of social learning in groups of chimpanzees (Biro et al., 2010; Hobaiter & Byrne, 2010; Humle, Snowdon, & Matsuzawa, 2009). As on-going field sites continue to compile evidence, new behaviours are constantly emerging. Abilities once thought restricted to humans, and then to chimpanzees, are now being seen in monkey species as well (Mannu & Ottoni, 2009; Perry, 2009), and will most likely appear in a greater range of species once the length and intensity of study increases across field sites. The addition of field experiments also holds much scope for the future (Biro et al., 2003; Gruber et al., 2009).

### 5.5. Conclusion

The discovery of tool manufacture in wild chimpanzees in the 1960s led to the redefining of what was “uniquely human” (van Lawick-Goodall, 1968). Since then, as outlined in Chapters 1 and 2, additional discoveries have continued to decrease the range of tool behaviours unique to our species, with chimpanzees displaying impressive tool repertoires. Despite this, human tool technology remains remarkable in terms of its breadth and complexity. The main part of this thesis compared the social learning abilities of chimpanzees and children on a tool modification task, in an attempt to better understand potential differences which might drive the human advantage. Several key findings are particularly instructive regarding the nature of tool use and social learning in

chimpanzees and children. First, both species socially learned how to build a tool from separate parts, and further persisted in faithfully using this method, even at the cost of efficiency two-weeks later. That the more subtle technique was only learned by the children, despite several chimpanzees innovating the process, suggests that children attend more to actions, or alternatively, that children are more socially motivated to solve difficult techniques. This latter explanation is perhaps justified given that children (but not chimpanzees) who learned with end results only continued copying the method faithfully when no longer required in the post-sessions. Additionally, the lack of a cumulative effect in wild chimpanzee tool technology may be the result of the inability to innovate technological additions which involve planning, rather than the inability to socially learn new techniques. Finally, the studies outlined in this thesis have shown that there is much scope for the use of video demonstrations, which permit conspecific demonstrators, without sacrificing experimental control. Further tests are required in order to better understand the nature of the cognitive processes supporting tool use in humans and other animals, and the methodology employed in these studies offers a promising avenue of research.

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## Appendix A. Pilot Study Participants

<b>Group</b>	<b>Sex</b>	<b>Test</b>	<b>Name (DOB)</b>
Q2	M	Poke	Nick (7/4/1988)
Q2	M	Poke	Chinook (25/8/1988)
Q2	F	Poke	Gigi (1962)
Q2	F	Poke	Polly (1963)
Q2	F	Poke	Mandy (8/9/1984)
Q2	F	Poke	Bria (31/8/1995)
Q3	M	Poke /Rake	Gimp (1969)
Q3	M	Poke /Rake	Samson (14/9/1984)
Q3	M	Poke /Rake	Magic (24/7/1992)
Q4	M	Rake	Ajax (1/1/1978)
Q4	M	Rake	Adonis (9/2/1975)
Q4	M	Rake	Skeeter (12/7/1977)
Q4	M	Rake	Armond (4/11/1986)
Q4	M	Rake	Kareem (4/1/1989)

## Appendix B. Behavioural Ethogram for Pilot Study

### **Tool directed behaviours:**

<b>Behavioural Code</b>	<b>Description</b>	<b>Coding</b>
<b>Contact Rod</b>	Contact of any duration with the small rod.	Frequency and Duration
<b>Contact Tube</b>	Contact of any duration with the tube. This behaviour was coded in addition to other tube contact behaviours (i.e. if poke hole is coded, contact tube is also coded).	Frequency and Duration
<b>Poke Hole</b>	Insertion of a finger/ tongue into the hollow end of the tube.*	Frequency
<b>Look Hole</b>	Looking inside the hollow end of the tube	Frequency
<b>Pull Attempt</b>	Pulling outward on the protruding end of the internal rod.*	Frequency
<b>Push Attempt</b>	Pushing inward on the protruding end of the internal rod.*	
<b>Touch End</b>	Touching the protruding end of the internal rod without pulling or pushing.*	Frequency
<b>Combine Attempt</b>	The subject attempts to insert the rod into the tube.	Frequency
<b>Combine Success</b>	The subject successfully inserts the rod into the tube.	Frequency

\* Attempts made with the mouth and hand were coded separately

### **Food Retrieval, Poke:**

<b>Behavioural Code</b>	<b>Description</b>	<b>Coding</b>
<b>Touch Metal</b>	Any contact with the feeding chute, not including the behaviours below.	Frequency
<b>Insert Metal</b>	Any insertion into the feeding tube. Finger, rod, and tube insertions were all coded separately.	Frequency
<b>Look Metal</b>	The subject looks up into the feeding chute.	Frequency

### **Food Retrieval, Rake:**

<b>Behavioural Code</b>	<b>Description</b>	<b>Coding</b>
<b>Close Success</b>	Successfully obtaining a grape placed 20 cm away.	Frequency
<b>Close Attempt</b>	Raking attempts made to obtain a grape placed 20 cm away not resulting in retrieving a grape.	Frequency
<b>Far Success</b>	Successfully raking in a grape placed 55cm away.	Frequency
<b>Far Attempt</b>	Raking attempts made to obtain a grape placed 55 cm away not resulting in retrieving a grape.	Frequency

\*Successes and attempts made with the rod, tube, and any other object were coded separately

Appendix C. Mean Rates of Behaviour for Each Subject

*Tool Directed Behaviours:*

Subject	Condition	Contact Rod	Contact Tube	Duration Rod (secs)	Duration Tube	Poke Hole	Look Hole	Pull Attempt	Push Attempt	Touch End	Combine Attempt	Combine Success
Nick	Poke	1.5	3.5	12.5	57.5	0	0	0	0	0	0	0
Chinook	Poke	1.5	4.0	20	17.5	0	0	0.5	0	0	0	0
Gigi	Poke	3	7	15.5	43.5	0.5	1	0.5	0.5	0	0	0
Polly	Poke	1	1	7	333.5	0.5	1	3.0	0	1	0	0
<b>Mandy</b>	Poke	8	14.75	59	223.5	3.25	1.75	5.0	1	1	0.5	1
Bria	Poke	0	4	0	427	6.5	5.5	3.5	1.5	1	0	0
<b>Samson</b>	Poke/Rake	12.7	14.7	139	207	1	0.3	1.3	0	0	1	1
Gimp	Poke/Rake	5	7	40.7	157	0.3	0.3	0	0	0.3	0.3	0.3
Magic	Poke/Rake	3.3	5.0	139	112	1.5	2	1	0	1.3	0	0
Ajax	Rake	2	3	271.5	180.5	0.5	0.5	0	0	0	0	0
Adonis	Rake	1.5	0.5	17	1	0	0	0	0	0	0	0
Skeeter	Rake	1	1	4.5	24	0	0	0	0	0	0	0
Armond	Rake	2	6	2	544.5	0.5	0.5	1.5	0	1	0	0
Kareem	Rake	2.5	8	38.5	535.5	0.5	0	0	0	0	0	0

\*Highlighted cells are for the two subjects who successfully combined the two tools.

*Food Retrieval Behaviours:*

<b>Subject</b>	<b>Condition</b>	<b>Touch Metal</b>	<b>Insert Metal w/Body</b>	<b>Insert Metal w/Tool</b>	<b>Look Metal</b>	<b>Close Success w/Tool</b>	<b>Close Attempt w/Tool</b>	<b>Far Success w/Tool</b>	<b>Far Attempt w/Tool</b>
<b>Nick</b>	Poke	4.0	3.0	0	0	-----	-----	-----	-----
<b>Chinook</b>	Poke	4.5	0.5	0	0	-----	-----	-----	-----
<b>Gigi</b>	Poke	9.0	1.0	1.0	0.5	-----	-----	-----	-----
<b>Polly</b>	Poke	1	0	0	0	-----	-----	-----	-----
<b>Mandy</b>	Poke	18.5	2	1	0.5	-----	-----	-----	-----
<b>Bria</b>	Poke	4	1.5	2.5	0	-----	-----	-----	-----
<b>Samson</b>	Poke/Rake	13	4	11	0	8	2	0	2
<b>Gimp</b>	Poke/Rake	1	5	3	2	4.5	1	0	3
<b>Magic</b>	Poke/Rake	4	3	1	1	0.5	0.5	0	0
<b>Ajax</b>	Rake	-----	-----	-----	-----	0	0	0	0
<b>Adonis</b>	Rake	-----	-----	-----	-----	0	0	0	0
<b>Skeeter</b>	Rake	-----	-----	-----	-----	0.5	0	0	0
<b>Armond</b>	Rake	-----	-----	-----	-----	21	4	0	1.5
<b>Kareem</b>	Rake	-----	-----	-----	-----	13.5	2.5	0	4.5

\*Highlighted cells are for the two subjects who successfully combined the two tools.

Appendix D. Subject Demographic Information and Scores on the Combine and Alternative Method Indices (M = Mother-reared, N = Nursery-reared, U = Unknown).

<b>Subject</b>	<b>Condition</b>	<b>Sex</b>	<b>Age</b>	<b>Rearing</b>	<b>Combine</b>	<b>Alternative</b>
Nowi	Combine	M	25	N	14	6
Joey	Combine	M	36	U	14	2
Keno	Combine	M	17	M	14	6
Coco	Combine	F	24	N	14	3
Kaya	Combine	F	18	N	14	4
Helga	Combine	F	42	U	13	6
Oreo	Combine	F	21	N	12	8
Becca	Combine	F	17	N	12	6
Kehg	Combine	M	26	M	6	2
Khuta	Combine	M	28	M	6	6
Kiht	Partial	F	19	N	14	12
Kelley	Partial	F	42	U	14	6
Simba	Partial	M	37	U	14	10
Kalioni	Partial	M	16	M	13	6
Alpha	Partial	F	24	M	6	6
Tang	Partial	F	40	U	6	8
Huhni	Partial	M	16	M	6	6
Nahagio	Partial	F	26	N	3	1
Haakid	Partial	M	18	M	3	7
Jake	Partial	M	20	M	2	2
Betty	Alternative	F	34	M	8	6
Josie	Alternative	F	18	M	6	6
Kukui	Alternative	M	24	M	6	6
Michon	Alternative	F	26	M	6	8
Hobbes	Alternative	M	18	N	6	6
Gisoki	Alternative	M	25	M	6	2
Sandy	Alternative	F	36	U	6	2
Krog	Alternative	M	16	M	5	3
Gracie	Alternative	F	16	N	3	2
Tabu	Alternative	M	17	M	2	2
Jane	VideoControl	F	37	U	14	6
Judy	VideoControl	F	40	M	6	6
Sindee	VideoControl	F	9	M	6	6
Bernadette	VideoControl	F	30	N	6	6
Maynard	VideoControl	M	36	U	6	2
Ehsto	VideoControl	M	12	M	6	9
April	VideoControl	F	28	M	5	3
Oscar	VideoControl	M	18	N	5	1
Totoni	VideoControl	M	13	M	4	6
Moose	VideoControl	M	38	U	3	1
Judumi	No Video	M	17	N	14	12
Chechekul	No Video	F	26	N	10	14
Beta	No Video	F	14	M	6	6
Kakaichu	No Video	F	27	M/N	6	10
Huey	No Video	M	18	M	6	4
Pierre	No Video	M	46	M	6	2
Muffin	No Video	F	27	M	5	5
Staun	No Video	M	24	M	5	5
Angie	No Video	F	33	U	2	6
Simon	No Video	M	40	U	2	4

## Appendix E. Description of Statistical Procedures

The following formula was used following Siegel and Castellan (1989) for multiple comparisons between treatments after obtaining a significant Kruskal-Wallis test:

$$\left| \bar{R}_u - \bar{R}_v \right| \geq z_{\alpha/k(k-1)} \sqrt{\frac{N(N-1)}{12} \left( \frac{1}{nu} + \frac{1}{nv} \right)}$$

where  $\left| \bar{R}_u - \bar{R}_v \right|$  is the difference between the average rankings for all pairs of groups and the value of  $z_{\alpha/k(k-1)}$  is the abscissa value from the unit normal distribution above which lies  $\alpha/k(k-1)$  percent of the distribution.

This is the most conservative method. Alternatively multiple Mann-Whitney U tests using bonferroni's correction might be used, leading to the same results:

### Chimpanzee Study:

Those in the Combine-and-Retrieve demonstration scored significantly higher on the combine scale than those in the Video Control (Mann Whitney  $U = 12.5$   $p = 0.003$ ) Control (Mann Whitney  $U = 13.5$   $p = 0.004$ ), or Alternative Method (Mann Whitney  $U = 8.0$   $p = 0.001$ ).

### Child Study:

#### **Combine Index**

Participants who saw the Combine-and-Retrieve demonstration scored significantly higher on the combine scale (Median = 14) than those in the Alternative Method condition (Mann Whitney  $U = 7.00$ ,  $p = 0.0001$ ) and Control conditions ( $U = 0.5$ ,  $p = 0.0001$ ).

#### **Alternative Method Index**

Those in the Alternative Method condition scored higher on the Alternative Method index than those in the Combine-and-Retrieve ( $U = 8.5$ ,  $p = 0.0001$ ), Retrieve-Only ( $U = 11.5$ ,  $p = 0.001$ ), and Control condition ( $U = 3.5$ ,  $p = 0.0001$ ).

Appendix F. Demographic Data and Demonstrator Assignments for Experiment 2.

<b>Subject</b>	<b>Sex</b>	<b>Age</b>	<b>Rearing</b>	<b>Combine Score</b>	<b>Demonstrator</b>
Junie	F	42	U	13	Coco
Rhoda	F	45	U	6	Coco
Mae	F	43	U	12	Coco
Chester	M	12	M	6	Coco
Pacer	M	36	U	6	Coco
Nahja	F	14	N	14	Kiht
Cheopi	F	20	N	14	Kiht
Ahkimel	M	25	N	10	Kiht
Cody	M	18	M	14	Joey
Radar	M	18	M	4	Jane

Appendix G. Participant Age, Sex, and Scores on the Combine and Alternative Method Indexes

<b>Condition</b>	<b>Age</b>	<b>Sex</b>	<b>Combine</b>	<b>Alternative</b>
Combine & Retrieve	30	F	13	8
Combine & Retrieve	31	F	12	2
Combine & Retrieve	34	F	14	4
Combine & Retrieve	37	M	14	4
Combine & Retrieve	38	F	14	4
Combine & Retrieve	39	F	14	6
Combine & Retrieve	44	F	14	2
Combine & Retrieve	45	M	8	2
Combine & Retrieve	45	M	14	10
Combine & Retrieve	52	M	14	2
Combine & Retrieve	52	F	14	2
Alternative Method	30	F	2	8
Alternative Method	31	M	2	10
Alternative Method	34	F	6	10
Alternative Method	38	F	2	8
Alternative Method	39	M	6	14
Alternative Method	41	M	2	14
Alternative Method	41	M	2	14
Alternative Method	42	F	14	4
Alternative Method	43	M	2	14
Alternative Method	49	F	2	14
Alternative Method	53	F	2	14
Retrieve-Only	29	M	2	4
Retrieve-Only	30	M	2	2
Retrieve-Only	31	M	2	10
Retrieve-Only	32	F	10	6
Retrieve-Only	38	M	14	6
Retrieve-Only	39	M	14	8
Retrieve-Only	41	M	2	2
Retrieve-Only	47	M	14	8
Retrieve-Only	52	F	8	4
Retrieve-Only	53	M	14	2
Retrieve-Only	54	F	14	4
Control	29	F	2	2
Control	30	M	2	2
Control	31	F	2	6
Control	31	M	2	2
Control	37	M	6	4
Control	39	M	8	4
Control	42	M	2	2
Control	46	F	2	2
Control	50	M	2	2
Control	51	F	2	6
Control	54	F	6	4

## Appendix H. Sample Head Teacher Letters and Parental Consent Forms

To the Head Teacher / Playgroup Leader:

### **A study of tool use in young children**

Financed by the Overseas Research Award Scheme and the School of Psychology, University of St. Andrews, we are beginning a study in nurseries and playgroups of how young children learn how to make tools. We would like to include two to four year old children in your nursery and I am writing to ask for your permission to come and discuss this with you.

The aim of the project is to understand how children begin to learn how to construct and use tools. We are interested in how much children rely on watching others to learn about tools, as opposed to their own individual exploration. Each session will only take a few minutes and is designed to be like a game so that the children will enjoy the experience. The study is divided into two phases. First, the child will watch a short video clip of another child constructing a tool and retrieving a sticker out of a box. The child will then be given with the opportunity to play with the tool parts herself in order to retrieve a sticker. Next, a few days later, the child will be presented with the same task. This time we will make it possible to retrieve the sticker without constructing a tool to see if this has an effect on whether or not the child still builds the tool. All children will be provided with a sticker at the end of the session if they have not successfully retrieved one.

Each session would be video-taped to allow us to analyse the data later. These tapes will be kept securely and will be erased after publication. Should we ever wish to show video clips at a conference to illustrate the results, we confirm that we shall only do so after consultation with the parents concerned. The children's participation will be treated with complete confidentiality and only we will have knowledge of his/her individual performance. All work will be carried out by myself, Elizabeth Price, and I have been subject to a successful police check (Enhanced Disclosure Scotland). The research has also been cleared by the University Teaching and Research Ethics Committee.

I hope you will feel able to help. I enclose copies of a letter and consent form for parents. At the end of the project, we shall provide a written report and be happy to offer a verbal one too. I look forward to hearing from you.

Yours sincerely,

Elizabeth Price and Andrew Whiten  
Contact: ep98@st-andrews.ac.uk

# PARENTAL CONSENT FORM

**Project Title**

*Social Learning of Tool Construction in Children*

**Researcher(s) Name(s)**

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**Consent**

The purpose of this form is to ensure that you are willing for your child to take part in this study and to let you understand what it entails. Signing this form does not commit you to anything you do not wish to do and you are free to withdraw at any stage.

I hereby give my consent for my child to be included in this study. I understand that I or my child can withdraw at any point. I understand that names of participating children will be held confidentially at the University of St. Andrews, and that anonymity will be preserved in ensuing publications.  Yes  No

I hereby give my consent for my child to be videotaped. I understand that all tapes will be wiped following publication. If researchers wish to show video clips at conferences that include my child, this will only proceed with my written permission.  Yes  No

I am willing to be contacted at a later date if my child's videoed image is to be used.  Yes  No

I would like more information. Please contact me at (email or phone number):

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**Name in Block Capitals** \_\_\_\_\_

**Signature** \_\_\_\_\_

**Date** \_\_\_\_\_

### Appendix I. Raven Subject Demographic Information

(DOB = Date of birth, HR = hand-reared; PR = parent-reared)

Subject	Sex	DOB	Rearing	Housing	Study
Ilias	M	16/03/2004	Wild born, HR	KLRS, with Columbo	Study 1 & 2
Columbo	F	19/03/2004	Zoo Born, HR	KLRS, with Ilias	Study 2
Lo	M	12/03/2004	Zoo born, HR	Wels Zoo, with Thea	Study 1
Thea	F	16/3/2004	Wild born, HR	Wels Zoo, with Lo	Study 1
Hugin	M	1995	Zoo born, HR	KLRS, with Dora	Study 1
Dora	F	12/03/2004	Zoo born, HR	KLRS, with Hugin	Study 1
Nemo	M	19/03/2004	Zoo born, HR	KLRS, with Gwaihir*	Study 1
Rumo	M	21/03/2008	Wild born, HR	KLRS with 3 Juveniles	Study 1 & 2
Jörg	M	21/03/2008	Wild born, HR	KLRS with 3 Juveniles	Study 1 & 2
Mojo	F	21/03/2008	Wild born, HR	KLRS with 3 Juveniles	Study 1 & 2
Pia	F	21/03/2008	Wild born, HR	KLRS with 3 Juveniles	Study 1 & 2
Manon	F	1990	Wild born	Edinburgh Zoo	Pilot and Model for Study 2
Hugo	M	2003	Zoo born PR	Edinburgh Zoo	Pilot and Study 2

\* Nemo's mate was removed during her trials, after which time she resided alone.

