INVESTIGATING SUCCESS BIASED TRANSMISSION, AND LONG-TERM MEMORY CAPABILITIES, IN CHIMPANZEES AND CHILDREN: IMPLICATIONS FOR CUMULATIVE CULTURE.

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Abstract

Cumulative culture denotes the arguably human capacity to build on the developments of our predecessors. Factors such as imitation, teaching and cultural transmission biases have been identified as important for cumulative culture. In this thesis factors with implications for cumulative culture were investigated in chimpanzees and 4-to 5-year old children. Two experiments were designed to assess success biased copying in chimpanzees (and children) and a third study investigated chimpanzees' retention and transfer of complex tool use skills. Information pertaining to success derived from others' performances influenced both chimpanzees and children's subsequent actions during a video based foraging task and token exchange task. Specifically, some of the first evidence for public information use and payoff biased transmission was documented in both species and thus suggests that a lack of such assessment abilities does not underlie the lack of cumulative culture in chimpanzees. In the final empirical study, some of the first evidence for appreciable long-term memory and improvements in the utility of complex tool manufacture was documented in chimpanzees. High fidelity retention of (socially) learned information is important for cumulative culture, where behaviour must be retained with sufficient fidelity for it to be reproduced. This is especially so where, for example, tool use is required to access temporally rare resources (e.g. nuts falling certain months of the year/seasonal resources).

INVESTIGATING SUCCESS BIASED TRANSMISSION, AND LONG-TERM MEMORY CAPABILITIES, IN CHIMPANZEES AND CHILDREN: IMPLICATIONS FOR CUMULATIVE CULTURE.

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Table of Contents

Declaration

This thesis is of my own original work and has not been submitted for any other award than stated above. Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature.

This work was completed under the guidance of Dr Rachel Kendal and Dr Emma Flynn, Durham University.

Copyright

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This thesis is dedicated to the late Kelley (chimpanzee) and Frankie Blacklock (human)

Chapter I

Introduction

Humans exemplify what it is to be social. The pinnacle of our social and cultural adaptations is the capacity for cumulative culture; an amalgamation of new and old thought that has crucially enabled culture to evolve with adaptive significance to our species (Mesoudi, 2011). The progressive nature of our culture is evident in the technological, medical and scientific knowledge humans possess today. This ability to build upon the achievements of one's forbearers appears to be restricted to *Homo sapiens,* but, the reasons why other animals, arguably, lack cumulative culture (e.g. Galef, 1992; Tennie, Call, & Tomasello, 2009) are not yet well understood. Theoretical accounts have predicted that the processes and mechanisms underpinning cumulative culture are manifold, yet, empirical investigation of many of these attributes across species remains in its early infancy.

In driving cumulative culture, particular emphasis has been placed upon innovation (beneficial modification to cultural traits required for cultural progression) and complex social learning mechanisms (imitation and teaching allowing the propagation and maintenance of cultural variants; Tomasello, 1999). The propagation of adaptive innovations is, of course, a defining feature of this cumulative process; however, other factors are also involved (Dean, Vale, Laland, Flynn, & Kendal, in press; Laland, 2004; Tomasello, 1999). In this thesis, the cognitive basis of cumulative culture, above and beyond innovation and social learning mechanisms, was investigated. Cognitive and social factors with implications for a species' cultural complexity were investigated in two primate species; humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) through investigation of: (i) success based social information use, (ii) payoff biased copying (a cultural transmission bias), and (iii) long-term memory capabilities in chimpanzees. Where possible 4-to 5-year old children participated as a comparison group. As the specific forms of success and payoff based social information use investigated in this thesis were previously undocumented in children, it was of independent interest to explore this unchartered territory. The similarity of experimental procedures employed with children and chimpanzees allowed similarities and differences in their socio-cognitive architecture to be identified to shed light on attributes important for these species' cumulative cultural capability.

Before turning to the empirical research, presented as stand-alone published/to-be-published papers, the proceeding section clarifies and introduces common terms, themes and experimental methods appearing in this thesis. First, as this thesis considers payoff and success based social information use, the main terminology and concepts pertaining to the literature of cultural transmission biases (encompassing payoff and success copying strategies) are outlined. As cultural transmission biases are reliant upon social learning, different forms of social learning mechanisms and processes are then outlined and defined. Finally, long-term memory is briefly considered. In the light of many of these themes being expanded upon in the following chapters, the proceeding section provides only a brief overview of pertinent concepts and their relevance to cumulative culture.

Cultural Transmission Biases

As noted, why humans possess sophisticated cultural variants unseen in the broader animal kingdom remains a challenging question (Lewis & Laland, 2012) . The first step towards answering this question is to understand cultural transmission (Cavalli-Sforza & Feldman, 1981). One area of interest in this regard has been the study of cultural transmission biases (also termed social learning strategies), that influence the spread of cultural variants and innovations (Henrich, 2001; Laland, 2004; Rendell, Fogarty, Hoppitt, Morgan, Webster & Laland, 2011). Transmission biases denote evolved heuristics that aid copying decisions by isolating when it is advantageous to copy others and by directing copying events towards beneficial behaviour and information (Henrich & McElreath, 2007; McElreath, Bell, Efferson, Lubell, Richerson & Waring, 2008). Transmission biases are predicted to be adaptive since they can protect against an overreliance on social learning leading to outdated and unreliable information (Laland, 2004; Rogers, 1988) and as they reduce the heavy cognitive load that can otherwise occur through gathering and processing large amounts of social information (i.e. if multifarious trait contents are sampled and assessed) or extensive use of trial and error learning (Henrich & McElreath, 2007).

Various classifications for transmission biases have been proposed. Strategies have been delineated into those relating to ‘whom’ one should copy, ‘when’ one should copy and ‘what’ to copy (Laland, 2004; Mesoudi & Whiten, 2008). This latter class of ‘what’ strategies are variously also known as ‘content’ or ‘direct’ biases since copying is influenced by a feature of the cultural variant itself rather than, for instance, an attribute of the person being copied (an ‘indirect’ bias: Boyd & Richerson, 1985; Rendell et al., 2011). For example, individuals may be biased towards attending to and copying information congruent, rather than incongruent, to previously held beliefs (Henrich & McElreath, 2007). This example is similar to, and in some cases could be mediated by, confirmation bias in which preferred information is that which confirms current beliefs.

‘Who’ strategies refer to heuristics based on particulars of potential models (‘model based biases’, an ‘indirect’ bias), also noted, in early classifications, to include frequency dependent copying strategies such as ‘copy the majority’ (Laland, 2004; Mesoudi & Whiten, 2008a). More recently, ‘when’ one should copy (‘state dependent biases’), ‘who’ one should copy (model biases) and ‘frequency dependent biases’ (e.g., ‘copy the majority’) have been classified as divisions encompassed under the broad label of ‘context’ biases (Rendell et al., 2011). Context biases are known as ‘indirect’ biases (Boyd & Richerson, 1985) as they are not based on trait content but on attributes of potential models (e.g. copy successful individuals: Mesoudi, 2008), trait frequencies (e.g. copy traits increasing in frequency: Toelch, Bruce, Meeus, & Reader, 2010) or states of the observer (e.g. copy when personal information is outdated, unreliable, or when uncertain: Kendal, Coolen, & Laland, 2009). Much of the research effort concerning transmission biases has focused on these context biases. For example, humans learn from prestigious (Henrich & Henrich, 2010), knowledgeable (Henrich & Broesch, 2011) and successful models (Wisdom & Goldstone, 2010), allowing selective learning from models likely to bear beneficial information (Henrich & Broesch, 2011). Such success biased strategies are well positioned to facilitate cumulative culture, through filtering out potentially poor models that may possess suboptimal, fitness-neutral or maladaptive behaviour. In particular, payoff biased copying, in which copying is dependent upon ‘direct’ performance proxies (payoffs), should promote behavioural improvement in populations. This is because payoff biased copying constitutes a more direct form of copying than other model based biases (e.g. copy older, successful or dominant individuals) as payoffs that relate to specific behaviours are sampled rather than general model characteristics. Interestingly, payoff biased copying rules have been termed both ‘indirect’ and ‘direct’ forms of biased copying (Kendal, Rendell, Pike & Laland, 2009; Rendell et al., 2011). As payoff biased copying is dependent upon the payoff to trait and not the trait content itself, in this thesis payoff copying is considered an ‘indirect’ bias. Nevertheless, payoff copying is considered a more direct form of copying than general success copying.

One of the main concepts investigated in this thesis is success and payoff biased social information use. As cultural transmission biases are discussed in greater detail in the forthcoming chapters, this next section now turns to a brief and non-exhaustive outline of social learning mechanisms and processes; prerequisites for transmission biases.

Social Learning Mechanisms: The ‘How’

Cultural transmission biases require a capability to socially transmit information between organisms; to be selective in copying one first requires social learning capabilities. In this thesis, the question of whether social learning is selectively employed according to behavioural success and payoffs was investigated (Chapters III and VI), but not underpinning social learning mechanism. Nevertheless, there is discussion of social learning mechanisms and processes throughout the thesis and thus, in this section social learning mechanisms are briefly defined, drawing upon the recent and comprehensive classification provided by Hoppitt and Laland (2008) (see also Heyes, 1994; Whiten & Ham, 1992).

Social learning is broadly taken to denote altered behaviour that results from exposure to another organism or its behavioural outcome (Heyes, 1994). In the past century, considerable research effort has been devoted to animal social learning mechanisms. This has led to the classification of a considerable number of social learning mechanisms and processes. These include local enhancement, stimulus enhancement, social facilitation, response facilitation, emulation and imitation (Hoppitt & Laland, 2008), which are now defined.

Many cases of animal learning are parsimoniously explained by facilitation and enhancement processes (Galef, 1992). In, perhaps, their simplest form, an elicited action can occur due to the simple presence of other organisms; termed social facilitation (Zajonc, 1965). Social facilitation has been documented in male zebra finch (*Taeniopygia guttata)*, who produce more song when in proximity of conspecifics than when alone (Jesse & Riebel, 2012). Similarly, capuchin monkeys have been shown to consume novel food faster, and eat more, when conspecifics were present, compared to when alone (Visalberghi & Addessi, 2000). Response facilitation can involve a similar arousal affect, but a response by an organism serves to promote a comparable end response in the observer (Byrne, 1994). This has been shown in domestic fowl (*Gallus gallus domesticus*), for whom the act of preening encouraged conspecific preening engagement (Hoppitt, Blackburn, & Laland, 2007). Thus, the presence of others, either engaging in the same activity (response facilitation) as the observers or not (social facilitation), can influence observer's activity levels.

Enhancement processes include the presence of an organism at a particular space in the environment increasing the chance that an observer, too, will visit this space (Thorpe, 1956). This, termed local enhancement, may occur through aggregation or attraction to locations via other organism's presence (Hoppitt & Laland, 2008). There are numerous examples of animals using other organisms as location cues, with birds (Midford, Hailman, & Woolfenden, 2000), primates (King, 1994), fish (Laland & Williams, 1997; Webster & Laland, 2012) and rats (Laland & Plotkin, 1993) all demonstrating local enhancement effects. Enhancement processes can also be directed towards specific stimuli rather than location. This, termed stimulus enhancement, is said to occur when an organism's interaction with a stimulus increases the likelihood that the observer then interacts with the stimuli (Heyes, 1994; Spence, 1937). Like local enhancement, there are numerous documented cases of stimulus enhancement in animals. Japanese quail (*Coturnix coturnix japonica*), for example, have been shown to reverse their preferred choice of male mating partner after viewing a conspecific female interact with an un-preferred male; an effect observed when the two males switched locations (controlling for local enhancement) (Galef & White, 1998; White & Galef, 1999).

Cumulative culture - in allowing complex traits to diffuse within populations and preserve across generations - requires high fidelity trait transmission; specifically imitation and teaching (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Tomasello, 1999). Accordingly, researchers have been interested in the question of whether other species teach and, particularly in chimpanzees, whether they imitate (Horner & Whiten, 2005; Tennie, Call, & Tomasello, 2012; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Imitation is posited to differ from other social learning processes in that it requires the copying of behavioural acts, while other forms of social learning relate to social information regarding environmental features such as food/object locations or pertinent stimuli (Heyes, 1994). While there is evidence to suggest that chimpanzees are capable of imitation (Whiten, 1998; Whiten et al., 2009), they may principally rely upon less exact copying mechanisms (Tennie et al., 2009; Tennie et al., 2012). One such mechanism is emulation. Emulation is a term used to describe the reproduction of the *results* of demonstrator actions (Hoppitt & Laland, 2008; Tomasello, 1990; 1996; Call & Carpenter, 2002). That is, upon observing a con- or hetero-specific's effect on a feature of the environment, observers recreate the observed affect without replicating behavioural movements (Tomasello, 1998). Three forms of emulation have been distinguished; termed affordance learning, end-state emulation and object movement re-enactment (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Specifically, affordance learning captures occurrences of identifying how things work (material properties) by observing others; object movement re-enactment refers to the copying of conspecific object movements (and not bodily movements which would constitiute imitation); and end-state emulation captures the re-recreation of a conspecific's actions end state (Whiten et al., 2009). Evidence suggests that chimpanzees may opt for emulative, over imitative copying but depending upon context (Horner & Whiten, 2005).

Considerable research effort has been given to determining social learning mechanisms in chimpanzees. Now it is established that chimpanzees are social learners (e.g. Horner & Whiten, 2005), it is important to investigate other factors that have implications for their cultural progress. As noted above, one such factor is copying heuristics that can promote the propagation of *efficient* behaviour as opposed to copying just *any* information (reviewed in Rendell et al., 2011). A second yet often overlooked factor with implications for a species extent of cultural complexity is long-term memory (LTM), which is now discussed.

Long-Term Memory

For social learning to occur, organisms require various forms of memory to encode and retain observed behaviour long enough to respond to social information. Some forms of social learning processes likely require only limited memory. The elicitation of pronounced activity in the presence of others (social facilitation), for example, is likely to impose very little, if any, memory demands above processing sensory information. However, other social learning mechanisms that allow the propagation of complex behaviours and their results require encoding and storage of social information. Also, functional definitions of social learning require a delay between observation and a learners' matching behaviour. Indeed, even stimulus and local enhancement require memory upon an observed organism ceasing interaction with a specific stimuli or presence at a location. Learning, whether social or asocial (individual trial and error learning), requires memory.

For cumulative culture, two aspects of memory are likely important. First, memory capacity, that dictates the level of complexity of information an organism encodes and stores, is crucial for, and a potentially constraining feature of, the level of cultural trait complexity and cultural breadth in a population. Second, the length of time information is stored, is crucial for retaining a cultural trait in a population long enough for transmission to occur and to prevent cultural loss. In both cases, LTM is essential; LTM enables large amounts of information to be stored and for long periods (Wood, Baxter, & Belpaeme, 2012). Significant LTM capabilities should support large cultural repertoires by increasing the amount of information that can be stored as well as for how long. This contrasts with working memory that stores small amounts, or chucks, of visual and auditory information transiently (Baddeley, 1992; Cowan, 2001; Miller, 1956). In considering factors that have implications for a species cultural complexity, it is therefore important that memory capabilities are investigated (Vale, Flynn & Kendal, 2012).

Overview of General Methods

When investigating cognitive and social factors with implications for cumulative culture, chimpanzees, in particular, are of interest. This is not only because of their shared ancestry with humans, but because they possess a rich culture (Whiten et al., 1999) and are capable of social learning (Hopper et al., 2007; Horner & Whiten, 2005; Whiten, 1998; Whiten, Custance, Gomez, Teixidor, & Bard, 1996; Whiten et al., 2007) and innovation (Reader & Laland, 2002). This raises the question of why chimpanzees, who are capable of acquiring information socially, culminating in diverse cultures (Whiten et al., 1999), appear to be restricted in their capacity for cumulative culture. This thesis was designed to shed light on this question.

Work on social learning strategies highlights the key role that contextual factors and trait content plays in the use of social or asocial information (Rendell et al., 2011). The experiments in this thesis investigate public information use, payoff biased learning, and tool manufacture retention in very specific, controlled settings with captive chimpanzees and in Western children tested within a learning environment (primary schools). Although the comparative approach can provide an important first step in determining what makes humans unique (with comparisons across broader phylogenies allowing evolutionary convergences and divergences to be identified), the use of captive animals has its limitations. Specifically, it has been argued that issues arise when generalising beyond one’s sample since developmental differences experienced by captive and wild animals can yield different cognitive abilities (i.e. captive chimpanzees may not display species typical traits and abilities: Boesch, 2007). Note that the same issue has been postulated to arise when generalising from Western samples to the larger human population (Boesch, 2007). Thus, caution is required when generalising the present results to larger human and chimpanzee populations. The findings presented in this thesis should be viewed as ancillary and supplementary to data derived from the wild, yet essential to uncover underpinning social and cognitive attributes that may otherwise be intractable from observational studies conducted in natural settings (see Tomasello & Call, 2008 for discussion).

Boesch (2007) recognises that controlled experiments are ‘preferable’ when underlying variables responsible for observed behaviour are difficult to pinpoint in the wild. The investigation of social learning and transmission biases constitutes one such case, since, in the wild it is difficult to separate social from personal information use and to isolate learning strategies without manipulating factors such as model attributes (e.g. to test for age/dominance dependent copying strategies) and payoffs (to test for success and payoff biases). Accordingly, the tight experimental control afforded by experimental studies, often unachievable in the wild, is often *necessary* to identify the cognitive and social attributes. Boesch (2007) posits that in such examples, valid cross-species comparison requires the presentation of closely matched experimental conditions to both samples. To this end, in the comparative studies presented in this thesis, experimental protocols were as equivalent as possible (e.g. demonstrators for each species were their conspecifics; similar or versions of the same apparatus were used with each species). Experimental differences included the use of stickers for children and food for chimpanzees and a reduction of task durations to maintain motivation in children. These differences reflect what

Tomasello and Call (2008) describe as necessary changes to accommodate species' differences in motivation that have functional equivalence (i.e. ethical considerations of providing food rewards to children for 30 minutes and chimpanzees' low, if not, absent motivation for stickers, requires different reward use with similar motivating qualities across species). In sum, the experimental protocols in this thesis allowed valid cross-species comparisons to be made, which are of interest for the identification of species differences or similarities in cognitive and social attributes.

In this thesis, comparisons are drawn between adult chimpanzees and human children. Again, this method has its limitations (e.g. biasing results towards older chimpanzees), yet, should be considered beneficial in some cases. For example, as Nielsen (2009) highlights, the absence of cognitive or socio-cognitive attributes in juvenile chimpanzees does not predict that they are absent in older individuals. With the question of human uniqueness in mind, early investigation, therefore, benefits from first establishing whether species are capable of certain tasks prior to the establishment of when developmentally they arise (Nielsen, 2009). As success and payoff biased copying had previously not been established in chimpanzees, it was justifiable to first test these capabilities in adult chimpanzees. Conversely, as these copying rules had been established in human adults (Mesoudi, 2011; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012), it became of interest to establish whether children too display such capabilities (taking a developmental stance). Justification for comparing children and adult chimpanzees can additionally, and reasonably, be inferred when experiments are particularly easy for adult humans. This would seem the case for the public information study (Chapter III below), which requires a simple determination of differential feeding rates to inform resource selections. In such cases it may be assumed that more scientific gain results from investigation with children whose capabilities may be constrained by development. In this thesis, success biased learning is investigated in 4-to 5-year old children. Children of this age were of interest as they have been shown to be capable of cumulative cultural learning (Dean, Kendal, Schapiro, Thierry & Laland, 2012).

Aim and Thesis Structure

The aim of this thesis is to shed light upon factors important for cumulative culture, with focus given to chimpanzees and children. Chapter II begins by reviewing current empirical and theoretical findings relating to cumulative culture, taking a comparative stance. In this chapter, various factors thought to contribute to whether species' can, or cannot, build upon the cultural developments of past generations are reviewed, including social learning strategies. Chapter III marks the beginning of the empirical investigations, starting with the question of whether chimpanzees and 5-year old children are capable of differentiating a 'resource rich' from a 'resource poor' task box by monitoring the foraging performance of a conspecific (public information use). Evidence for public information use was documented in both chimpanzees and children, who used the graded foraging success (rate of food consumption) of a demonstrator to select the rich resource. Chapter IV, investigates success biased copying in greater detail, with focus given to whether payoff biased copying rules are employed by chimpanzees and 4-to 5-year old children to maximize reward gain. This large scale, group based, comparative study found evidence for use of a more sophisticated payoff biased copying rule in chimpanzees than in children, albeit, children were quicker to implement a copying rule, requiring less social learning opportunities. In Chapter V, the final empirical paper investigates chimpanzees' ability to recall and transfer complex tool behaviour following a 3.6 year hiatus between the initial learning event and re-test. Despite the significant imposed delay, chimpanzees retained specific tool use methods which were generalized to a similar but novel task. Finally, in Chapter VI the findings of all three empirical studies are discussed in detail with regard to their implications for cumulative culture, particularly in chimpanzees. Possible directions for future research are also provided in this chapter.

This thesis is presented in publication format. Each empirical chapter therefore includes a separate introduction, method, results, discussion and reference section. The status of publication is indicated in each chapter (excluding Chapter VI containing the general discussion).

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Chapter II

Human cumulative culture: a comparative perspective

This chapter reviews the theoretical and empirical evidence concerning cumulative culture in both human and nonhuman animals. The proceeding work has been accepted in *Biological Reviews* and is currently in press. Authorship is stated below. I, and Lewis Dean, contributed equally to the manuscript.

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Abstract

Many animals exhibit social learning and behavioural traditions, but human culture exhibits unparalleled complexity and diversity, and is unambiguously cumulative in character. These similarities and differences have spawned a debate over whether animal traditions and human culture are reliant on homologous or analogous psychological processes. Human cumulative culture combines high-fidelity transmission of cultural knowledge with beneficial modifications to generate a ‘ratcheting’ in technological complexity, leading to the development of traits far more complex than one individual could invent alone. Claims have been made for cumulative culture in several species of animals, including chimpanzees, orangutans and New Caledonian crows, but these remain contentious. Whilst initial work on the topic of cumulative culture was largely theoretical, employing mathematical methods developed by population biologists, in recent years researchers from a wide range of disciplines, including psychology, biology, economics, biological anthropology, linguistics and archaeology, have turned their attention to the experimental investigation of cumulative culture. We review this literature, highlighting advances made in understanding the underlying processes of cumulative culture and emphasising areas of agreement and disagreement amongst investigators in separate fields.

How is culture ‘cumulative’?

On 20th July 1969 Neil Armstrong spoke the immortal words, “That’s one small step for man, one giant leap for mankind”. Landing the Eagle lunar module on the moon was a huge achievement for humanity, but it was one that resulted from a series of many small steps. This crowning achievement of human endeavour was not planned and devised by Armstrong alone, but by a huge team, deploying ballistics, electronics, materials science and radio communication technologies reliant on theoretical and experimental research carried out over several centuries. Whilst the achievement of individual scientists and engineers may be ground-breaking, technological progress virtually always depends upon the work that goes before it.

The focus of this review is cumulative culture, the ability of humans to ratchet up the complexity of cultural traits over time. The example of the Apollo mission demonstrates that humans are able to increase the complexity of their technology and knowledge over many episodes of social transmission, by building on the developments of their predecessors. This ratcheting up in the complexity of cultural traits, frequently across multiple generations, has been proposed to be the hallmark of human culture (Enquist & Ghirlanda; Mesoudi, 2011; Richerson & Boyd, 2005), but the cognitive and social processes upon which it relies remain poorly understood. Here a comparative perspective is potentially informative. While claims have been made that certain animals possess cumulative culture in rudimentary form, these are disputed and the human capacity for cumulative culture is clearly unparalleled in the animal kingdom. The question of what underlies this difference in human and animal cultures was featured in *Science* magazine’s ("So much more to know," 2005) list of 125 things we don’t know that we need to, as the answer to this question has far-reaching implications for how we view our place in nature.

Herein we review the current theoretical and empirical evidence addressing cumulative culture in both human and non-human animals. In doing so, we explore how human culture differs from non-human culture, before turning to the potential social and cognitive processes that may hold the key to our species’ unique cumulative cultural capability.

Culture in animals

Defining culture. The term ‘culture’ is used by researchers from a broad range of disciplines, including biology, psychology, archaeology, and social and biological anthropology, with each discipline drawing on different epistemological and ontological assumptions. As Sterelny (2009) points out, these different definitions of culture are not stipulative, they are hypothesis-choosing. Thus, through formulating a definition, researchers have determined their focus, thereby limiting both what is investigated and how it is investigated. Using different definitions, the focus of the study of culture can cover over 11,000 species (Lumsden & Wilson, 1981) or be restricted to humans (Kroeber & Kluckhorn, 1952). The definitions ascribed to culture can impose constraints on which learning processes are deemed to underlie culture [e.g. “Culture is information capable of affecting individuals’ phenotypes, which they acquire from other conspecifics by teaching or imitation” (Boyd & Richerson, 1985, page 33)]. Moreover, the definition also dictates whether culture is treated as the physical expression of specific behaviour patterns (van Schaik et al.,

2003) or as the ideas and beliefs which lie behind behaviour patterns (D'Andrade, 2008).

Here, our primary agenda is to compare the cultural capabilities of humans and other animals, and accordingly we adopt a definition that lends itself to this objective. Following Laland & Hoppitt (2003), we define culture as “group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information”. This established, we now consider what is known about culture in non-human animals.

The animal culture debate

Alongside the alternative definitions that different researchers apply to culture, there are also disagreements about the quality of the evidence necessary for a given species to be deemed ‘cultural’ (Galef, 1992; Laland & Galef, 2009; Laland & Hoppitt, 2003). For instance, Lefebvre & Palameta (1988) summarise nearly 100 reports of traditional behavioural patterns in animal species, including mammals, birds and fish, suggesting that animal traditions are taxonomically widespread. Although these authors did not classify these phenomena as ‘culture’, to the extent that the observation of a tradition can be regarded as evidence for social transmission, these species are potentially candidates for animal culture. However, it is difficult to establish unequivocally that social transmission underlies natural diffusions and inter-population behavioural variation, since individual animals might independently have been shaped by ecological conditions to perform the focal behaviour. For this reason, some researchers seek additional evidence that natural traditions are socially transmitted, for instance, relying on translocation experiments or careful analyses of the development of the behaviour. In reviewing field experiments, Reader & Biro (2010) concluded that social learning has been unequivocally demonstrated in 20 different species in the wild, including in honeybees, birds and mammals, and across a range of contexts, including foraging, predator avoidance and habitat choice. Whilst these experiments do not necessarily test whether the behaviour patterns are group typical, they do establish that the relevant information is socially transmitted. However, given that many hundreds of species of animals have been shown to be capable of social learning through experiments in captivity, this list almost certainly substantially underestimates the extent of natural animal tradition.

Primatologists Whiten & van Schaik (2007) restrict culture to those species with traditions in at least two different behavioural domains, specifically chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.) and white-faced capuchin monkeys (*Cebus capucinus*). Whiten et al. (1999) gathered data from seven long-term chimpanzee field sites providing evidence for 39 behaviour patterns judged to be cultural by field workers, including food-processing techniques, such as nut-cracking, methods of parasite inspection, and social customs, such as hand-clasp grooming. Likewise, orangutans have been proposed to show 24 social and foraging traits (van Schaik et al., 2003), while foraging traditions have been documented in white-faced capuchins (Panger et al., 2002), as have social games (Perry et al., 2003- detailed in section IV.3.b). Thus, although Whiten & van Schaik (2007) argue that culture is not unique to humans, they argue that there is only evidence of culture in primates.

These claims have been criticised by other researchers concerned that the reports of culture in primates are based upon purely observational studies, with no experimental evidence that the behavioural variation is indeed a result of socially transmitted information and not some other factor (Galef, 1992; Laland & Hoppitt, 2003; Tomasello, 1994). While such experimental procedures are available (e.g. manipulations in which individuals are experimentally transferred between populations, or populations are transferred between sites), and have been applied to some fish species (Helfman & Schultz, 1984; Warner, 1988), they are not feasible for primates. More recently, less disruptive methods have been developed for identifying social learning in the field (Kendal, Galef, & van Schaik, 2010; Laland, Kendal, & Kendal, 2009).

These examples illustrate that even amongst researchers who argue that animals have culture, there is disagreement on how widespread culture is. As these arguments are fully expanded elsewhere (e.g. Laland & Galef, 2009), we turn to the specific focus of this review, that of cumulative culture.

Cumulative culture

The idea of cumulative culture is integral to the work of cultural evolutionists (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981), who have developed mathematical models, based on those used in evolutionary biology, to examine how cultural innovations are introduced and spread within a population. Whilst this work was primarily focussed on culture in humans, other researchers have been interested in a comparative approach to culture. Comparative psychologist Michael Tomasello coined a metaphor commonly used to illustrate cumulative culture, that of the ‘ratchet’ (Tomasello, 1994). Tomasello argued that loss of a cultural trait across generations is prevented by high-fidelity information transmission conferred by accurate social learning processes, creating the opportunity for modifications of the cultural trait to be devised, ratcheting up its complexity or efficiency. Over time, repeated modifications result in cultural traits that are too complex to have been invented by a single individual (Tomasello, 1994, 1999; Tomasello, Kruger, & Ratner, 1993). Several researchers have argued that this cultural ‘ratchet’ is a unique feature of human culture (Boyd & Richerson, 1996; Heyes, 1993; Tomasello, 1994; Tomasello, Kruger & Ratner, 1993). Theoretical analyses provide support for the link between high-fidelity transmission mechanisms and cumulative culture: irrespective of the rate of innovation, cumulative culture cannot emerge without accurate transmission (Lewis & Laland, 2012; but see Pradhan, Tennie, & van Schaik, 2012). Pradhan, Tennie & van Schaik (2012) suggested that increased sociability, thus an increase in social-learning opportunity, may be sufficient for cumulative culture to occur, although some researchers argue that high-fidelity transmission is not present in non-humans (Tennie, Call & Tomasello, 2009).

Some researchers have discussed the accumulation of a large number of behavioural traits (e.g. knowledge of different foods) as cumulative culture (van der Post & Hogeweg, 2008). However this accumulation does not necessarily involve modifications over time, or any ratcheting up in complexity or efficiency. Cumulative culture may occur alongside the accumulation of knowledge or behaviour patterns, but there is a key difference between the two. Henceforth, we describe as *accumulation*, the addition of knowledge or behaviour patterns to the behavioural repertoire of an individual or population [akin to ‘step-wise traditions’, as proposed by Tennie et al. (2009)], and restrict use of the phrase *cumulative culture* to the modification, over multiple transmission episodes, of cultural traits (behavioural patterns transmitted through social learning) resulting in an increase in the complexity or efficiency of those traits.

Evidence for Cumulative Culture

Human cumulative culture: Historical evidence

Human culture is clearly cumulative, with innovations being built upon the knowledge of previous generations and ideas from different disciplines and populations combined to formulate new traditions and technologies. Lehman (1947) and Basalla (1988) both documented the invention, refinement and propagation of novel innovations across various technological and academic disciplines (see also: Ziman, 2000). Lehman (1947) found that there had been rapid advancement in the academic fields of chemistry, genetics, geology, mathematics, medicine and public hygiene, education, entomology, botany, philosophy, and operatic and symphonic music. Using historical sources documenting the number of books published or the number of 'outstanding contributions' to a field as judged by several recognised historians, Lehman (1947) demonstrated exponential growth in these fields on an historical timescale (from 1000–1600 AD through to the 20th Century). Although Lehman's (1947) data may be somewhat subjective, he used multiple sources for the definition of an 'outstanding contribution' in a particular field. He illustrates that by building upon previous knowledge, humans accelerated their discovery of knowledge. Indeed he predicted that in the near future this acceleration would continue and mechanisation would become more important and widespread, a prediction that, superficially, appears to be true. While Lehman (1947) did not explicitly examine whether cumulative culture is occurring, it is reasonable to assume that the contributions reviewed are built on previous contributions (Enquist, Ghirlanda, Jarrick, & Wachtmeister, 2008).

Basalla (1988) documents how many innovations, often characterised as invented by ‘geniuses’, are part of a continuum of technological development and application of old technology to new areas. For example, Whitney’s cotton gin, which was patented in 1794 and was used to separate short staple cotton from pods, built upon a long line of Indian charkhi machines that had separated long staple cotton from pods, and other agricultural and milling machinery that was available at the time. Similarly, when Guglielmo Marconi received a Nobel Prize in 1909 for transmitting radio signals across the English Channel and the Atlantic Ocean he had built upon, and applied, the pioneering research of physicists such as Hertz and Righi (Basalla, 1988).

Whilst these historical sources illustrate that human culture is cumulative, with notable inventions building on the ideas of others, they do not provide experimental evidence of cumulative modifications to cultural traits.

Empirical research

Several researchers have investigated cumulative modifications to behavioural traits using artificial 'generations' in the laboratory. In these diffusion chain experiments, participants take part in a task in series; thus the first participant will act as demonstrator to the second participant, who will in turn act as demonstrator to the third participant and so forth (see Mesoudi & Whiten, 2008 for a review).

Kirby, Cornish & Smith (2008) set up a diffusion chain experiment in which novel words (sequences of lower-case letters) were paired with coloured shapes with an arrow indicating a movement pattern. Individuals were trained with a set of shape/movement and word pairs. They were then tested, having to write down the words paired with both previously seen shapes/movements and, unknown to the participant, unseen shapes/movements. As mistakes in recall of shape/movement and word pairs were made across 'generations' in the experiment, the artificial language became less diverse with an accompanying reduction in transmission errors. Indeed, in some chains transmission errors were reduced to zero as languages increased not in complexity but in ‘learnability’. Over the course of the experiment, the structure of the ‘language’ increased, with words for each colour and each movement type increasing in similarity. This increase in structure, the authors suggest, was the reason why the language was transmitted with fewer copying errors. They also argue that the increased structure, representing an increasingly efficient artificial language by the end of the experiment, represents cumulative improvement in the trait.

Also using a transmission chain design, Flynn (2008) presented children with puzzle boxes in which a reward was held in place by a series of defences. Children received an initial demonstration containing both task-irrelevant actions (which had no bearing on gaining the reward) and task-relevant actions (which allowed reward retrieval). The aim was to assess whether children would copy both the functional and non-functional actions, or whether the irrelevant actions would be filtered out gradually along the diffusion chain. Flynn (2008) found that children did parse out task-irrelevant actions, often quite early in the diffusion chains. Thus the technique that the children employed was gradually modified across the laboratory ‘generations’, creating a more efficient means to gain the reward. Flynn (2008) argues that this modification of the procedure represents a cumulative improvement in efficiency and, therefore, a cumulative cultural process.

Much of the laboratory-based evidence concerning cumulative increases in the complexity of human (simple) technologies was provided by Caldwell (Caldwell & Millen, 2008; Caldwell & Millen, 2010a). Experimental micro-populations were set simple tasks, such as making paper aeroplanes or constructing towers with uncooked spaghetti and plasticine. Participants were told the aim was to build a plane that flew as far as possible or a tower that was as tall as possible. By using overlapping laboratory generations in the population, of variously two to four individuals, they were able to expose naïve individuals to skilled individuals. Using this ‘micro-society’ replacement design, they found that over 'generations' the performance of the technology (the mean distance flown by a plane or the mean height of a tower) increased. Designs within chains were more similar than those between chains, suggesting the formation of traditions, with individuals learning socially about design aspects of the technology.

A striking finding was that the level of conservatism of design was higher when pay-offs were less predictable (Caldwell & Millen, 2010a). In this experiment there were two measuring protocols; in one condition spaghetti towers were measured immediately upon completion, whilst in a second condition the towers were measured five minutes after completion and following their transfer to a table upon which was a desk fan. The increase in uncertainty about whether the tower would remain standing in the breeze from the fan decreased the amount of modification made to designs over the chain compared to towers that were measured immediately, raising the possibility that in more risky situations the ratcheting up of cumulative cultural traits may be hindered.

Caldwell & Millen (2009) applied the transmission chain design to examine the mechanisms underlying cumulative changes in cultural traits, in this case making paper aeroplanes. Participants were assigned to one of several conditions in which they could gain information through different mechanisms, by observing others construct planes (imitation), teaching, and seeing the planes others had made (emulation), or a combination of these mechanisms. They found that any one of these mechanisms was sufficient to elicit a cumulative improvement over the laboratory generations. It remains to be seen whether this pattern is characteristic of multiple tasks, particularly more complex tasks. Plausibly, high-fidelity information transmission (e.g. as is potentially facilitated by language, teaching or imitation) might be necessary for the transmission of more complicated technology.

The empirical study of cumulative cultural changes in humans is relatively young, but the results so far give an interesting insight into the process. A moot point is whether these findings will hold up when more challenging tasks, those less likely to be invented by a single individual, are deployed.

Non-human cumulative culture

Compared to the empirical investigation of cumulative culture in humans, that in other animals is both scarce and controversial.

Evidence from the wild

Based on observations of animals in the wild, some researchers have claimed that other species show cumulative culture. As these observations must allow a comparison with the cumulative culture observed in humans, we suggest the following criteria be deployed to guide identification of cumulative culture in other animals. First, there should be evidence that the behavioural pattern or trait is socially learned and any variation in the character is not solely due to genetic or environmental factors (Laland & Janik, 2006). Second, there must be evidence that the character in question changes over time in a directional or progressive manner. This requires evidence that it has been transmitted between individuals through social learning over repeated episodes. It also requires evidence that the character has changed in the transmission process to achieve an enhanced level of complexity. For practical reasons, a useful yardstick is that the character should be beyond what a single individual could have invented alone (Tennie et al., 2009) (Table 1). The evidence for cumulative transmission may come from long-term field studies, archaeological finds or some other source. However, we emphasize that the occurrence of similar, but non-identical, behaviour patterns in different populations (whether for the same purpose or different purposes), does not constitute evidence that one evolved from the other, and that supplementary evidence (e.g. observational, archaeological) will be required to demonstrate that variation in the character is attributable to ratcheting, and that cumulative change occurs within a historical lineage. The appearance of similar methods for performing a task in different populations may reflect the fact that there is a salient, or easily discoverable, method of performing that task and not evidence of shared ancestry. Cultural evolution is likely to occur over a shorter time scale than genetic evolution, which may also alter behaviour, but over a longer time period.

Boesch (2003) proposes three chimpanzee behavioural patterns that he believes show the hallmarks of cumulative modifications. The first is nut-cracking behaviour, displayed by different populations across Africa. In particular, western populations use tools, such as hammer stones, to crack nuts, and Boesch (2003) believes this is an elaboration of an ancestral behaviour pattern of hitting nuts on the substratum to smash them. This behaviour pattern has, according to Boesch (2003), been further modified with the use of anvil stones and, in some cases, a second, stabilising stone. However, the latter claim remains uncorroborated. Moreover, it is unclear whether even the most complex variant of nut cracking, that including hammer, anvil and stabilising stone, is too complex for one individual to have invented (Tennie et al., 2009). Archaeological analyses by Mercader et al. (2007) found that chimpanzee nut-cracking stone technology could date as far back as 4,300 years ago, suggesting that there has been little behavioural modification during that time. Thus, evidence from the archaeological data and contemporary assessment of the behaviour patterns suggest that, even if modifications have been added to nut cracking, these are not obviously more complex than one individual could have invented alone.

The second behaviour pattern outlined as cumulative by Boesch (2003) is ectoparasite manipulation in the three eastern chimpanzee communities of Budongo, Mahale and Gombe. At all three sites leaves are used to inspect the parasites that have been removed during grooming; at Budongo the parasite is placed on a leaf when removed. However, at Mahale individuals fold the leaf and then cut it with their nail. At Gombe there is a variant in which several leaves are piled on top of one another before the parasite is placed on the top and inspected. However, these are small modifications and there is no direct evidence that what has been described as the ‘modified’ behaviour pattern is derived from the ascribed ‘ancestral’ behaviour pattern. Whilst the two hypothetically ‘derived’ behaviour patterns could each have evolved from the hypothesised ‘ancestral’ character, it remains possible that each variant could have been invented independently.

The third behaviour pattern highlighted by Boesch (2003) is a modification of the context for an existing behaviour pattern and the possible addition of a separate technology to it. This is the digging of wells in dry environments, which, it is argued, is translated to contexts in which water sources are contaminated where the additional use of leaf sponges is observed. The addition of leaf sponging to well digging may be regarded as an increase of complexity of one behaviour pattern, and thus representative of cumulative culture, although it is not clear that the combination of these existing behaviour patterns is outside of the capacity of a single individual to invent. Also, the digging of wells in polluted areas is the application of a known behaviour in a new context (an ‘innovation’, see Reader & Laland, 2003), not an increase in complexity, and represents *accumulation* (Tennie et al., 2009).

Another chimpanzee behavioural trait hypothesised to be the result of modifications to an ancestral trait is the tool set observed in some populations. The complex tool sets observed at some sites, most notably in the central African communities, appear to be used, in sequence, for different aspects of the same foraging behaviour (Boesch, Head, & Robbins, 2009; Sanz & Morgan, 2007, 2009; Sanz, Schoning, & Morgan, 2009). One tool is normally used to puncture the outside of a nest of ants or bees. Other tools are then used to widen the hole to allow greater access to the food within. Finally, a smaller stick tool is used to gather honey, ants or larvae. In one study this ‘collector’ stick was modified to increase the surface area (Boesch et al., 2009; Sanz et al., 2009), the bark being removed and the wood below chewed to make it more brush-like. These tool sets contrast with other populations in which similar behaviour is performed, but with a single tool (Humle & Matsuzawa, 2002; Whiten et al., 1999). Once again, there is no direct evidence that any of the single-tool or proposed ‘simpler’ behaviour patterns are ancestral to the multiple-tool or more elaborate variants. Whilst these tool sets may be a case of simple cumulative culture, without the required evidence it is currently not clear that they are more complex than a single individual could invent alone.

Perry et al. (2003) reported a number of social conventions that arose in a population of capuchin monkeys that are also suggestive of cumulative culture.

These social games appear to have derived from the existing hand-sniffing behaviour (Perry et al., 2003), which has been observed in some populations. These social games (the hand-in-mouth, hair-in-mouth and toy-in-mouth games) emerged in succession, within one group, with the latter two appearing to be modifications of the first (Perry et al., 2003). However, whilst this represents an interesting case of modifications to a social behaviour pattern, all modifications appear to have been initiated by one individual, Guapo, a young male in the group. Although this demonstrates the ability of individuals in the species to make small modifications to a behaviour pattern, it does not represent a multi-generational or even multi-individual behavioural modification. Thus, in the absence of evidence for repeated bouts of transmission and refinement, this example too fails to provide clear evidence for cumulative culture, and is better characterised as several bouts of individual learning building upon one another.

More recently, white faced capuchins have been observed performing the ‘eye poke’ social convention, documented as the poking of a conspecifics finger into the eye of another (Perry, 2011). ‘Eye-poking’ (to oneself) has interestingly been reported occasionally to occur concurrent with the ‘hand sniff’ (Perry, 2008), representing conjunction of the two conventions. Importantly however, this eye-poke convention, along with the other reported social conventions, seems to have been reinvented in different groups/locations (Perry, 2011), providing further support that these behaviours are not beyond what individuals can invent for themselves. Moreover, there is as yet no evidence that eye-poking with hand sniff is in any sense superior to the hand sniff alone, which means this variation may well be characterised better as cultural drift (in which random changes have occurred, without selection). Hence, these examples, while representing interesting social traditions, cannot yet be said to be cumulative.

Stone-handling behaviour in Japanese macaques is present in different forms at sites throughout Japan, although its adaptive significance is unknown (Huffman, Nahallage, & Leca, 2008; Leca, Gunst, & Huffman, 2010; Leca, Gunst, & Huffman, 2007; Nahallage & Huffman, 2008). Some variants of the behaviour are almost ubiquitous, while others are rare, leading to the hypothesis that some individuals may be specialists, who have created new behavioural variants from existing ones (Leca et al., 2007). However, once again, there is no evidence that even the most complex of the stone-handling behaviours is outside a single individual's capacity to invent, and the putative refinements are not unambiguous improvements. If these traits are non-adaptive, as it is claimed (Leca et al., 2007), then there would seem to be little reason for conservatism in the behaviour and, therefore, we might expect to see great diversity in stone-handling modifications in Japanese macaques through a drift-like process (Caldwell & Millen, 2010b). This would mean that, rather than any one stone-handling behaviour building in complexity (or efficiency) upon another, each behaviour may simply represent the corruption of an existing stone-handling behaviour, inaccurately transmitted between individuals, without any further addition of complexity. Note that, we do not dismiss accidental mutations or inaccurate transmission as playing a role in cumulative culture but that, for ratcheting to occur, beneficial 'accidents' would be preferentially retained.

Circumstantial evidence for cumulative modifications can also be found in New Caledonian crows *Corvus moneduloides* (Hunt & Gray, 2004; Seed, Clayton, & Emery, 2007). The species uses several tools, the most studied of which are constructed from *Pandanus* leaves, which are used for foraging. Hunt & Gray (2003) document three different designs of these tools: narrow, wide and stepped. Amongst the stepped designs, between one and four steps are used. These patterns vary geographically across New Caledonia. It has been claimed that the variation in *Pandanus* tool design across New Caledonia is most parsimoniously explained as cumulative variation (Hunt & Gray, 2003). Hunt & Gray (2003) propose that the wide tools are ancestral with the narrow and stepped types derived from them. The variation in stepped tools has also been proposed to be a series of modifications to the original one-step design (Hunt & Gray, 2003). However, like chimpanzee's tools, there is no direct evidence that these lineages are correct and that the different tool types are not individual innovations, each invented from scratch. The evidence for social learning in the wild is also equivocal, suggesting there is a significant level of individual invention (Holzhaider, Hunt, & Gray, 2010) and evidence from captivity indicates that New Caledonian crows may possess an inherited predisposition for tool use and tool manipulation (Kenward, Rutz, Weir, & Kacelnik, 2006; Kenward, Weir, Rutz, & Kacelnik, 2005).

The difficulties of interpreting putative examples of cumulative culture in wild populations, as summarised in Table 1, being at the same time suggestive but inconclusive, has led some researchers to work on captive populations, to examine experimentally whether animals are capable of cumulative cultural learning.

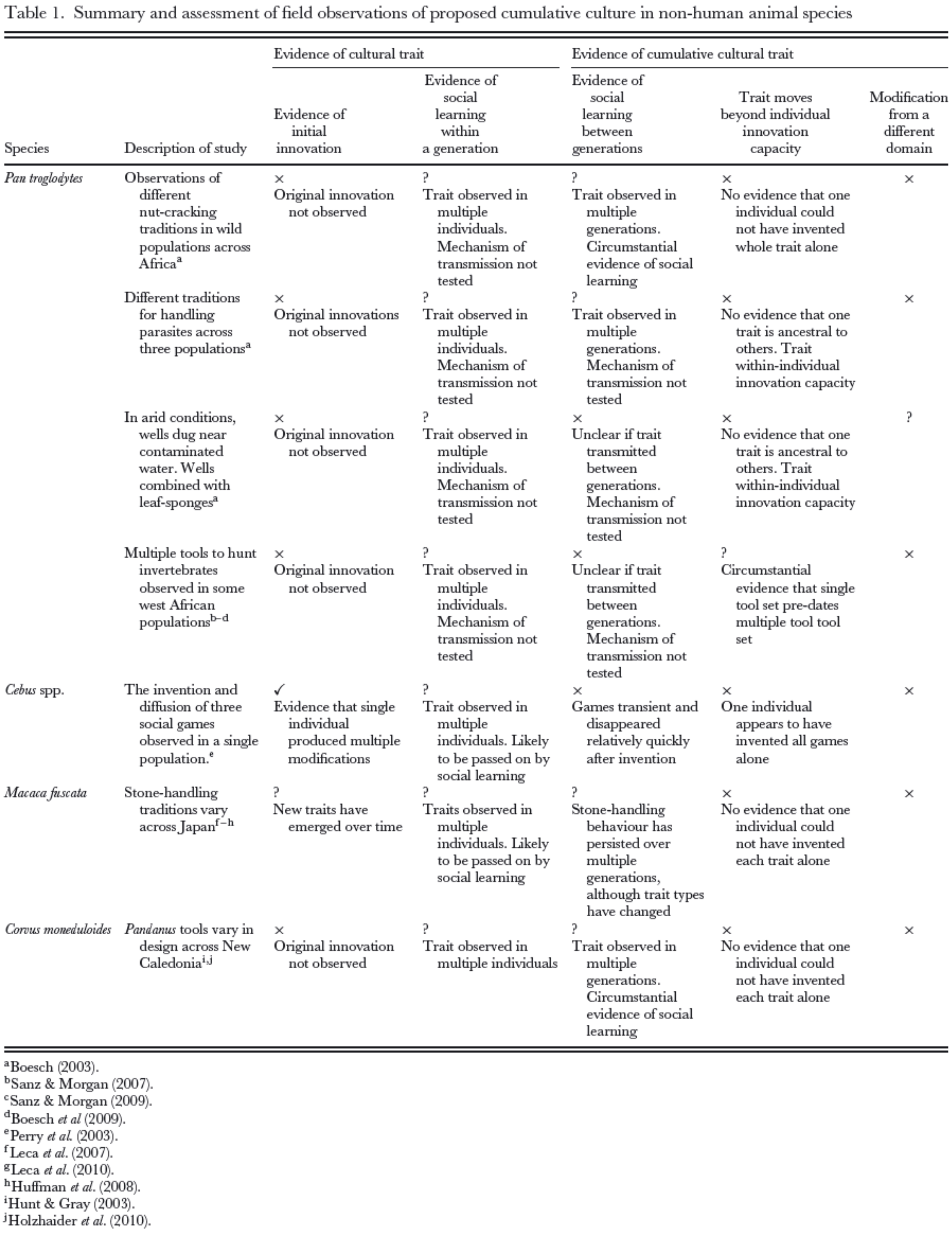

Table 1. Summary and assessment of field observations of proposed cumulative culture in non-human animal species

		Evidence of cultural trait		Evidence of cumulative cultural trait		
Species	Description of study	Evidence of initial innovation	Evidence of social learning within a generation	Evidence of social learning between generations	Trait moves beyond individual innovation capacity	Modification from a different domain
Pan troglodytes	Observations of different nut-cracking traditions in wild populations across Africa[a]	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	? Trait observed in multiple generations. Circumstantial evidence of social learning	× No evidence that one individual could not have invented whole trait alone	×
	Different traditions for handling parasites across three populations[a]	× Original innovations not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	? Trait observed in multiple generations. Mechanism of transmission not tested	× No evidence that one trait is ancestral to others. Trait within-individual innovation capacity	×
	In arid conditions, wells dug near contaminated water. Wells combined with leaf-sponges[a]	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	× Unclear if trait transmitted between generations. Mechanism of transmission not tested	× No evidence that one trait is ancestral to others. Trait within-individual innovation capacity	?
	Multiple tools to hunt invertebrates observed in some west African populations[b–d]	× Original innovation not observed	? Trait observed in multiple individuals. Mechanism of transmission not tested	× Unclear if trait transmitted between generations. Mechanism of transmission not tested	? Circumstantial evidence that single tool set pre-dates multiple tool tool set	×
Cebus spp.	The invention and diffusion of three social games observed in a single population.[e]	✓ Evidence that single individual produced multiple modifications	? Trait observed in multiple individuals. Likely to be passed on by social learning	× Games transient and disappeared relatively quickly after invention	× One individual appears to have invented all games alone	×
Macaca fuscata	Stone-handling traditions vary across Japan[f–h]	? New traits have emerged over time	? Traits observed in multiple individuals. Likely to be passed on by social learning	? Stone-handling behaviour has persisted over multiple generations, although trait types have changed	× No evidence that one individual could not have invented each trait alone	×
Corvus moneduloides	*Pandanus* tools vary in design across New Caledonia[i,j]	× Original innovation not observed	? Trait observed in multiple individuals	? Trait observed in multiple generations. Circumstantial evidence of social learning	× No evidence that one individual could not have invented each trait alone	×

[a] Boesch (2003).
[b] Sanz & Morgan (2007).
[c] Sanz & Morgan (2009).
[d] Boesch *et al* (2009).
[e] Perry *et al.* (2003).
[f] Leca *et al.* (2007).
[g] Leca *et al.* (2010).
[h] Huffman *et al.* (2008).
[i] Hunt & Gray (2003).
[j] Holzhaider *et al.* (2010).

Empirical testing of non-human cumulative culture

The first explicit test of the capacity for cumulative cultural learning in non-human primates found little evidence that chimpanzees could accumulate modifications to their behaviour (Marshall-Pescini & Whiten, 2008). This test involved a puzzle box that could be opened in two ways, with the second, more complicated, method allowing access to nuts and a greater volume of honey than the first, simpler method, which just allowed animals to dip for honey. The chimpanzee subjects were allowed to manipulate the puzzle box in a baseline condition with no demonstration, resulting in two individuals out of 14 discovering the first, 'dipping' method, and one also discovering the more complicated method. When the dipping method was demonstrated by a familiar human demonstrator three more individuals managed to learn it. These animals then received a demonstration of the more complicated method; of the five individuals tested only one performed the more complicated method and this was the individual who had already discovered the method in the baseline trials.

Researchers have also drawn conclusions about cumulative culture from the results of experiments investigating other cognitive factors in chimpanzees. In an experiment in which subjects were required to obtain food by pushing it around a maze using a stick, five individuals discovered that by rattling the board on which the maze was placed, food could be obtained more rapidly (Hrubesch, Preuschoft, & van Schaik, 2009). The researchers altered the conditions in which animals could interact with the maze board, either taking away sticks to encourage the rattling technique, or bolting the maze down to prevent it. They found that individuals did not switch the technique they used and appeared to have become fixed upon the method they had already discovered. The authors argue that this behavioural conservatism may explain the lack of cumulative cultural evolution in non-humans.

Compound tool use, the combining of separate objects to make a meta-tool, has been observed in wild chimpanzees, on a handful of occasions and only in certain contexts (Boesch, 2003; Sugiyama, 1997). Price et al. (2009) tested captive chimpanzees, where subjects were required to put together two component tools to create an elongated single tool that could be used to retrieve an out-of-reach food reward. Chimpanzees were significantly more likely to learn to combine and use the tool when they had seen a video demonstration showing the tool being manufactured and used, than in other conditions, where individuals received a video demonstration of only part of the process. This suggests that the participants were able to modify a tool, which they then used to retrieve food suggesting that they may have the potential for rudimentary cumulative cultural learning. However, as some control subjects, who received no demonstration of the combining process, were also able to learn to make the complex tool, it clearly is not beyond a single individual's capabilities (Tennie et al., 2009).

The most comprehensive experimental attempt to investigate the factors that may underlie cumulative culture in animals to date was carried out by Dean et al. (2012). In a comparative study of sequential problem solving, these authors provided groups of capuchin monkeys, chimpanzees, and nursery school children with an experimental puzzle box that could be solved in three stages to retrieve rewards of increasing desirability. Stage 1 required individuals to push a door in the horizontal plane to reveal a chute through which a low-grade reward was delivered. Stage 2 required individuals to depress a button and slide the door further to reveal a second chute for a medium-grade reward. Stage 3 required the solver to rotate a dial, releasing the door to slide still further to reveal a third chute containing a high-grade reward. All stages could be completed through two parallel options, with sets of three chutes on both left and right sides. This two-action, two-option design aided evaluation of alternative social learning mechanisms and allowed two individuals to operate the puzzle box simultaneously. After 30 h of presentation of the task to each of four chimpanzee groups, only one of 33 individuals reached stage 3, with a further four having reached stage 2, and with each group having witnessed multiple solvers at stage 1 (experiment 1). Chimpanzee performance was not greatly enhanced by trained demonstrators (experiment 2). A similar pattern was observed in the capuchins: after 53 h, no individual reached stage 3 and only two individuals reached stage 2. Thus, the experiments provided no evidence for cumulative learning in chimpanzees or capuchins. These findings stand in stark contrast to those of the children, where despite a far shorter exposure to the apparatus (2.5 h), five out of eight groups had at least two individuals (out of a maximum of five) who reached stage 3, with multiple solvers at stages 2 or 3 in all but two groups. Dean et al. (2012) found that the success of the children, but not of the chimpanzees or capuchins, in reaching higher-level solutions was strongly associated with a package of sociocognitive processes —including teaching through verbal instruction, imitation, and prosociality — that were observed only in the children. Children’s individual task performance covaried strongly with the amount of teaching, imitation and other prosocial behaviours (donation of retrieved stickers) they personally received; those children that received less support were less likely to get to the higher cumulative stages of the task and all children who got to the final stage did so with, usually, at least two forms of social support (Dean et al., 2012). Thus, completion of all stages of the task was beyond that which an individual child could invent for his/herself. While this study does not represent a multi-generational approach, it provides evidence for the socio-cognitive factors necessary for cumulative learning to occur, and provides evidence of repeated bouts of elaboration and social transmission amongst the children.

In summary, at present, reports of cumulative culture in animal species remain subjective and circumstantial. Observations from the wild and captivity suggest that while some species are capable of modifying behaviour, these modifications do not seem to accrue across generations and do not clearly move beyond what individuals alone can invent for themselves (see also: Tennie et al., 2009). This suggests that while animals can transmit behaviour socially to create localised traditions, animal cultures are either not cumulative at all or cumulative in a highly restricted and simple manner.

Why are there Differences in Cumulative Culture between Humans and Non-humans?

The evidence that cumulative cultural evolution may be unique to humanity has led researchers to construct various hypotheses as to the critical processes that underpin human cumulative culture.

Hypotheses concerning the lack of Cumulative Culture in Non-humans

Some of the hypotheses focus upon species differences in social structure and inter-individual tolerance that might plausibly affect the spread of cumulative innovations. Others focus on cognitive mechanisms that may affect the constituent processes of cumulative culture.

Cognitive differences

The distribution of cumulative culture may be accounted for by the presence of cognitive mechanisms specific to, or substantially enhanced in, humans. However, researchers do not agree which particular processes are unique to humans and which may promote cumulative culture.

Innovation. An increased creativity, that is the ability to innovate, has been proposed to drive cumulative culture. Enquist et al. (2008) argue that cultural traits must be invented to spread within the population and be modified in a cumulative process. Whilst this argument is logical, there are extensive data documenting innovations in a range of species of primates (Reader & Laland, 2002) and birds (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009), yet comparatively little evidence for traditions and cumulative culture. These data suggest that innovation alone is not sufficient for cumulative culture. Indeed, a recent study suggests that innovation may act as a cultural catalyst, at least in the early stages of ratcheted technologies, functioning only to speed up the level of cultural complexity attained (Pradhan et al., 2012).

Conservatism. In contrast to the creativity of humans, it has been argued that non-humans are conservative in their actions. Some experimental studies have reported that non-humans, in particular chimpanzees, continue to use the first solution they discover even when a potentially more rewarding alternative is available to them (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). A recent demonstration of conservative behaviour in chimpanzees was provided by Hopper et al. (2011). In this study, chimpanzees preferentially exchanged the token they had seen a conspecific model exchange for food, even when the food received was of lower value than that which a second, alternative, token yielded. Interestingly, the two potential outcomes (high- or medium-value rewards associated with the two token types) were gained using the same behaviour (token exchange), yet there was little evidence of chimpanzees switching between the tokens despite all gaining experience with the alternative token, which in one group yielded the high-value rewards. However, the extent to which the two behavioural options were understood by the chimpanzees is unclear. Likewise, the role of the identity of the model in enhancing this conservatism is yet to be investigated, and may prove explanatory given that both models were of relatively high rank (Kendal, Hopper, Brosnan, Schapiro, Lambeth & Hoppitt, submitted).

Researchers have argued that the discovery or utilisation of a more rewarding solution is suppressed by the initial discovery of a task solution (Hopper et al., 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Whiten et al., 2009). Similar arguments concern a species propensity for functional fixedness, that is the inability to use items beyond their initially learnt affordances (Hanus, Mendes, Tennie, & Call, 2011). Specifically, it is thought that functional fixedness can occur from one's own experience with environmental features, canalising its use according to how such was personally used in the past. Alternatively, normative influence may play a role, such that one's cultural background or norms for item affordances could inhibit learning new item functions (Gruber, Muller, Reynolds, Wrangham, & Zuberbühler, 2011; Hanus et al., 2011). According to these arguments, cumulative additions to a solution would be increasingly likely to occur in species as conservatism (and/or functional fixedness) decreased. Wood, Kendal & Flynn (2013) have recently shown that children acquire multiple strategies to a problem, even where their first solution procured a reward of no lesser value than the alternative solutions they went on to use. Therefore, if humans are less conservative than chimpanzees, as suggested by Whiten et al. (2009), this may partly explain the prevalence of cumulative culture in the former relative to the latter. However, the aforementioned study of cumulative problem solving, in children, chimpanzees and capuchin monkeys (Dean et al., 2012), found no evidence for conservatism or behavioural inflexibility in any of the species.

It is important here to distinguish between conservatism as a mechanism and as an outcome. For example, if a species lacks the capability to copy in proportion to behavioural payoffs, beneficial demonstrated solutions may be neglected in favour of previously learned and rewarded solutions. Thus animals would fail to elaborate upon acquired behaviour and would consequently appear ‘conservative’. Conservatism, as a mechanism, however, posits that there exists a specific conservative learning strategy on the part of the animal.

Interestingly, behavioural flexibility rather than conservatism has recently been documented in captive orangutans. Lehner, Burkhart & van Schaik (2011) investigated orangutans’ (*Pongo pygmaeus abelii*) ability to modify previously used techniques when the previous behaviours were blocked. Three conditions were presented in which orangutans could retrieve syrup from a tube employing various tool methods, the two later conditions were successively more restrictive, forcing animals to alter the method they had used previously. The animals did switch to new techniques for gaining the food reward, demonstrating behavioural flexibility. The authors claim that two of the techniques built cumulatively upon other techniques, however there is no evidence that these new techniques were socially transmitted.

Imitation. The fidelity of transmission of behavioural traits between individuals has been proposed to be of key importance to the evolution of cumulative culture (Boyd & Richerson, 1985; Galef, 1992; Lewis & Laland, 2012; Tomasello, 1994). Imitation, learning the exact motor pattern of a behaviour from observing another individual, is argued by some researchers as central to human cumulative culture

(Boyd & Richerson, 1996; Tomasello, 1994, 1999), since it is the social learning process capable of supporting high-fidelity transmission. Thus individuals do not have to 'reinvent the wheel' when they learn a new behaviour.

Recent theoretical work suggests that imitation is not necessary for non-cumulative traditions, which can emerge from simple learning processes, such as local/stimulus enhancement coupled with reinforcement learning or from asocial learning when individuals are exposed to the same environment (van der Post & Hogeweg, 2008). These learning mechanisms, while sufficient to support durable traditions (Matthews, Paukner, & Suomi, 2010) or an accumulation of behavioural traits (van der Post & Hogeweg, 2008), would seem an insufficient foundation for cumulative culture insofar as enabling the accumulation of beneficial modifications to an existing behavioural trait, increasing its complexity. To the extent that local/stimulus enhancement results in low-fidelity transmission, as is widely thought (although we note that few hard data exist here), then Lewis & Laland's (2012) theoretical analysis would not expect it to result in cumulative culture. Thus, if a species is not capable of accurate imitation (or teaching) it is much less likely that it will be able to develop cumulative culture. In support of this theory, Dean et al. (2012) found that between species (capuchins, chimpanzees and children), and within species, performance with a cumulative problem-solving task correlated strongly with the degree of task manipulations performed by individuals that matched those of their predecessors at the task. It is noteworthy, however, that end-state emulation can result in high-fidelity social learning and thus imitation may not be as essential for cumulative culture but rather high-fidelity learning in general (Caldwell, Schillinger, Evans, & Hopper, 2012). However, end-state emulation may result in high-fidelity learning only in those tasks for which the end product can readily be recreated from viewing the action’s products, while imitation is required for process-opaque tasks (Acerbi, Tennie, & Nunn, 2011; Derex, Godelle, & Raymond, 2012). Object movement emulation may constitute another route to high-fidelity learning. For example, it has been shown that after viewing video footage of physical object movements only, through digital removal of a demonstrator’s behaviour, children’s object movements were comparable to when a full behavioural-object movement demonstration was viewed (Huang & Charman, 2005). Task difficulty and task demands are however likely to play an important role in whether forms of emulation are sufficient to optimise behaviour (Acerbi et al., 2011).

Why, then, when there is recent evidence that chimpanzees are capable of imitation (Horner, Whiten, Flynn, & De Waal, 2006; although see Tennie et al., 2012), do they not appear to have developed cumulative culture? There are various potential explanations for this. First, while chimpanzees have shown some capacity for imitation this may be the exception rather than the rule, with other social-learning mechanisms such as emulation or stimulus enhancement, associated with lower copying fidelity, responsible for much behavioural propagation (although see Caldwell et al., 2012; Hopper, 2010; Tennie et al., 2009; Tomasello, 1999). Moreover, comparative studies reveal substantive differences in the amount of imitation, and rate of imitative learning, exhibited by humans and chimpanzees (Dean et al., 2012; Hecht, Patterson, & Barbey, 2012; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Horner & Whiten, 2005), suggesting that while chimpanzees may be capable of imitation, they are not as proficient at it (or perhaps, as motivated to imitate) as humans. Second, there is a lack of evidence that when imitating chimpanzees formulate the copied agent’s intentions (Tomasello &

Carpenter, 2007). That is, compared to humans, chimpanzees may be less capable of rational imitation, or may be less able to imitate actions deliberately and consciously in order to achieve the same outcome as that inferred for the demonstrator. The ability to take into consideration the demonstrator's goals and intentions might plausibly facilitate cumulative culture, if this increased the accuracy of information transmission [although see arguments regarding imitation of irrelevant actions, or ‘overimitation’ in children (Horner & Whiten, 2005; Lyons, Damrosch, Lin, Macris, & Keil, 2011; Lyons, Young, & Keil, 2007)].

Adaptive filtering. Enquist & Ghirlanda (2007) argue that imitation alone cannot support cumulative culture. They argue that in the absence of adaptive filtering mechanisms, or strategies evaluating the consequences of observed behaviour, blind or random imitation is likely to occur. This creates a situation in which maladaptive traits are as likely to spread as adaptive traits. However, if individuals use rational imitation (Carpenter, Akhtar, & Tomasello, 1998; Gergely, Bekkering, & Kiraly, 2002) or reliable learning heuristics (Laland, 2004) dictating what (and whom, e.g. (Wood, Kendal, & Flynn, 2012) is copied, the replication of maladaptive or suboptimal traits could be reduced. In the case of chimpanzees, the absence of cumulative cultural evolution may also be related to an inability to evaluate the consequences, or payoffs, of observed behaviour. It has yet to be established whether chimpanzees, and indeed other animals, possess an adaptive-filtering process that serves to remove maladaptive behaviour, but there are reasons for doubting that this is the key to the absence of cumulative culture in animals. That is because the demonstrating animals themselves are likely to exhibit adaptive filtering, since individuals disproportionately perform productive, high-payoff behaviour, leaving the pool of variants available to copy a selective set of tried-and-tested solutions (Rendell et al., 2010).

Teaching. Teaching is behaviour that functions to impart knowledge, and differs from other forms of social learning in requiring an active and costly investment by the tutor into the learning of the pupil (Caro & Hauser, 1992). Teaching frequently requires the teacher to infer the current knowledge state of the pupil to allow an appropriate level of support (Flynn, 2010); however, inferring knowledge states in other animals is difficult. The distribution of teaching may be wider than previously thought, with experimental evidence in meerkats (*Suricata suricatta*), pied babblers (*Turdoides bicolor*), ants (*Temnothorax albipennis*) and bees (*Apis* spp) (Franks & Richardson, 2006; Raihani & Ridley, 2008; Thornton & McAuliffe, 2006), although whether the teaching in non-humans is consanguineous to human teaching remains debatable (Hoppitt et al., 2008; Premack, 2007). Teaching may be particularly important for the transfer of cumulative modifications, as it functions to promote the fidelity of knowledge transfer, potentially allowing specific behavioural patterns to be transmitted between individuals until such a time as beneficial modifications appear (Boyd & Richerson, 1985; Tomasello, 1999). Indeed, teaching can be characterised as behaviour that functions specifically to enhance the fidelity of information transmission. A recent mathematical analysis of the evolution of teaching (Fogarty, Strimling, & Laland, 2011) found that cumulative culture broadens the range of conditions under which teaching is favoured by selection, leading to the hypothesis that teaching and cumulative culture may have coevolved. This finding is consistent with the findings of the aforementioned experimental investigation of cumulative culture (Dean et al., 2012), which reported strong positive correlations between how much teaching a child received from other children and how well they performed on the cumulative culture puzzle-box task.

Complex communication. Alongside teaching, human language, a uniquely complex communication system (Cheney & Seyfarth, 2010; Hauser, Chomsky, & Fitch, 2002; Pinker & Jackendoff, 2005; Tomasello, 1999), may promote cumulative culture, again through facilitating accurate transmission. Language allows the transmission of intentions and complex behaviour patterns between individuals and the facilitation of easy and 'cheap' pedagogy; greatly enhancing teaching. Language has also enabled humans to compile written records of the beliefs, ideas, innovations and technologies of our predecessors, which provides protection against cultural loss, as well as enabling access to the knowledge from outside individuals' social networks. Language, both in the form of verbal and linguistic notation therefore, could enable high-fidelity transmission of modifications to existing behavioural traits, facilitating cumulative culture (Carpenter, 2006; Csibra & Gergely, 2005; Tomasello, 1999; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Consistent with this, Dean et al. (2012) found that children's performance in the cumulative task covaried with the amount of verbal instruction they received from other children.

Prosociality. The evolution of prosociality, enabling cooperation between individuals, increased tolerance, and the shared motivations of individuals has been proposed to support the evolution of cumulative culture (Tomasello, 1999; Tomasello & Call, 1997; Tomasello et al., 2005; Tomasello & Moll, 2010). The argument states that if individuals cooperate they will be able to work on a task together, allowing naïve individuals to get closer to and thus learn from a knowledgeable individual (Tomasello & Call, 1997). Working together also allows two or more individuals to discover solutions to a task and to pool their information, thus providing the opportunity for two separate solutions to be combined or modified (Tomasello, 1999). If individuals share motivations they are able to recognise that another individual has a goal and intentions, and potentially are able to assist others to achieve their goal (Tomasello et al., 2005). Shared intentionality, in which individuals recognise that others, who may not even be present at the time, share their goals and intentions, can facilitate the modification of a behaviour pattern by many individuals, over many transmission episodes and, therefore, the evolution of cumulative culture (Tomasello et al., 2005; Tomasello & Moll, 2010). Indeed, Dean et al. (2012) also highlighted a significant role for prosocial behaviour (donation of retrieved rewards to others) in the success of children in their cumulative problem-solving task. These authors hypothesised that such prosocial behaviour signified an understanding of shared motivations and served to scaffold the learning of naïve individuals.

In summary, a number of cognitive differences have been proposed to explain the evolution of cumulative culture. However, it seems unlikely that one cognitive trait could explain the evolution of cumulative culture by itself. Instead there may be differences in a suite of cognitive traits between species [e.g. socio-cognition: teaching, imitation, pro-social behaviour and complex communication (Dean et al., 2012; Tomasello, 1999)], which collectively afford the high-fidelity information transmission, social tendencies, and motivations necessary for cumulative culture.

Social learning strategies

Whilst social learning may often provide a cheaper and quicker method of learning than asocial learning (Rendell et al., 2010), theoretical models suggest that it should not be used indiscriminately (Boyd & Richerson, 1985a; Laland, 2004). Rather, to enhance fitness individuals should use social learning strategies, or cultural transmission biases, to dictate when to collect social information and from whom to acquire it (Boyd & Richerson, 1985; Kendal, Coe, & Laland, 2005; 2009; Laland, 2004). Certain social learning strategies have been proposed to be important to the evolution of cumulative culture.

Conformity. One such strategy is conformity, defined as the propensity to disproportionately copy the most frequent behavioural trait in the population, over and above the chance expectation (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Whiten, Horner, & De Waal, 2005). Our definition of conformity differs from that deployed in social psychology, which focuses on the normative and social influence acting on the copying of (incorrect) decisions, originating from the work of Asch (1955) (Morgan & Laland, 2012). Mathematical models reveal that conformity is favoured under a wide range of conditions (Henrich & Boyd, 1998) and contributes to the high-fidelity transmission required for cumulative culture. However, Eriksson, Enquist & Ghirlanda (2007) found that conformity hindered the spread of adaptive variants, with individuals who adopt cultural traits at random being more successful than those who adopt a conformist strategy. Eriksson et al.'s (2007) model encompasses temporal variation in the environment but not a spatial component, thus preventing sub-populations from forming and, therefore, conformity from evolving within them. Thus the model fails to provide a realistic approximation of human demography and the geographical parameters that influence behaviour and trait transmission.

Conformity, defined as copying the behaviour displayed by the majority of individuals rather than disproportionate copying of the behaviour of the majority, was recently shown in chimpanzees and two-year-old children (Haun, Rekers, & Tomasello, 2012). Specifically, after observing three conspecifics demonstrating the same behaviour (each dropping a ball into a coloured box) or one individual demonstrating a different behaviour three times (dropping a ball three times into a different coloured box), chimpanzees and children copied the behaviour of the majority. By contrast, orangutans showed no such majority-biased copying when exposed to the same experimental procedure. While this study makes an initial step towards investigating general majority-biased transmission in different primate species, interpretation of these data is open to debate (T. Morgan, personal communication). As noted by Haun et al. (2012), further investigation in this area is needed, particularly to isolate the influence of unbiased or random copying in such tasks, as unbiased copying itself is frequency dependent. The testing of conformity bias, defined as a disproportionate likelihood of copying the most frequent trait in a population, is required before drawing conclusions on the effect conformity has on other animals' social transmission and their opportunities for cumulative culture. Furthermore, avoidance of the minority response or the undemonstrated option could have played a role in the behavioural responses observed in chimpanzees and children (T. Morgan, personal communication). Further data will help clarify majority-biased learning in these species.

Kandler & Laland (2009) modelled the spread of cultural traits, derived through independent innovation or cumulative modification, with different levels of conformity bias (defined as disproportionately copying the most common cultural variant) to the transmission of the traits. They found that strong conformity (in which it was difficult for frequency-independent traits to invade) tended to hinder the spread of novel innovations within the population, irrespective of whether the innovation was beneficial or not, as individuals would fail to switch to a new variant. Conversely, under a weaker conformity bias a beneficial variant could spread within the population. Some individuals would switch after determining that the new variant was more beneficial, and this was enhanced as the trait became more common by individuals using a conformist learning bias. Weak conformity was, therefore, suggested to be adaptive, since it resulted in a greater proportion of individuals adopting the beneficial variant. Such ‘weak conformity’ is apparently supported by the equivocal or conditional empirical evidence for conformity in humans (Coultas, 2004; Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Efferson et al., 2007; Eriksson & Coultas, 2009; McElreath et al., 2008; McElreath et al., 2005; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). Thus the impact of conformity, and, indeed, the extent to which species do conform, is currently unclear.

Selective copying. Mathematical models have also suggested that selective copying of successful behaviours or successful individuals, when coupled with the opportunity to learn asocially, can strongly affect cumulative cultural evolution (Ehn & Laland, 2012). Ehn and Laland (2012) propose an ‘individual refiner’ strategy, which first uses social learning, and then refines through individual learning, and continues to do so irrespective of the level achieved. This strategy generates high fitness across a broad range of conditions, leads to high amounts of socially transmitted behaviour in the population, and accumulates significantly more innovations over the generations than other strategies.

Wisdom & Goldstone (2010) recently demonstrated this sensitivity to the performance of others in the laboratory by exposing human participants to a computerised game. When trying to solve the game, participants had access to the choices of the other participants and could choose to copy their task solutions. The investigators also manipulated whether participants could see the payoffs relating to the task solutions of the other participants. Overall the results indicated that when neighbour scores were visible, groups attained higher overall scores with more pronounced cumulative improvement across rounds than those in the invisible score condition. These results indicate that identifying and copying successful individuals may play an important role in human cumulative evolution.

Likewise, Morgan et al. (2012) exposed humans to a series of cognitive puzzles, in which they were able to view the choices of others. In addition to conformist transmission, they found that participants were able to improve their performance using a proportional observation strategy, copying demonstrators in proportion to the level of reward the demonstrator received (Schlag, 1998). The participants also used (conditional) proportional imitation strategies, whereby individuals copy the behaviour of others in proportion to how much better the other's payoff is than their own (Schlag, 1998). Game theory analysis has established that this strategy optimises cumulative cultural learning (Schlag, 1998).

Empirical evidence of the presence of 'copy successful behaviour' and 'copy if dissatisfied' strategies in non-human animals is currently limited to a handful of studies. Galef, Dudley & Whiskin (2008) reported evidence for a 'proportional reservation' strategy, as set out by Schlag (1998), in female Norway rats (*Rattus norvegicus*). Rats exposed to energetically dilute diets displayed a greater propensity to copy the food choices of demonstrator rats than did energetically satisfied rats, with the propensity to copy being proportional to the level of nutritional deprivation. However here the dissatisfaction was not with regard to the payoffs of a particular behavioural trait and the copying behaviour may also be interpreted as a manifestation of a ‘copy when uncertain’ strategy in nutritionally deprived rats (Kendal et al., 2009*)*.

There is also some evidence that nine-spined sticklebacks (*Pungitius pungitius*) adopt a proportional observation strategy (Kendal, Rendell, Pike, & Laland, 2009; Pike, Kendal, Rendell, & Laland, 2010). After gaining personal experience of two food patches, containing different densities of food, focal fish observed conspecifics feeding at the same resource sites, however the food densities of the patches were manipulated, such that the fish’s personal experience no longer predicted the food density. When subsequently given the choice of food patch, focal fish tended to copy the social information in proportion to the demonstrators’ payoff (Kendal, Rendell et al., 2009; Pike et al., 2010).

Social learning strategies depend upon the underlying cognitive capacity for social learning and may also be influenced by social structure and tolerance. Given the evidence for social learning strategies in other animals, it seems unlikely that these alone could explain the evolution of cumulative culture. However, it is possible that humans may implement particular strategies, such as payoff-based copying, more efficiently, by virtue of their possessing higher fidelity transmission mechanisms.

Social structure

In humans, differences in population size, connectedness and social structure are thought to alter the ease with which complex behaviour patterns can be transmitted between individuals, thus accounting for the observed distribution of cumulative culture (Hill et al., 2011; Kline & Boyd, 2010; Powell, Shennan, & Thomas, 2009). In animals, social structure is normally measured by factors such as the dominance gradient (the ability of low-ranking individuals to win fights with higher ranking individuals), amount of social play, the intensity of aggression within populations and the frequency of conciliatory displays (Thierry et al., 2008). In species with a steep dominance gradient, social factors may hinder the invention and spread of cumulative modifications. A recent mathematical model of cultural progression found that increasing the number of tolerant knowledgeable individuals is expected to generate higher levels of technological complexity, with tolerance thought to be essential in the initial stages of cultural progression (Pradhan et al., 2012). Thus, social structure may account for some variation in the extent of cumulative culture (Burkart & van Schaik, 2010; Coussi-Korbel & Fragaszy, 1995).

Monopolisation. By monopolising resources and scrounging from low-rankers, dominant individuals may exploit those lower in the social hierarchy and prevent them from accessing novel resources (Lavallee, 1999; Soma & Hasegawa, 2004). In an experiment investigating tool use in free-ranging captive brown capuchins (*Cebus apella*), Lavallee (1999) reported that the alpha male would frequently chase low-ranking individuals away from a tree stump that contained resources of honey. Out of a group of 11 individuals, four never had the opportunity to interact with the task and others were also constrained in the amount of time they could spend at the resource. Similar findings have been reported in a study of social learning in wild lemurs (*Lemur catta*, Kendal, Custance, Kendal, Vale, Stoinksi et al., 2010). In a review of the primate literature, Reader & Laland (2001) found that there were more reports of innovations in low-ranking individuals than in high- or mid-ranking individuals. If low-ranking individuals have a greater propensity to innovate than high-ranking individuals but, because of the activities of dominants, experience restricted opportunities to interact with novel resources, or to perform any innovative behaviour they devise, then innovation may be curtailed. This, coupled with the reported decreased likelihood of individuals observing novel behaviour by low rankers compared to high rankers (Coussi-Korbel & Fragaszy, 1995; Kendal et al., submitted), means that the population may not be able to exhibit cumulative social learning.

Scrounging. Several studies have reported a relationship between the level of scrounging, or kleptoparasitism, that individuals commit and the amount that they learn socially (Beauchamp & Kacelnik, 1991; Caldwell & Whiten, 2003; Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997; Midford et al., 2000), although the direction of this relationship varies. Some studies have found that social learning was inhibited by scrounging (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997), leading to the hypothesis that, when able to scrounge, individuals do not learn cues about the task from the demonstrator, but rather learn that the demonstrator itself is a source of food (Beauchamp & Kacelnik, 1991; Giraldeau & Lefebvre, 1987). Scrounging, by inhibiting learning about the task itself, might therefore restrict the spread of social information, thereby hindering cumulative culture.

However, other researchers have found that scrounging enhanced the learning of observers regarding a novel extractive-foraging puzzle box (Caldwell & Whiten, 2003; Midford et al., 2000). In these studies animals able to scrounge performed better when given the opportunity to interact with the novel task, than those that were not permitted to scrounge. The researchers argue that scrounging promoted closer observation of the novel behaviour pattern and attendance to cues of the puzzle box, rather than simply associating the demonstrator with food, which allowed the scrounger to learn a behaviour pattern more efficiently (Caldwell & Whiten, 2003).

Social learning may also depend upon species' social tolerance levels (Caldwell & Whiten, 2003; Coussi-Korbel & Fragaszy, 1995; Fragaszy & Visalberghi, 1989). Animals that display greater social tolerance of one another (more egalitarian species) may exhibit enhanced social learning with scrounging, since the co-action and close proximity allows the observers to learn from the demonstrator more effectively. By contrast, scrounging may have an inhibitory effect on social learning in despotic animals (displaying lower social tolerance) due to a reduction in the opportunity for co-action and subsequent ability of dominant individuals to access the resources (Coussi-Korbel & Fragaszy, 1995). An important contributing factor in the development of cumulative culture, thus, may be a species' level of social tolerance, with species displaying high social tolerance, such as *Homo sapiens*, able to transfer more complex information. However, since cumulative culture is not found in all egalitarian species, and a lack of social tolerance was not found to contribute to a lack of cumulative culture in chimpanzees or capuchins (Dean et al., 2012) factors other than social tolerance must also contribute to its evolution.

Demography

Demographic factors have also been proposed to influence cumulative culture. Powell et al. (2009, 2010) proposed that the changes in human culture during the late Pleistocene, observed in the archaeological record, are explained by demographic factors. Using simulation models building on a model of Henrich's (2004), Powell et al. (2009, 2010) found that high population densities and high migration rates between subpopulations resulted in accumulation of modifications and increased complexity in technologies (see also Kline & Boyd, 2010). They hypothesise that population dynamics may have played an important part in the acceleration of cumulative cultural change around 50 thousand years ago (kya). However, a key assumption of the models is the pre-existence of cognitive capacities for social learning and cumulative culture in humans, therefore, clearly demography alone is insufficient to generate cumulative culture without these cognitive capabilities. Hill et al. (2011) highlight various hunter–gatherer group-composition properties unique among the primates that may have implications for the emergence of cumulative culture. These include hunter–gatherer bands being composed of a large proportion of non-kin (suggesting cooperation between unrelated individuals), flexible patterns of male and/or female dispersal, maintained lifelong social bonds (Chapais, 2011; Rodseth et al., 1991) and bands forming constituent parts of larger social networks. A likely by-product of these group structures is pronounced social transmission and continued flow of cultural practices, knowledge and ideas between bands and sub-populations, accentuating the probability that traits will accumulate within and across populations. By contrast, for chimpanzees, (affiliative) contact between communities is composed almost exclusively of female migration, upon which contact with the natal group is lost (Chapais, 2011). Thus we see that human band compositions are especially well suited to cultural transmission on a large scale. As such, a species' demography may play an important role in whether or not their culture has accumulated over generations.

Enquist et al. (2010) investigated how the number of animals an individual is able to copy affects the persistence of a cultural trait over time. They used mathematical models to investigate under what conditions copying a single cultural 'parent' could support a stable culture. They found that multiple cultural parents were typically necessary for a stable culture as, unless perfect transmission was possible, then copying of single cultural parents would result in the proportion of individuals expressing a trait decreasing generation after generation. This suggests that a population with overlapping generations and the opportunity for learning from multiple individuals promotes cultural transmission.

Whilst a larger population size has a positive effect on the development and sustainability of complex cumulative culture, small, isolated populations may also lose cultural complexity. The best-known example of cultural loss is the island of Tasmania, where humans arrived about 34 kya and were isolated from the mainland between 12 kya and 10 kya (Henrich, 2004). Subsequently, the Tasmanians lost all but 24 items in their toolkit, compared to a toolkit of hundreds on mainland Australia. Thus, when Europeans arrived in the 18th century there was no bone technology, no skills for making winter clothing and no ability to fish as seen in mainland Australian aborigine populations (Henrich, 2004). In modelling the data Henrich (2004) found that as population size dropped it became much easier for losses of behavioural traits to occur due to small copying errors. The isolation of Tasmania meant that the small population could rapidly lose technologies, with little chance of innovations from within their population or from migrant individuals.

The Tasmanian example is replicated with other populations in the Pacific Ocean. Kline & Boyd (2010) found that in Pacific islands the population size and rate of contact with other populations correlated with the complexity of the marine foraging technology. Whilst acknowledging that complex technologies may increase the carrying capacity of the population, the authors speculate that the influx of migrant ideas and range of ideas from a larger population allow modifications to cultural traits to be made more rapidly, ratcheting up complexity.

In summary, the size, network structure and mobility of populations may impact upon the number of cultural traits that a population can sustain. Clearly demography alone cannot account for the initial development of individual cumulative cultural traits, otherwise it would be widespread in nature. However, population size will influence the speed at which technologies ratchet up in complexity, and the level of diversity maintained (Pradhan et al., 2012).

Efficiencies and complexities

Throughout this review, there has been discussion of empirical work and field observations that focus on an increase in complexity over time. The ratchet effect, as originally described by Tomasello (1994), specifically referred to increases in complexity with social transmission. This increase in complexity is hypothesised to have created the many artefacts, institutions and complex technologies that humans display across populations (Tomasello, 1999).

However, we wish to emphasise that in cumulative culture (specifically relating to material culture, as has been the focus of this review), combined with complexity (modification by addition), there must also be changes in efficiency (reduction in the time, effort, energy or cost of production, and/or increase in usability of the product). It is likely that cultural traits that simply become more complex, with no improvements in efficiency, would simply become too complex for individuals to learn or gain sufficient benefit to justify learning them. For example, Mesoudi (2011) posited a limit to cumulative complexity due to the costs of acquiring a complex trait from the previous generation within a lifetime. An obvious example of the proposed requirement for improved efficiency alongside complexity is that of computing technology; computers have become more compact, and user friendly, as they have become more powerful.

Some studies featured in this review have solely focussed on cumulative improvements in efficiency (Flynn, 2008; Kirby et al., 2008). Flynn (2008) finds that the imitation of causally irrelevant actions (or ‘over-imitation’), as seen in other experiments with humans (Horner & Whiten, 2005; Nielsen & Tomasello, 2010; Wood et al., 2012), reduces over laboratory generations with children employing rational rather than blind/faithful imitation, making the technique used to solve the task more efficient. Similarly, the decrease in diversity, and thus increase in efficiency, of Kirby et al.’s (2008) artificial languages relies on mistakes made by individuals. Indeed, the structured manner in which individuals made language-learning ‘mistakes’ resulted in the structure that emerged in the language, in turn enabling efficient language learning.

To take an alternative example, New Caledonian Crows are observed to make a variety of different pandanus tools (Hunt & Gray, 2003). However, Sanz et al. (2009) assert that these tools do not enhance the efficiency with which the crows can gain food, they are simply additions to the tool which increase its physical complexity. We see this as an empirical issue: if evidence can be provided that step tools are more efficient than other tools then (provided these tools also meet the other criteria outlined in Table 1) they may yet prove to be a case of cumulative culture. Likewise, we may posit a similar argument for the stone-handling of Japanese macaques which may increase in complexity yet, as there is no apparent ‘purpose’ to the behaviour, do not increase in efficiency. Finally, there are examples in human culture in which ceremonial or decorative items become more complex to manufacture, independent of their original function (functioning instead, for example, as signs of wealth, position, skill or power) and thus without increases in the efficiency with which a target is achieved (Basalla, 1988). For example, the Torres Strait Islanders created ornate decorative (turtle shell) fish hook ornaments that were worn by married women (Hedley, 1907, cited by Florek, 2005), creating complex, carved, symbolic cultural artefacts that did not increase the efficiency of the items' original fishing function (although the efficiency with which it acted as a display could be investigated). In sum, addition to artefact or trait complexity without benefit (e.g. efficiency) carries the potential to lead to suboptimum cultural variants that are more difficult to copy (added complexity). In so far as beneficial additions are not incorporated we may hypothesize that cultural change is occurring rather than cumulative cultural *improvements*.

We emphasise that whilst cumulative culture primarily drives the complexity of cultural traits, the efficiency with which the trait is transmitted, executed, and enables achievement of its intended purpose, may also change. Thus the interplay between the complexity and efficiency of cumulative cultural traits potentially influences how traits evolve with some showing increasing efficiency and reducing complexity (e.g. language change in the laboratory), some increasing complexity and increasing efficiency (e.g. computing technology) and others increasing complexity and reducing efficiency (e.g. symbolic culture). It is noteworthy that symbolic culture, in which, for example, traditional dance may become more complex over time, without enhancing the efficiency of the behaviour, may have other social benefits (e.g. display of skill through more complex displays). As long as beneficial modifications occur, and provided examples also meet the other criteria outlined in Table 1, they should be considered examples of cumulative culture. We believe that how cultural variants change over time is a neglected aspect of research into cumulative culture, which warrants further investigation.

Conclusions

(1) Historical evidence suggests that human culture is cumulative, with successive generations building on what went before. This evidence is supported by empirical data, which suggests that humans are able to observe other individuals and modify what they have seen.

(2) Although some researchers have argued that certain non-human species ratchet up the complexity of cultural traits, the evidence that non-humans have cumulative culture is weak. Presently there is no evidence that any species, except humans, have cumulative culture. Some evidence from the wild suggests that modifications have been made to the behavioural traits of some animals, but evidence that these were socially transmitted is lacking.

(3) There have been a number of different hypotheses advanced for the evolution of cumulative culture. Current evidence supports the view that a package of sociocognitive capabilities (including teaching, imitation, verbal instruction and prosocial tendencies) present in humans, but absent or present to a lesser extent in other animals, underpins cumulative cultural learning, probably because it promotes high-fidelity information transmission.

(4) Currently, studies of cumulative culture often focus solely on increases in trait complexity. However, evidence from historical reports and experimental investigations suggest that there are also associated changes in trait efficiency, which warrant investigation.

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Chapter III

Public Information Use in Chimpanzees (*Pan troglodytes*) and Children (*Homo sapiens*)

This chapter investigates whether chimpanzees and children use public information to assess resource abundance, a necessary skill for payoff based transmission biases (see chapter IV). Specifcially, this study focusses on whether the foraging success of a conspecific influences observers' resource decisions. This chapter has been accepted for publication in the *Journal of Comparative Psychology* with the following authorship:

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Abstract

The discernment of resource quality is pertinent to many daily decisions faced by animals. Public information is a critical information source that promotes quality assessments, attained by monitoring others' performance. Here we provide the first evidence, to our knowledge, that chimpanzees (*Pan troglodytes*) use public information to guide resource selection. Thirty-two chimpanzees were presented with two simultaneous video demonstrations depicting a conspecific acquiring resources at a fast (resource-rich) or slow (resource-poor) rate. Subsequently, subjects selected the resource-rich site above chance expectation. As a comparison, we report evidence of public information use in young children. Investigation of public information use in primates is pertinent as it can enhance foraging success and potentially facilitate payoff biased social learning.

Introduction

Social learning denotes behavior or learning that is altered according to other organisms' presence, behavior or behavioral products (Heyes, 1994). A large body of evidence indicates that many animal species are capable of social learning (Brown & Laland, 2003; Galef & Giraldeau, 2001; Reader & Biro, 2010; Reader & Laland, 2002), culminating in regional variation in behavior, suggestive of tradition or culture (Perry, 2011; van Schaik et al., 2003; Whiten et al., 1999). Wild chimpanzees, in particular, display one of the broadest cultural repertoires recorded, with geographical variation in food extraction and processing methods as well as social behavior, thought to be underpinned by social learning rather than genetic or ecological factors alone (Whiten et al., 1999). Ancillary studies of captive chimpanzees support claims that social learning plays a role in regional behavioral variation in the wild (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010; Whiten, Horner, & de Waal, 2005; Whiten et al., 2007). Indeed, both arbitrary behavioral traditions (Bonnie, Horner, Whiten, & de Waal, 2007) and foraging traditions (Horner, Whiten, Flynn, & de Waal, 2006) have been shown to emerge through social learning in this species.

A trend exists in the social learning literature to document how chimpanzees socially acquire foraging techniques (Hopper et al., 2007; Horner & Whiten, 2005) and, more recently, from whom they learn (Horner et al., 2010). In particular, focus has been given to the question of whether chimpanzees imitate (broadly defined as the copying of behavioral actions) or rely on other social learning processes (Hopper, Lambeth, Schapiro, & Whiten, 2008; Tennie, Call, & Tomasello, 2006); a question that remains a topic of debate (Tennie et al., 2009; Tennie et al., 2012). Additionally, work on model-based biased social learning has begun to document selective copying with regard to whom it is that chimpanzees attend to and from whom they copy. Chimpanzees, for example, have been shown to preferentially copy dominant over low-ranking conspecifics, and selectively attend to the food associated behavior of older or same-aged individuals (Biro et al., 2003; Horner et al., 2010; Kendal et al., submitted).

One area of interest that has received relatively little attention addresses whether social information influences chimpanzees' decisions of where to forage; whether the foraging successes of others act as a cue to locating the most abundant food resources. When animals feed, they produce information, often inadvertently, through their performance, activity and decisions as well as in their by-products. This information can then be used by others as cues to resource locations (Danchin, Giraldeau, Valone, & Wagner, 2004). Theoretical modeling suggests that social learning (resulting in joining feeding conspecifics) outcompetes individual sampling in changing environments where resources with high payoffs are associated with a high probability of samplers failing to find food (Arbilly, Motro, Feldman, & Lotem, 2011). Thus, for species that experience a variable food supply, where nutritional food sources can be devoid of food (e.g., seasonal fruits, Basabose, 2004; Watts, Potts, Lwanga, & Mitani, 2012), attending to foraging conspecifics may prove an adaptive strategy. While the question of whether graded foraging performances cue resource quality judgments in primates remains understudied, evidence of the capacity to source and use social information to locate food resources has been documented in various primate species. The presence of a conspecific at one of two opaque food containers (local enhancement), for instance, can act as a social cue used by chimpanzees to locate a container baited with food (Itakura, Agnetta, Hare, & Tomasello, 1999). Similarly, Tonkean macaques (*Macaca tonkeana*) have been shown to use both olfactory and visual residual signs, produced as a by-product of conspecific feeding, to locate distant food sources of the same type (Drapier, Chauvin, & Thierry, 2002).

Social cue use has been documented in all four great ape species (*Pan troglodytes, Pan paniscus*, *Gorilla gorilla gorilla* and *Pongo pygmaeus abelii*) (Buttelmann, Call, & Tomasello, 2008). Specifically, various behavioral cues consistent with attempts to extract hidden food from one of two locations were used by subjects to infer the location of the hidden food sources. For example, a preference was displayed for baited containers, which the experimenter smelled and attempted to bite open, compared to those that were only smelled. Interestingly, Buttelmann and colleagues (2008) found that when subjects possessed personal knowledge of the absence of food in both containers, despite differential behavioral cues performed on the containers, subjects selected at random. Thus, social information use was dependent on subjects' own knowledge states (i.e., personal information) and when personal and social information conflicted, a preference was displayed for the reliable, personal information; a "copy (only) when uncertain" strategy (Kendal, Coolen et al., 2009; Kendal, Coolen, van Bergen, & Laland, 2005). More recently, chimpanzees have been shown to remember (inaccessible) locations at which they observed a human hide food items, and when eliciting the aid of a human to gain the hidden food items, they directed them first to items of high quality (Sayers & Menzel, 2012). Thus, the chimpanzees were able to store and use both personal information regarding resource quality and social information regarding location of resources following a delay. What is novel about the current study is an investigation of whether chimpanzees use social cues to assess resource *quality* (public information *sensu* Valone, 1989) and use this to guide their choice of a resource location.

Although studies have shown that primate species use social cues to locate hidden food (Buttelmann et al., 2008; Itakura et al., 1999) and that feeding conspecifics can socially facilitate other animals food consumption (Visalberghi & Addessi, 2000), little is known regarding whether primates are capable of discerning food abundance based on conspecifics' foraging successes. One of the main daily decisions facing foragers is, of course, how to optimize energetic returns. When social information acts as a cue to resource quality it is termed 'public information' (Valone, 1989). Public information, specifically, is a term derived from behavioral ecology, that, rather than referring to any information that is public (available to others), is confined to social information sourced from others' performances conveying cues regarding quality (Valone, 1989; Valone, 2007; Valone & Templeton, 2002). This can include cues to abundant resources, successful breeding partners, habitats and breeding sites and the quality of potential competitors (Valone, 2007). Public information use does not necessitate complex social learning processes; it can occur via local enhancement (Webster & Laland, 2012), feeding rate (Coolen, Bergen, Day, & Laland, 2003) and food related collective commotion (Laidre, 2013).

Public information use has been assessed in the common marmoset (*Callithrix jacchus*) (Voelkl & Huber, 2007). Marmoset pairs (demonstrator-observer) were presented with four pairs of opaque containers filled with wood chips, some of which were baited with food. The marmosets could forage simultaneously, with visual access to each other, but were separated by wire mesh. Equally, paired containers were positioned adjacent to one another but separated by mesh, so that resource sites matched for marmoset pairs. The ‘demonstrator’ marmoset was informed of food locations and thus, the ‘observer’ marmoset could maximize its foraging success by synchronizing its search for food with that of the demonstrator. Contrary to expectation, however, the availability of this social information did not enhance foraging success.

In chimpanzees, auditory information can signal resource quality. Chimpanzees, upon locating food, produce rough-grunt vocalizations that differ according to the producer’s food preferences (Slocombe & Zuberbühler, 2006), offering important resource quality information. Slocombe and Zuberbühler (2005) showed that a chimpanzee altered his foraging strategy according to playbacks of a high- versus low-quality food response, suggesting rough-grunts served as a social signal to resource quality. Overall, food searching behavior was found to be prolonged and more thorough upon hearing rough grunts produced in response to the high-quality food. Food searching additionally tended to be longer at the resource sites that were associated with the rough grunt played. Thus, rough grunts may constitute an important source of auditory public information.

In Experiment 1, we aimed to examine whether chimpanzees use visual public information - differential foraging behavior of a conspecific - to identify the most abundant food source, in the absence of vocal signals. Public information is predicted to be widespread in nature, promoting greater accuracy in environmental assessments (Valone & Templeton, 2002). Yet, research into public information use has largely been confined to species of birds and fish (Valone, 2007). The study of public information in chimpanzees is vital for understanding what social information contributes to the daily decisions made by this species, including whether public information facilitates resource maximization. Public information use was recently reported in chimpanzees (Martin, Biro, & Matsuzawa, 2011), where observers used models' behavioral actions to solve a matching to sample task. However, as the copying of behavioral decisions was not confined to resource quality (as required for the strict use of 'public information' *sensu* Valone, 1989), to date, whether chimpanzees discern patch profitability by monitoring the relative success of conspecifics is unknown.

We employed a variant of Coolen, van Bergen, Day and Laland's (2003) methodology, to examine whether chimpanzees use graded information of a conspecific foraging at a food-rich and food-poor site to inform their own foraging decisions. Simultaneous videos of a conspecific acquiring resources at two locations, each differing in terms of the rate at which food was gained (food-rich versus food-poor), were presented. Subsequently, observer chimpanzees were given access to the resource sites, and their selections recorded. Employing video-based social stimuli with chimpanzees (Hopper, Lambeth, & Schapiro, 2012) offers the advantage of presenting the same unfamiliar model at each foraging site, thus controlling for any model-based biases (Rendell et al., 2011). This is important due to the established influence of social dynamics, age, and perhaps previous track record of success (Biro et al., 2003; Horner et al., 2010; Kendal et al., submitted) to whom it is that chimpanzees attend and from whom they learn. As bird and fish species use public information (Valone, 2007), and given chimpanzees' sensitivity to behavioral cues in foraging situations, their discerning auditory food signals (Slocombe & Zuberbühler, 2005) and their ability to engage in observational learning (Martin et al., 2011), we predicted that chimpanzees would display the ability to use public information.

We were additionally interested in the ability of 5-year-old children (*Homo sapiens*) to use public information as, to our knowledge, whether children use public information to discern reward quality has yet to be empirically investigated. In Experiment 2, we replicated the chimpanzee study with 5-year old children (*Homo sapiens*), using a similar methodology. This follows previous studies that have focused on the socio-cognitive skills of both chimpanzees and children, finding that young children constitute an appropriate group to which chimpanzees can be compared (Dean et al., 2012; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Horner & Whiten, 2005). Similar to chimpanzees, the feeding behavior of children shows susceptibility to social context. Children's food preferences, for example, have been shown to alter in accordance with peer preferences (Birch, 1980a). Similarly, children's food intake and preferences have been documented to positively correlate with those of parents and other adults of the same subculture (Birch, 1980b; Orlet Fisher, Mitchell, Wright, & Birch, 2002), while the amount of food consumed has been shown to vary according to one's own size and social partner size (Salvy, Romero, Paluch, & Epstein, 2007). Given the social influence on feeding behavior and that children readily respond to social information (Lyons et al., 2011; Wood, Kendal, & Flynn, 2012), it is predicted that children would use public information as a cue to resource quality.

Experiment 1: Chimpanzees

The purpose of this study was to establish whether individual chimpanzees would assess resource quality by monitoring the relative foraging success of a conspecific feeding, or retrieving stickers, at different rates (public information use).

Subjects. Thirty-nine chimpanzees participated; three were discounted as they did not interact with the resource boxes during a pre-testing phase (see procedure) and four were discounted due to inattention to the demonstrations. The remaining 32 chimpanzees (16 male) ranged in age from 15 to 44 years (*M* = 30). Following previous studies, a dominant female (Hopper et al., 2011), unfamiliar chimpanzee served as the demonstrator. Subjects were housed at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) facility in Bastrop, TX USA. The KCCMR is fully accredited by the AAALAC-I. The chimpanzees were group housed with access to enriched indoor and outdoor enclosures with climbing facilities. Subjects had participated in previous video social learning tasks (Hopper et al., 2012) and had past exposure to video for enrichment. No food or water deprivation was used during this study which was approved by the Life Sciences Ethical Review Committee, Durham University and the Institutional Animal Care and Use Committee of The University of Texas MD Anderson Cancer Center.

Video Stimuli. Video demonstrations showed a model acquiring rewards (peanuts) at different rates (rich: approximately every 12secs, poor: approximately every 84secs; see Table 1) from two boxes (21.5 H x 10 W x 30 L cm). To achieve this, the boxes had a small hole situated at the back through which the food items were dispensed by the experimenter. The demonstrator could then retrieve the food items by reaching inside an opening at the front of the box. Thus, the peanuts themselves were barely visible whilst the foraging/eating actions of the demonstrator were. The two boxes, resource-rich and resource-poor, were colored either yellow or black. To allow counterbalancing of the box color constituting the rich resource sites

Table 1.

Time (minutes. seconds) at which single rewards were dispensed during demonstrations

Pan		Homo	
Resource-Rich	Resource-Poor	Resource-Rich	Resource-Poor
0.05	0.05	0.06	0.06
0.17		0.12	
0.29		0.18	
0.41		0.24	
0.53		0.30	
1.05		0.36	
1.17		0.42	
1.29	1.29	0.48	0.48
1.41		0.54	
1.53		1.00	
2.05		1.06	
2.17		1.12	
2.29		1.18	
2.41		1.24	
2.53	2.53	1.30	1.30

during the test sessions, four video demonstrations were captured (yellow rich; black poor; black rich; yellow poor, with the same demonstrator used in all demonstrations). To ensure that the demonstrator sourced individual peanuts at the predetermined rates, where appropriate video demonstrations were edited slightly using Picture Motion Browser and Windows Live Movie Maker. Video editing consisted of cutting and/or looping subsections of the demonstrations. All recordings were captured with a Sony Handycam.

Figure 1. Model retrieving rewards from the resource boxes (video demonstrations stills)

Design and Procedure

Pre-tests. As neophobic reactions to novel objects can occur in chimpanzees, a habituation stage was performed to expose subjects to the resource boxes prior to running the experiment. Chimpanzees were given sequential, color counterbalanced, exposure to the baited resource boxes. Chimpanzees that did not retrieve a grape from both boxes during this session (*N*=3) were eliminated from the study. This pretest identified subjects who lacked the motivation to participate and/or those that would fail to select a resource box in test sessions due to neophobic responses to the apparatus.

Color preference was assessed using a dichotomous preference paradigm (Hopper et al., 2011). In 10 successive, counterbalanced and unrewarded trials, the experimenter simultaneously held one cylindrical token (yellow/black) in each hand and chimpanzees selected one via gesture. No color preferences were observed (yellow token selections from 10 trials $M = 4.81$, $SD = .90$; binomials, all $p > .05$, $N = 36$).

Experimental Test. Chimpanzees were tested individually and voluntarily within their indoor compartments (ca. 2.4x2.4x1.8m^3). Demonstrations were presented on two computer monitors (48.26 cm) on separate trolleys (85 H x51 W x51 L cm) located adjacent to one another (separated by cf. 40cm). The two opaque boxes (yellow/black), from which the demonstrator retrieved resources, were positioned in front of the trolleys behind an occluding barrier, and positioned (left/right) to match the box color depicted in the corresponding video. The color (yellow/black) constituting the resource rich patch and the side (left/right) it was presented were counterbalanced. All subjects received one trial only. Test sessions were video recorded.

Following the demonstrations, the resource boxes were simultaneously revealed by removal of the occluding barrier and pushed toward the subjects. The resource boxes were designed such that the observers could not see the food rewards inside until they had placed their hand inside the hole at the front. Resource selection was defined as the first resource box the subjects touched. The unselected box was then removed by the experimenter to prevent chimpanzees from gaining rewards from both boxes. Upon box selection, chimpanzees could retrieve the food item from their chosen box. To reduce food intake, and since only one trial was conducted with each subject, resource boxes were each baited with one banana piece only, irrespective of box quality. This also prevented potential olfactory cues arising from a large amount of food placed in one box only. Subjects were allocated up to two minutes to make their selection, after which the trial would be terminated and the subject discounted. In practice all selections were made in less than 13 seconds and no individuals were discounted. Subjects' attention (head orientation) to the videos was noted at 10-second intervals, and those (*N* = 4) not meeting a criteria of attention at ≥ 6 10-second intervals, were discounted.

Statistical Analysis. Due to the small sample size and dichotomous dependent variable, non-parametric statistics were used. First we investigated whether the number of resource rich selections differed from chance (50%) using the Binomial Test. Mann-Whitney U-Tests were conducted to ascertain whether subject age, latency to box selection and attention levels differed according to resource selection (rich/poor). Whether resource selection differed according to sex, the video-sets viewed (yellow rich/black rich) and the sequential order of box presentation during the pre-test habituation phase, was assessed using Chi Square and Fisher's Exact (where contingency tables contained expected values of below 5) Tests. Binomial Tests were additionally used to assess side and color biases in resource selections (chance = 50%).

Results

As predicted, the majority (22 of the 32) chimpanzees selected the resource-rich box following presentation of the demonstrations (binomial, *p* = .03, one tailed, 95% CI [.53, .84]; see Figure 2). The mean time taken to select a resource box was 4 seconds (*SD* = 3). No significant differences were observed between age (*U* = 74.50, *N* = 32, *p* = .15), sex (χ^2 (1) = 2.33, *p* = .25), latency to selection (*U* = 94.50, *N* = 32, *p* = .54) or attendance (*U* = 95.50, *N* = 32, *p* = .57) as a function of the resource box selected.

There was no significant difference in resource box selection following the demonstration as a function of the box presented first during the box exposure pretest (χ^2 (1, 32) = 2.32, *p* = .25). Resource box selections did not differ according to the different video-sets needed to counterbalance color and resource richness (FET: *N* = 32, *p* = 1. 00). Moreover, the chimpanzees displayed no side bias (binomial: *N* = 32, *p* = .38, left *N* = 13 and right *N* = 19) nor color bias (binomial: *N* = 32, *p* = .86, black *N* = 15 and yellow *N* = 17).

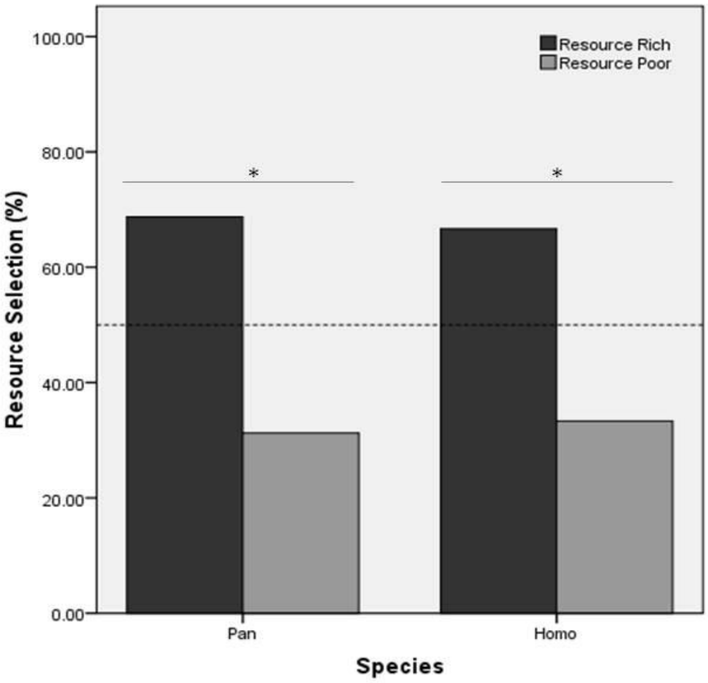

Figure 2**.** Resource-rich and resource-poor selections (%) per species. Dotted line represents chance level, *=*p*<0.05.

Experiment 2: Children

Experiment 1 showed that chimpanzees discerned resource quality from video demonstrations. We now turn to the question of whether children use public information to assess resource quality. The child study methodology was identical to the chimpanzee study except for changes, detailed below, to accommodate species differences.

Participants. Thirty-six 5-year-old children (17 male) were recruited from three primary schools in the North East of England. A single female child, unfamiliar to the participants (aged 5 years), acted as the demonstrator, via video, for all children.

Video Stimuli. Video presentations were shorter in duration (1 minute 40 seconds) than for the chimpanzees and, due to retention of the overall resource quantities presented (rich 15 versus poor 3), the rate at which each reward was dispensed at the resource rich location was increased (from every 12 to every 6 seconds; see Table 1). Stickers constituted the resource due to the ethical considerations of provisioning consumables. The boxes consisted of two opaque hemisphere-shaped plastic containers (total surface area 763.41 cm^2). As children display color preferences (Boyatzis & Varghese, 1994), the boxes were differentiated by pattern (large or small black squares). Upon retrieving stickers, the demonstrator placed them in an opaque cup. This prevented a stack of stickers accumulating which could have served as an additional cue for the children, relative to chimpanzees where rewards were immediately consumed by the demonstrator.

Design and Procedure. Testing was conducted in a quiet room at each child’s school away from the rest of their class. Each child participated in one trial only. Participants were told by an experimenter (GV), “I would like you to watch videos of a girl getting stickers, and then after the videos you will get a chance to find stickers” and given verbal prompts (“are you watching the videos?”, “can you see what the little girl is doing?”) if attention lapsed. It is noteworthy, that children were encouraged to attend to the videos by experimenter prompting, with no verbal prompts given to the chimpanzees. Following the videos, the occluding barrier was removed to reveal the resource boxes and children were instructed, “You can have a look in the boxes now”. Participants were allocated up to one minute to make a resource selection, defined as the first box touched or gestured toward. The chosen box was then opened to retrieve the stickers. The number of baited stickers in the resource rich and resource poor boxes matched the number obtained by the demonstrator in the corresponding videos (15 and 3, respectively). As the data was derived from one trial only, the number of stickers gained did not influence the study results.

Results

As predicted, 24 of 36 children selected the resource rich location, which is above that predicted by chance alone (binomial test: $p = .03$, one tailed, 95% CI [.51, .82] see Figure 2). Average time to box selection was 6 seconds (*SD* = 5). Resource selection was not related to sex ($\chi^2(1) = .22$, $p = .73$) or box selection latency ($U = 95.50$, $N = 36$, $p = .10$). No side (binomial test; $N = 36$, $p = .24$) or box pattern preferences (binomial test; $N = 36$, $p = .62$) were observed. There was no significant difference in the species’ tendencies to choose the ‘rich’ patch ($\chi^2(1) = .03$, $p = 1.00$).

Discussion

Chimpanzees and children are capable of social learning (Horner et al., 2006). Numerous studies have documented that group specific traditions occur in these species through differential copying of knowledgeable conspecifics (Flynn & Whiten, 2008; Whiten et al., 2005; Whiten et al., 2007). Such studies have tended to concentrate on the copying of behavioral methods, often using tools, of gaining a food reward i.e., (novel) food extractive behavior. Less is known about whether social information relating to differential food abundance guides primates’ subsequent foraging decisions. The ability to discriminate between resource qualities using public information allows profitable food sources to be identified and visited with potentially greater accuracy than if using personal information alone (Arbilly et al., 2011; Valone, 2007). Our results indicate that chimpanzees, and 5-year-old children, possess this ability, interestingly showing high concordance in public information use across species. Thus, in addition to attending to social cues to locate food sources (Buttelmann et al., 2008; Itakura et al., 1999), chimpanzees and children were able to select reward sources according to the graded acquisition (of food/stickers) performance of a conspecific. Children and chimpanzees thus performed at comparable levels despite methodological differences including verbal attention prompts for children and not chimpanzees and the provisioning of stickers versus consumables.

Foraging decisions rely on various cognitive skills. Route planning, cognitive maps, memory of food sources, travel time, competition for food and likelihood of patch depletion can all influence decisions of where to forage (Noser & Byrne, 2010). Much of this information is derived from personal experience; however, social foragers are afforded an additional information source derived from others' activities (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Our results suggest that public information sourced from conspecific foraging success may, in addition to personal information (Beran, Evans, & Harris, 2008) and auditory signals (Slocombe & Zuberbühler, 2006), aid in locating quality resources in chimpanzees and hence constitute one more factor among many that could contribute to foraging decisions

The use of public information has many implications. Primates may optimize foraging efficiency through exploiting inadvertent social information manifested in the foraging activity of conspecifics (Arbilly et al., 2011). In the present study, the relative number of times or the rate at which the demonstrator reached inside each resource box to acquire reward items, and the subsequent consumption activity for chimpanzees, could constitute potential cues by which resource quality was determined. Future investigation would benefit from control conditions to isolate the cues utilized to discern resource abundance. The inclusion of consumption only and reward retrieval without consumption would prove beneficial conditions in this regard.

Public information use can allow patch estimation to occur without engaging in personal sampling (Coolen et al., 2003). Public information may therefore aid decisions of food approach through an assessment of whether food sources will support additional foragers without direct food contest. That is, use of public information could benefit foragers through conflict avoidance by allowing a predetermination of whether approach would likely result in conflict due to low resource abundance versus safer approach to more abundant non-monopolizable food sources. When public information is derived from successful dominant foragers, an ability to use it following the departure of that individual may prove beneficial for subordinate observers (McQuoid & Galef, 1992). Chimpanzees have been shown to remember, following a delay, locations they previously saw a human hide food and to ‘direct’ a human helper to hidden food of high quality first (Sayers & Menzel, 2012). This, along with other numerous studies, show that chimpanzees are capable of delayed social information use (Bering, Bjorklund, & Ragan, 2000; Bjorklund, Yunger, Bering, & Ragan, 2002). It is worth noting however that where food is markedly limited, public information will be of little value, even after a delay, since due to depletion, food consumption depends upon who discovers it first

(Giraldeau, Valone, & Templeton, 2002). In this context, reliance upon personal information would best serve the forager. Thus considerations of public and personal information use are pertinent to chimpanzees, a species in which fission-fusion dynamics are pronounced, as they allow assessment of resource distribution and abundance, factors that can underwrite party size (Aureli et al. 2008).

Public information has the potential to aid foraging activity through signaling patch depletion (Fraser, Ruxton, & Broom, 2006; Templeton & Giraldeau, 1995). It is of interest that chimpanzees and children selected the resource box associated with the demonstrator retrieving rewards at the fastest rate. This suggests that the faster feeding rates did not signal patch depletion. While increased feeding rate can mark rapid food depletion, sustained high rates should signal food abundance and slower (or reducing) rates should indicate limited food supply. Finding that chimpanzees and children displayed a preference for the resource supporting rapid food retrieval is in line with reports that species are attracted to food sites at which feeding rate is faster (Coolen et al., 2003; Coolen, Ward, Hart, & Laland, 2005). To investigate whether public information provides cues to patch depletion, it would be of interest to examine the influence of demonstrator foraging success, varying success (x retrieval attempts with no food obtained) and the feeding rate (gradual reduction versus increase rate of food obtained) in addition to utilizing real-time demonstrations.

While chimpanzees in this study displayed a preference for the rich resource box, it remains unclear whether this finding would hold in a group context. Video footage of a foraging demonstrator, theoretically, could have alleviated any competitive foraging demands that would otherwise occur in more naturalistic group settings, including dominance factors (Emery Thompson, Muller, Kahlenberg, &

Wrangham, 2010; Muller & Wrangham, 2004; Sapolsky, 1992). This scenario is beneficial for the establishment of whether chimpanzees *can* use public information, but nevertheless does not allow an assessment of whether they *do* use public information more generally in the wild (Boesch, 2007, 2008). In groups, factors such as the dominance rank of those already foraging, the number of foragers, food distribution (monopolizable or not) and species level foraging strategies (e.g., contest and/or scramble competition) will likely play a prominent role in foraging decisions (Murray, Eberly, & Pusey, 2006; Murray, Mane, & Pusey, 2007).

Moreover, in chimpanzees, foraging strategies also differ according to sex and reproductive status. Lactating females tend to visit fewer of the available high value resources per day than do sexually receptive females and males, but stay at resource locations longer (Bates & Byrne, 2009). Males, in contrast, have been shown to use linear daily foraging paths, indicative of a strategy of combining foraging needs with territorial defense (Bates & Byrne, 2009). Accordingly, although chimpanzees in this study showed public information use, individual foraging strategies employed in the wild, including patch departures, are mediated by optimizing food intake, and other factors such as sex specific needs. Thus, foraging decisions in this species represents a complex process that may not only rely on personal and public information, but one that is also variable according to individual needs.

To understand decision making in chimpanzees (and children) it is important to determine the information sources underpinning behavioral actions. In this study we demonstrated that public information derived from differential foraging success can influence subsequent foraging decisions. How human and non-human primates weight personal and public information, especially when they conflict (Kendal, Coolen et al., 2005), and how social dynamics (Coussi-Korbel & Fragaszy, 1995), such as dominance rank, influence public information use, represent further important questions. Moreover, the pertinence of public information, especially in species displaying traditions (Laland & Galef, 2009), lies in its use enabling payoff assessments of resources without participating in personal sampling which can be costly in terms time and energy losses (Valone, 2007). To this end, public information has the potential to facilitate informed payoff biased copying decisions, whereby individuals adopt behaviors in proportion to their profitability. One aspect of import to cumulative culture, in which cultural traits and behaviors become more complex and efficient across generations such that a single individual could never invent the trait within its lifetime (Tennie et al., 2009), is recognizing when a behavioral option is a beneficial modification which should be incorporated into the existing cultural trait (Laland, 2004). Public information may promote rudimentary 'copy if better strategies' (Schlag, 1998, 1999), allowing the 'ratcheting up' (Tennie et al., 2009) of cultural traits (e.g., technology) over generations. If quality assessments - made through monitoring the relative payoffs gained by conspecifics, or one's self, using different traits - encourages the social acquisition of beneficial trait modifications (e. g. food processing techniques), these could have potential consequences for cultural evolution. Specifically, it is possible that cumulative culture, which is widely held to be responsible for humanity's success (Kendal, Rendell, Pike, & Laland, 2009), depends upon use of "payoff biased" social learning strategies. Whether public information use may promote selectivity in what is copied through facilitating such payoff biased social learning, and whether use of such cultural transmission biases (Rendell et al., 2011) is instrumental in the observed cross-species distribution of cumulative culture (Dean et al., 2012), requires further investigation.

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Chapter IV

Payoff Biased Copying in Chimpanzees (*Pan troglodytes*) and Children (*Homo sapiens*)

In the previous chapter, a form of success copying, specifically ‘public information use’ was established in chimpanzees and children. This Chapter investigates a specific form of copying related to the success of others, specifically, payoff biased transmission in chimpanzees and children. This research remains in preparation and has not been submitted to a journal. Likely journals are *Current Biology* and *PLoS ONE*. Authorship is displayed below.

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Abstract

Payoff biased copying allows beneficial cultural modifications to be incorporated into observers' repertoires, having important implications for cultural progression and cumulative culture. In this study we investigated whether chimpanzees (*Pan trogodytes*) and 4-and 5-year old children (*Homo sapiens*) copy according to three payoff copying rules: Proportional Imitation, in which copying depends upon payoffs to demonstrators and self; Proportional Observation, in which copying is dependent upon payoff to demonstrators only, and; Proportional Reservation, in which copying is dependent upon satisfaction with reward to self only. Using an exchange task, groups received personal experience with one token type and its corresponding reward. Participants in the model Seeded condition then observed a model exchange an alternative token for a different reward of greater, equivalent or lesser value than the first reward, depending on group. In the following open diffusion sessions, unlimited access was given to both token types. Our results indicated that both children and chimpanzees showed differential token exchange according to token payoffs. Specifically, we report the first tentative evidence that children utilised a Proportional Observation strategy and chimpanzees a Proportional Imitation strategy. The implications of these payoff biased copying rules in each species' extent of cultural evolution are discussed.

Introduction

Cumulative culture, denotes the progressive enhancement of cultural complexity and efficiency, to the extent that individuals cannot invent these cultural products within their own lifetime (Dean, Vale, Laland, Flynn & Kendal, in press; Tomasello, 1999; Tomasello & Wrangham, 1994). Why other animals that are capable of acquiring information socially may lack, or are extremely limited in, this process of cultural ratcheting (Tomasello, 1990; Tomasello, Kruger, & Ratner, 1993) and, relatedly, what human cognitive adaptations have moulded our own cultural evolution (Griffiths, Kalish, & Lewandowsky, 2008) remain significant questions (Dean et al., in press). A suite of psychological attributes, inclusive of sophisticated social (imitation and teaching; Fogarty, Strimling, & Laland, 2011; Lewis & Laland, 2012) and asocial (innovation and modification: Ehn & Laland, 2012) learning mechanisms, prosociality (Dean, Kendal, Schapiro, Thierry & Laland, 2012), shared intentionality (Tomasello, Carpenter, Call, Behne, & Moll, 2005), cooperative processes (Tennie, Call & Tomasello, 2009), social tolerance (Coussi-Korbel & Fragaszy, 1995), language (Carruthers, 2013) and transmission biases (Rendell, Fogarty, Hoppitt, Morgan, Webster & Laland, 2011) have all featured as factors thought to be influential in cultural progress. However, whether these factors influence the level of cultural development exhibited by different species has only recently been under empirical investigation (Dean et al., 2012; Marshall-Pescini & Whiten, 2008). In this study, we take the first comparative step to establish whether transmission biases play a role in two primate species' (*Pan troglodytes* and *Homo sapiens*) propensities to optimize behavioural efficiency in their use of social information; a key capability for cumulative culture.

Social learning strategies, sometimes called transmission biases (Boyd & Richerson 1985), refer to evolved heuristics that influence when, whom and what to copy (Laland, 2004; Mesoudi & Whiten, 2008; Rendell et al., 2011). In facilitating selective copying these biases contribute both to whether, and the extent to which, cultural variants spread in populations. Transmission biases are theorized to confer fitness benefits to social learners by improving the quality of culturally transmitted information (Chudek, Heller, Birch, & Henrich, 2012). Specifically, they may protect against indiscriminate social learning and an overreliance on social information that could otherwise promote the uptake of maladaptive, unreliable or outdated information (Laland, 2004).

Confirmation for the predicted selective and adaptive use of social learning has been provided by recent empirical studies (Kendal, Coolen, van Bergen & Laland, 2005). Children, for example, copy adults more faithfully than peers (Wood, Kendal & Flynn, 2012), prestigious (preferentially attended to) individuals rather than those not attended to (Chudek et al., 2012), and more accurate models rather than less accurate models (Birch, Vauthier, & Bloom, 2008; Brosseau-Liard & Birch, 2010). Adult humans have been shown to: engage in state dependent strategies such as 'copy when uncertain' (Flynn & Smith, 2012; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2011), employ frequency dependent strategies (e.g. 'copy rapidly increasing traits'; Toelch, Bruce, Meeus & Reader, 2010) and copy according to model attributes (e.g. copy successful and prestigious individuals; Atkisson, O'Brien, & Mesoudi, 2012; Mesoudi, 2008). Surprisingly, investigation has only just begun to explore the possible transmission biases present in our closest living relatives, chimpanzees, showing that they preferentially attend to older individuals (Biro, Inoue-Nakamura, Yamakoshi, Sousa & Matsuzawa, 2003), copy individuals who are simultaneously dominant, successful, and older (Horner, Proctor, Bonnie, Whiten & de Waal, 2010), ‘copy when uncertain’, ‘when of low rank’, as well as ‘copy dominants and knowledgeable individuals’(Kendal et al., submitted).

A particular, yet understudied, subset of transmission biases comprise of strategies that relate to an aspect of the model’s competency and success. Success biased copying constitutes a model-based bias, also termed an ‘indirect transmission bias’ (Boyd & Richerson, 1985), in which a measurement or proxy of model success contributes to learning likelihoods, rather than the trait itself. Success copying rules are well positioned to facilitate the propagation of beneficial traits by extracting adaptive information (Baldini, 2012). The conditions under which success biased copying rules emerge within populations, and how they influence the propagation and optimization of cultural variants, have begun to be explored through theoretical models and simulation studies. Success-based copying, for instance, has been shown to outcompete asocial learning, random copying and conformist bias in multimodal fitness landscapes in an arrow-head design computer simulation (Mesoudi & O'Brien, 2008a). Concomitant empirical studies have highlighted the role of success biased copying in optimizing participant performances, supporting theoretical findings. Mesoudi and O’Brien (2008b) showed that human participants, who employed a ‘copy successful individuals’ strategy in a multimodal fitness landscape, outperformed asocial learners during a virtual arrow-head design task. Extending these findings, Mesoudi (2011) showed that humans preferentially employed a ‘copy successful individuals’ strategy over other social learning strategies (conformity, random copying and trait averaging). Furthermore, visibility of information regarding the success of others (based on trait combinations) has been shown to promote overall performance levels through discriminate social learning and the propagation of innovations (Wisdom & Goldstone, 2010). Specifically, success feedback, when available, was used in 79% of copying events in the form of a ‘copy the most successful player’ strategy. Success-opaque task situations, by contrast, constrained a participant’s performance and task efficiency (Wisdom & Goldstone, 2010).

A more ‘direct’ bias is that based on payoffs which allows individuals to copy the behaviour of others depending upon the payoffs associated with a given behaviour and not due to any other model characteristic (e.g. their general ‘success’). Payoff biased learning may be particularly important for cumulative culture as copying judgements are made according to a ‘direct’ proxy for the observed trait or behaviour (trait-payoff), rather than for example, judgements of the value of a model that can promote maladaptive trait hitchhiking (Boyd & Richerson, 1985). Denrell and Lui (2012) recently demonstrated this; when success was dependent on progressive accumulation of accomplishments it failed to provide a consistent indication of skill since early chance events impacted on later success. Similarly, Mesoudi and O’Brien (2008b) found that participants employing a ‘copy successful individuals’ rule copied non-functional arrow-head attributes (i.e. their colour) along with functional attributes (e.g. their length and width).

Theoretical and empirical considerations have focussed on transmission biases where ‘success’ is defined as specific trait payoffs that contribute to individual fitness and are specific to the task faced by the learner. Such payoff biased social learning has been shown to increase optimum choice discovery (McElreath, Bell, Efferson, Lubell, Richerson & McElreath, 2008) and to be favoured in temporally changing environments, often outcompeting other forms of learning (Nakahashi, Wakano, & Henrich, 2012). Furthermore, payoff biased social learning has been found to promote the uptake of rare cultural traits which is important in changing environments where optimum traits are likely to be few (Baldini, 2012). Uncertainty in behavioural payoff has additionally been found to have detrimental effects to cumulative culture, eliciting higher copying fidelity at the expense of cultural artifact refinement (Caldwell & Millen, 2010). These findings stress the importance of payoff information for successive cultural improvements across generations and iterative learning events.

Given the benefit of payoff biased transmission it may be expected that, when payoffs are known and assessed without too much cognitive load, payoff biased learning should be favoured over general success biased transmission. Economic consideration of payoff biased learning has yielded three copying strategies thought to enhance agent's copying decisions, namely: (i) Proportional Imitation (PI), where an individual copies the behaviour of another in proportion to how much better the demonstrator's payoff is than his/her own; (ii) Proportional Observation (PO), where individuals copy in proportion to the demonstrators' payoffs only, (iii) 'Proportional Reservation (PR)', also termed 'copy if dissatisfied', where individuals copy according to satisfaction with their own behavioural payoff (Schlag, 1998, 1999). These rules, particularly Proportional imitation, were found to confer benefits to the learner over 'copying the most successful' variant, which could lead to suboptimal trait copying, especially when a small number of models were sampled. Laland (2004) predicted that nonhuman animals' limited capacities for cumulative culture may be explained, in part, by the inability to determine whether behavioural alternatives displayed by others yield better payoffs than ones already in the observer's repertoire. Instead, it was proposed that animals may widely employ the less cognitively demanding strategy of 'copy if dissatisfied' (Proportional reservation), that omits an assessment of a demonstrator's rewards (Proportional observation) and comparing the observed rewards to rewards to self (Proportional imitation) (Laland, 2004). Initial support for these claims was provided by female Norway rats, who demonstrated a Proportional reservation strategy ('copy if dissatisfied') (Galef, Dudley, & Whiskin, 2008), though the dissatisfaction was in a general, rather than specific payoff related, sense (Kendal, Coolen & Laland, 2009). Nine spined sticklebacks and humans alike, in contrast, have been shown to use a Proportional observation strategy, with copying dependent upon a demonstrator's payoffs (Kendal, Rendell, Pike & Laland, 2009; Morgan, Rendell, Ehn, Hoppitt & Laland, 2011; Pike, Kendal, Rendell, & Laland, 2010). These studies notwithstanding, empirical investigation into payoff biased learning in species, including our own, remains in its infancy.

In the present study we test whether two primate species, chimpanzees and children, employ payoff biased copying strategies as outlined by Schlag (1998; 1999). Chimpanzees are of interest here since they show a comprehensive cultural repertoire (Whiten et al., 1999) and forms of social learning similar to our own (e.g. imitation and emulation). Chimpanzees are also capable of distinguishing rewards based on differential numerousness and quality both using personal (Beran & Beran, 2004; Beran et al., 2008; Hanus & Call, 2007) and public information (Vale, Flynn, Lambeth, Schapiro & Kendal, in press), a prerequisite for payoff biased social learning. Here, chimpanzees and children were tested in semi-naturalistic group settings, employing a variant of the token exchange paradigm (Brosnan, 2011). Exchange tasks have previously been employed to investigate primate species economic decision making skills, particularly in answer to inequity aversion. Importantly, such inequity aversion findings suggest that chimpanzees respond to rewards distributed to self and other when they are unequal, displaying elevated food and exchange refusal upon the partner receiving a better reward than the subject (Brosnan, Schiff, & de Waal, 2004; Brosnan, Schiff, & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; although see Brauer, Call & Tomasello, 2006). This implies that chimpanzees have the building blocks to support a Proportional imitation social learning strategy.

Payoff biased copying requires social learning. Social learning has also been investigated using token tasks (Bonnie, Horner, Whiten, & de Waal, 2007; Brosnan & de Waal, 2004; Hopper, Schapiro, Lambeth & Brosnan, 2011). Brosnan and de Waal (2004) showed that brown capuchin monkeys (*Cebus apella*) displayed a preference for a high-value (in terms of reward) token option following exposure to a conspecific exchanging this, over a low-value alternative. Conversely, Hopper and colleagues (2011) found that chimpanzee groups copied the token preference of a seeded model irrespective of whether the token was paired with a low or high value food reward. Key methodological differences likely explain these contrasting findings across species. These include, group testing (chimpanzees) versus dyadic testing (capuchins) and model demonstration of both token options (capuchins) versus one token option (chimpanzees). Accordingly, it is premature to conclude that chimpanzees lack the ability to optimize reward gains since task situations, and indeed other copying strategies such as ‘copy dominant individuals’, may have limited its expression.

The present study provisioned multiple tokens of two types to groups of chimpanzees and groups of children. Tokens differed in their outward appearance (contrasting shape and colour) and reward value (Small-Low-value or Large-Medium-value, depending on condition: see method section). To ensure that both token types were discovered by participants, individuals first gained experience with one token type before exposure to an alternative token type (model demonstrated: Seeded condition; non-demonstrated: Non-Seeded condition). This allowed an assessment of whether group members switched to exchange of this token alternative according to reward values and the presence of a trained model. It was hypothesized that both species would display application of payoff biased copying. Due to the novelty of this study, no specific strategy predictions were made. Given that payoff transmission influences the propagation of beneficial traits allowing culture to evolve, the identification of any differences across species may go some way in explaining the vast gap in cultural accumulation observed between ourselves and chimpanzees. Conversely, similarity in payoff biased social learning strategies across species will rule out the possibility of these rules being sufficient for cumulative culture to emerge to the differential extent observed between chimpanzees and humans.

Study 1: Chimpanzee Method

Participants

Eighty-three chimpanzees participated (M_{age}=29.96 years; 49 females). Following previous studies (Hopper et al., 2011), medium to high ranking females served as demonstrators. Participants were housed at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) facility in Bastrop, TX USA. The KCCMR is fully accredited by the AAALAC-I. The chimpanzees were group housed with access to enriched indoor and outdoor enclosures with climbing facilities. Asocial control participants (*N*=11) were tested individually and voluntarily within their indoor compartments (ca. $2.4\text{x}2.4\text{x}1.8\text{m}^3$). Six Asocial control participants were lost due to lack of participation. All other testing was group-based and conducted in the large outdoor enclosures (ranging from 5-11 chimpanzees per group). The majority of participants had previously participated in social learning investigations. No food or water deprivation was used during this study which was approved by the Life Sciences Ethical Review Committee, Durham University and the Institutional Animal Care and Use Committee of The University of Texas MD Anderson Cancer Center.

Materials and Procedure

Chlorinated polyvinyl chloride (CPVC) pipes formed non-edible tokens for exchange; elbow pipes coloured black (1.9cm diameter, height 7.5cm) and straight pipes coloured yellow (1.9cm diameter, length 20cm, Figure 1). Dichotomous colour preference tests revealed no colour preference for black or yellow in chimpanzees (procedure described in Appendix A).

Figure 1. Exchange Tokens

Tokens were distributed to the group via two token receptacles spatially separated by 3.96m and attached to the mesh of the enclosure (Figure 2). Yellow tokens were placed into a yellow receptacle and black tokens a black receptacle (33cm H x 33cm L x 28cm W). Each receptacle contained an internal gradient that ensured the dispensed tokens fell towards an opening in the front to allow easy token access. The token's colour representing the initially learned token reward and the side (left/right) on which it was presented were counterbalanced across groups. Food rewards were contained in two opaque and different coloured buckets (blue/green: height 38cm), with the colour of bucket holding the large-medium value (Large) reward counterbalanced across conditions. Food bucket colours did not match token/receptacle colours (i.e. black/yellow) to prevent possible over-cueing or over-simplification of the task. The food was cut into small pieces, approximately 2.5x 2.5cm (depth 0.5cm).

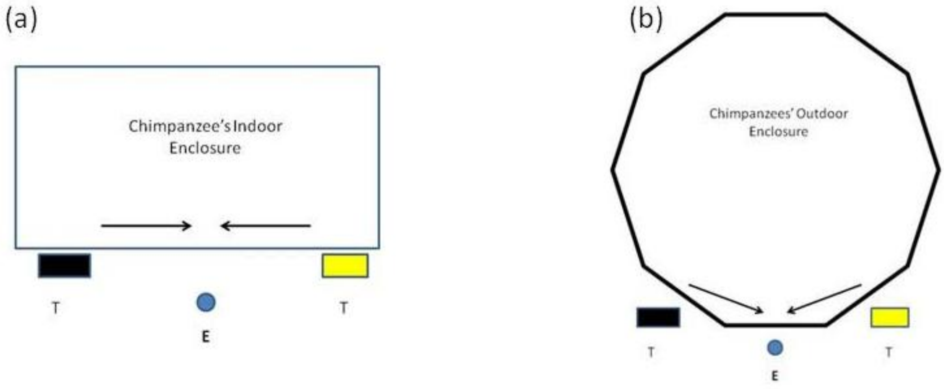

Figure 2. Chimpanzee experimental set-up (a: asocial condition; b: group conditions). Tokens were dispensed via two receptacles (T locations, yellow and black) positioned either side of the experimenter (E). Chimpanzees could retrieve tokens from either receptacle (T) during testing. To retrieve a reward, tokens had to be transported and exchanged at the central location (E). Rewards were concealed in two opaque buckets located either side of the experimenter (at location E).

Rewards for each token consisted of one carrot piece ('Small') or four apple pieces ('Large') (note we class apple as a medium value food as additional preference tests showed a clear preference for grape over apple; see Appendix A for details of preference test procedure). An additional motivation test showed that chimpanzees were motivated to exchange tokens for a single carrot piece (see Appendix A). Three reward conditions, dictating the value of the first personally learned ‘pre-experienced’ token and the value of the ‘alternative’ token, were presented; SS Condition (Small => Small); Condition SL (Small => Large); Condition LS (Large =>Small) (see Table 1).

Table 1.

Model and Reward conditions

Reward Condition	Token Value			Participation (Model Condition)		
	Pre-experienced		Alternative	Asocial	Non-seeded	Seeded
LS	Large	=>	Small	x	1 group	2 groups
SS	Small	=>	Small	x	1 group	2 groups
SL	Small	=>	Large	5 Pts	1 group	2 groups

Note: Small = 1 carrot piece, Large=4 apple pieces; x =no participants; Pt's = participants

The three conditions enable an assessment of the underlying learning strategies as follows (see Table 2): copy if dissatisfied (Proportional reservation) will be evidenced by a greater proportion of individuals proceeding to exchange the alternative token (demonstrated by the model) in conditions where their personally acquired reward is of low rather than high value. If participants are satisfied with the Large reward and dissatisfied with the Small reward we predict proportions of alternative tokens exchanged as follows: SS=1, SL=1, LS=0; Proportional observation (determined by demonstrator’s payoff only) evidenced by a greater proportion of individuals proceeding to the alternative token in conditions where the socially demonstrated reward is of high rather than low value. Given this strategy, we predicted that the proportion of alternative tokens exchanged would equal 1 in the SL condition, with lower but equal proportions exchanged in the SS and LS conditions; Proportional imitation (relative payoff to self and other) evidenced by a greater proportion of individuals progressing to the alternative token in conditions where the payoff to self is lower than the payoff to the demonstrator. Employment of this strategy was predicted to yield proportions of alternative tokens exchanged as follows: SL=1, SS=.5, LS=0.

To distinguish the role of social learning in token choices three model conditions were presented: Asocial controls (individuals tested away from their social group); Non-Seeded (tested in groups, no trained demonstrator of alternative token); Seeded (tested in groups with exposure to a trained demonstrator). For the Seeded condition, testing occurred in three stages; (i) Pre-experience phase wherein personal experience was gained within the group context with one token type only; (ii) Model observation phase wherein conspecifics observed a trained female demonstrator exchange a different token to that in the pre-experience phase; (iii) Open diffusion wherein all individuals had access to both token types. For example, individuals in the Seeded SS condition (see Table 1) exchanged the pre-experienced token for carrot during the pre-experience stage, observed a model exchange the alternative token for carrot, and in open diffusion sessions could exchange either token for carrot. Individuals in the Non-Seeded condition followed the same procedure as the corresponding Seeded condition except

Table 2.

Outline of Schlag's payoff biased copying rules according to the number of individuals likely to copy model token preference within reward conditions

Schlag's Payoff Strategies	Copy in proportion to…	Copying likelihood
Proportional Reservation	…satisfaction with own payoff only	SS>LS, where **SS=SL**
Proportional Observation	…the demonstrator's payoff only	SL>SS, where **SS=LS**
Proportional Imitation	…difference in payoff to self and demonstrator	SL>SS>LS

Note: LS=Large=>Small; SS=Small=> Small; SL=Small=>Large they did not receive the model observation phase. Asocial controls were conducted to provide an asocial comparison to group conditions, in which social learning was possible (both Seeded and Non-Seeded groups). This condition was run for the SL condition as it was the one of interest in relation to whether participants switch to the 'better' token through social learning.

Chimpanzees were exposed to a minimum of three, maximum of five, pre-experience (all model conditions) and model observation (Seeded condition only) sessions (see below for phase durations), until 60 percent of individuals personally exchanged 20 tokens/observed at least 10 model exchanges or the maximum of five sessions was reached. Cut off points were required to avoid certain participants obtaining extensive personal or social information, while others did not.

Model Training. Models were trained in isolation, out of view of their group members. Medium to high dominance bounds were used for model selection as the highest ranking female in each group would not always voluntarily isolate for training (or be motivated to train). Models were trained to exchange one token type by only rewarding exchanges with the desired token. Initially only the desired token was made available forcing the participant to exchange this token only. Multiple tokens of each type were then provisioned. Models were considered trained upon exchanging the desired token, when both were available, 10 consecutive times across two sessions. Each training session lasted between ca. 15-30 minutes.

Pre-Experience Stage: Personal Information. All groups and Asocial controls first gained experience with one rewarded token type. Both receptacles were present but only one was baited by the experimenter with multiple tokens of the same type. Chimpanzees could exchange tokens by giving or throwing tokens through the mesh at the exchange area (Figure 2, location E). For groups, each session lasted one hour. For Asocial controls, each session lasted 15-minutes, to avoid potential stress upon reintroductions to constituent groups. Note that pilot tests, with individuals not included in this study, showed that Asocial individuals exchanged approximately the same number of tokens (Mean = 10 exchanges in the first15 minute session) compared to a Non-Seeded group equivalent (11.8 exchanges during the first hour session).

Model Observation Phase/Social Information: Seeded condition. The model observation sessions were shorter than the pre-experience phase, with each session lasting 30 minutes. This was in an attempt to (i) minimize the potential for chimpanzees employing a ‘copy when personal information is outdated’ strategy (van Bergen, Coolen, & Laland, 2004), and (ii) to lessen the likelihood that individuals would copy the dominant model’s token preferences irrespective of token payoffs (Hopper et al., 2011).

Model observation sessions were conducted in the outdoor enclosure, in the absence of token receptacles, in a group setting. Sessions would begin when the model approached the exchange area. If necessary, the experimenter would call the model over to this area. The alternative token was handed to the model by the experimenter. To gain a reward, the model had to pull the token into her enclosure (through the mesh) before exchanging it back with the experimenter. All group members were free to observe model exchanges. Token provisioning was employed to control who received the token (i.e. model only), thus ensuring only social information was available to chimpanzees. Token receptacles were not baited as it was deemed unlikely that models (mid-to high-ranking females) were of sufficient dominance to gain access to a single token if placed in its receptacle. If conspecifics stole the alternative token from the model, the exchange was rewarded to avoid extinguishing the behaviour.

Testing Phase: Open Diffusions. Each group session lasted one hour (6 sessions conducted per group). Prior to tests, the experimenter and an additional person (care staff or researcher) simultaneously dropped 30 tokens into each token receptacle. Exchanged tokens were placed in one of two opaque buckets dependent on token type. Upon the yellow token bucket becoming half full and/or the black a quarter full (due to token size difference), receptacles were replenished with the exchanged tokens. After each exchange, food was provisioned by the experimenter. Model exchanges with the untrained token were not rewarded to encourage persistent trained token preferences. Again, session durations were reduced for Asocial controls (two 20-minute test sessions were conducted). All sessions were videotaped and narrated for later coding.

Data Scoring and Reliability

Exchange was defined as pushing, throwing or giving a token through the wire mesh of the enclosure at the exchange location. Exchanges, token type (pre-experienced or alternative), exchanger identity, time of exchange and conspecifics attending to the exchange (defined as within 3m proximity and head orientated towards exchanger/experimenter) were recorded. Food steals (successful gaining of food from the exchanger), steal attempts (unsuccessful attempt to gain exchanger's food) and scrounging (collection of fallen or discarded food) were also recorded. Stolen tokens, whereby a token was exchanged for reward by an individual other than the token retriever were noted. An independent coder assessed a subsection of the data (20 minutes per reward condition) for purpose of inter-rater reliability, recording participant identity, time of token exchange and the colour of token exchanged. High agreement was attained (token type exchanged: Kappa coefficient: .84, $p<0.001$). Due to high inter-rater reliability, we could be confident in the original coding which was retained for subsequent analysis.

Statistical Analysis

Where data violated parametric assumptions (normality and homogeneity of variance), non-parametric equivalents were used. The Levene's Statistic was employed to test homogeneity of variance and Shapiro-Wilk for normality testing. Data were transformed when transformation could meet test assumptions. Where necessary a constant was added to each data point (0.5) prior to transformation. SPSS Bonferroni adjusted *p*-values are reported for Post-hoc tests following ANOVAs only, otherwise (Bonferroni) corrected alpha* is specified. Demonstrator's behaviour was excluded from analyses, with the following exceptions: exchanges observed by conspecifics were included for the purpose of analysing attention levels to conspecific (including model) exchanges; token steals and food steals/attempts to steal/scrounging *from* models were included. Chimpanzees who failed to exchange a single token (of either type) were also excluded from the main analysis. Again, food steals/attempts to steal/scrounging *from* these participants were included.

Results

In this section we consider levels of token exchange during the three study phases (pre-experience/model observation/open diffusion). Levels of attention to conspecific exchanges are considered (as an indication of participants collecting social information) before turning to the levels of token exchange by model (to assess social learning) and reward conditions (to assess selective learning according to differential reward values).

Pre-Experience Phase**.** During the personal/pre-experience stage, participants exchanged 46 (Mean) tokens (*SD*=53.03; range 1-234); 12 participants exchanged less than 10, and 5 participants exchanged over 100, tokens. There was no difference in the number of tokens exchanged according to whether the token yielded the Large reward or Small reward (*U*=352.50, *p*=.885, *N*=57).

Model Observation: Seeded groups. During the model observation stage participants attended to 20 (Mean) exchanges (*SD*=16.54) with models exchanging 93 (Mean) tokens (*SD* = 30.54).

Attendance: Open Diffusion. Throughout the 6 hours of open diffusion, participants attended to 72 (Mean) conspecific exchanges (*SD*=60.68, range 2-277); 3 participants attended to less than 10, and 18 participants to more than 100 conspecific exchanges. Individuals in the Seeded condition attended to proportionally more alternative token exchanges (alternative conspecific exchanges observed/total number of conspecific exchanges observed; *M*=.553) than individuals in the Non-Seeded condition (*M*=.312; ANOVA: *F*(1,52)=21.308, p<.001, $\eta\rho^{2}$ =.291, Figure 3). There was also a main effect of reward condition on attendance (ANOVA: *F*(2,52)=19.640, *p*<.001, $\eta\rho^{2}$ =.430, Figure 3). Post Hoc tests revealed that the proportion of alternative token exchanges attended to was higher in SL (*M*=.664) groups than in LS groups (*M*=.317, *p*<0.001, 95% CI [.220, .473]) and SS groups (*M*=.451, *p*<0.001, 95% CI [.084, .341]). SS groups attended to a higher proportion of alternative tokens than LS groups (*p*=.044, 95% CI [.003, .2652] Figure 3). There was no interaction between reward condition and model condition (*F*(2,52)=1.092, *p*=.343, $\eta\rho^2$=.040).

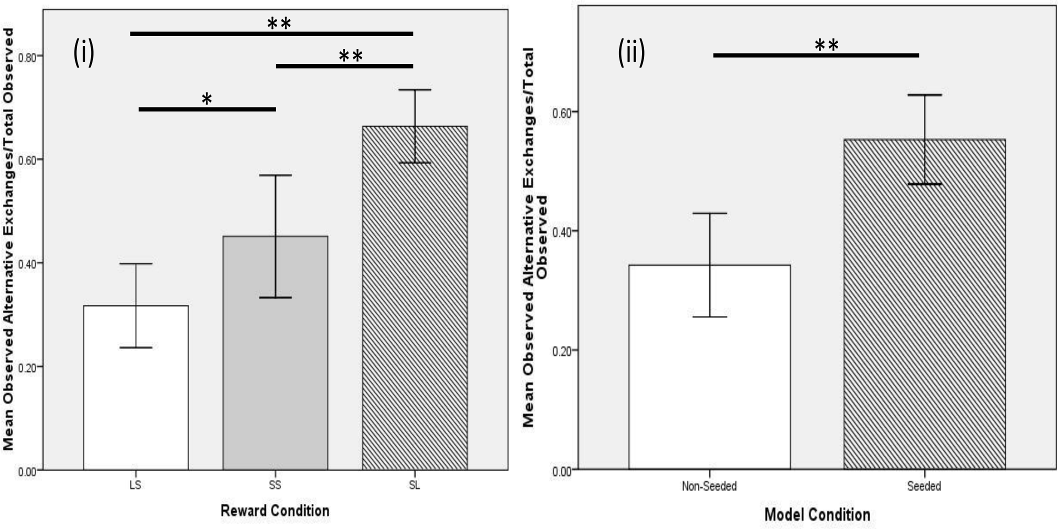

Figure 3. Attendance to conspecific exchanges made with the alternative token as a function of reward condition (i) and model condition (iii). Error bars represent 95% Confidence intervals. **p*<.05; ***p*≤.01.

Seeded Open Diffusion: Token Exchanges According to Reward Condition. Mean proportions of alternative tokens (alternative exchanged/total exchanged) exchanged significantly differed as a function of reward condition 2 =.155; Figure 9 below). Bonferroni post-hoc comparisons revealed the mean proportion of alternative tokens exchanged was significantly greater in the SL (.64) group than the LS (.29) group (*p*=.044). All other comparisons were not significant (*p*s>.05; SS *M*=.50). There was no significant association between the token exchanged first (pre-experienced/alternative) and reward condition (LS/SS/SL) (Fisher's Exact Test (FET): *N*=39, *p*=.559).

While no significant difference was observed between the levels of tokens exchanged by the LS and SS group (but note small sample sizes per reward condition), the pattern of exchanges (see Figure 4) was suggestive of a proportional imitation rule (SL>SS>LS).

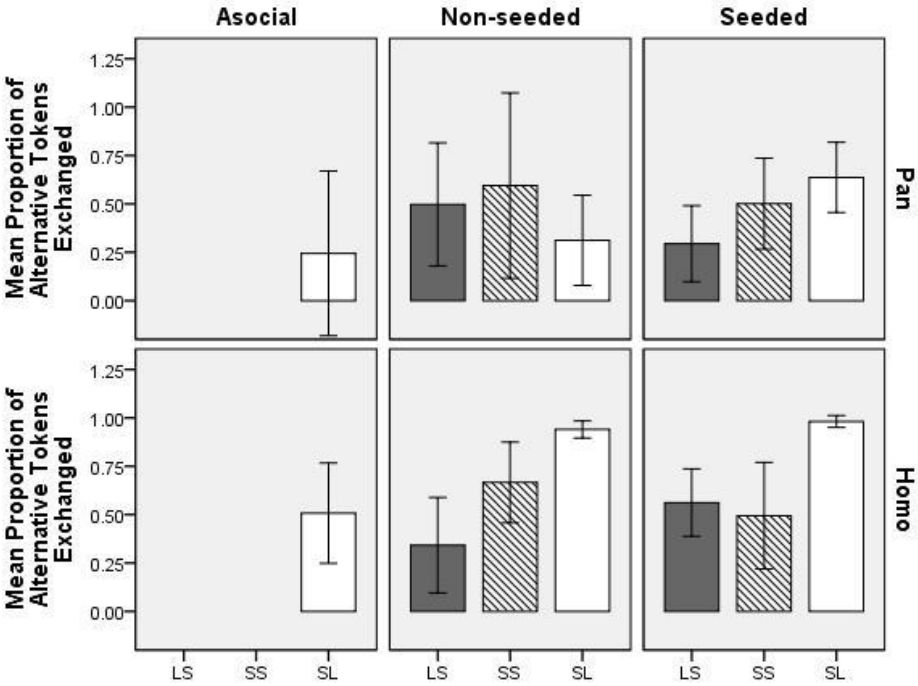

Figure 4. Alternative tokens exchanged according to model and reward condition and species. Error bars represent 95% confidence intervals.

The mean proportion of alternative tokens exchanged in the SL condition (*M*=.64) significantly differed from the predicted proportion of alternative exchanges given employment of a proportional imitation rule (1.00; One sample T-test: *t*(13)=-4.32, *p*=.001, 95% CI of the difference [-.55, -.19]). The mean proportion of alternative tokens exchanged by chimpanzees in the LS condition (.29) significantly differed from the predicted proportion of alternative exchanges (.00; One sample T-test: *t*(11)=3.29, *p*=.007, 95% CI difference [.10, .49]). There was no significant difference between the expected (.50) and actual (*M*=.50) proportion of alternative tokens exchanged in the SS condition (*t*(12)=.01, *p*=.99, 95% CI difference [-.23,.24]).

There was a significant difference in proportion of alternative exchanges made by chimpanzees in the LS (*M*=.29) condition and the predicted level of token exchange (equal to the SS condition: .50, One sample T-test: (*t*(11)=-2.30, *p*=.042, CI 95% difference [-.40, -.01]). Thus support for chimpanzees' employment of the Proportional observation rule was not found.

Non-Seeded: Open Diffusion Token Exchanges according to Reward Condition. There was no significant difference according to reward condition (LS/SS/SL) in the number of alternative tokens exchanged as a proportion of the 2=.130). A Fisher's Exact test revealed there was no significant association between the token type (pre-experienced/alternative) first exchanged and reward condition (LS/SS/SL) (*p*=0.064).

Individual Token preferences in Open Diffusion according to Reward Condition and Model Condition. Binomials were conducted to determine individual token choices, allowing each participant's overall preference to be identified (pre-experienced/alternative/ no preference: see Appendix B Table B2). A significant association was observed between reward condition and individual token preferences in the Seeded condition (FET: *p*=.027, see Figure 5 below). The number of individuals displaying a preference for the alternative token (alphas*=.0167) in the LS (N=0/12) and SL (N=8/14) conditions significantly differed (FET: *N*=26, *p*=.002, phi=.617). There was no difference in the number of individuals who preferred the alternative token between the LS and SS (4/13) conditions (*N*=25, *p*=.096), or the SL and SS conditions (chi: χ^2 (1,27)=1.899, *p*=.168). Overall, in the

Non-Seeded groups there was no significant association between reward condition and participant token preferences (pre-experienced/alternative/no-preference) (FET: *N*=19, *p*=.811).

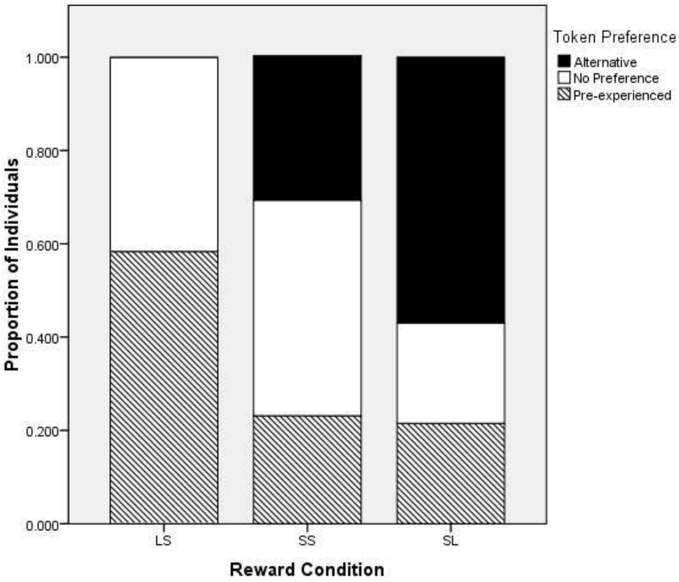

Figure 5. Token preferences displayed in the Seeded groups.

Exchange Patterns over time. Due to loss of statistical power and large confidence intervals, exchange performance over time was not statistically analysed for Non-seeded chimpanzees. This was due to small sample sizes and intermittent individual participation across test days. Inspection of Figure 6, nevertheless, indicates that the mean proportion of alternative tokens exchanged by Non-seeded chimpanzees was generally higher (SL condition) or lower (SS condition) by the final test session (day 6) than in their first test session (day 1). For seeded chimpanzees there was no significant main effect of time (day 1versus day 6) on the proportion of alternative tokens exchanged (*F*(1,20)=.109, *p*=.745). There was no significant interaction between time and reward condition (*F*(2,20) =.065, *p*=.937). Not accounting for reward condition, there was no significant difference in the proportion of alternative tokens exchanged by Non-seeded (*W*=12.00, *N*=8, *p*=.401) or Seeded (*W*=23, *N*=23, *p*=.575) chimpanzees on Day 1 and Day 6.

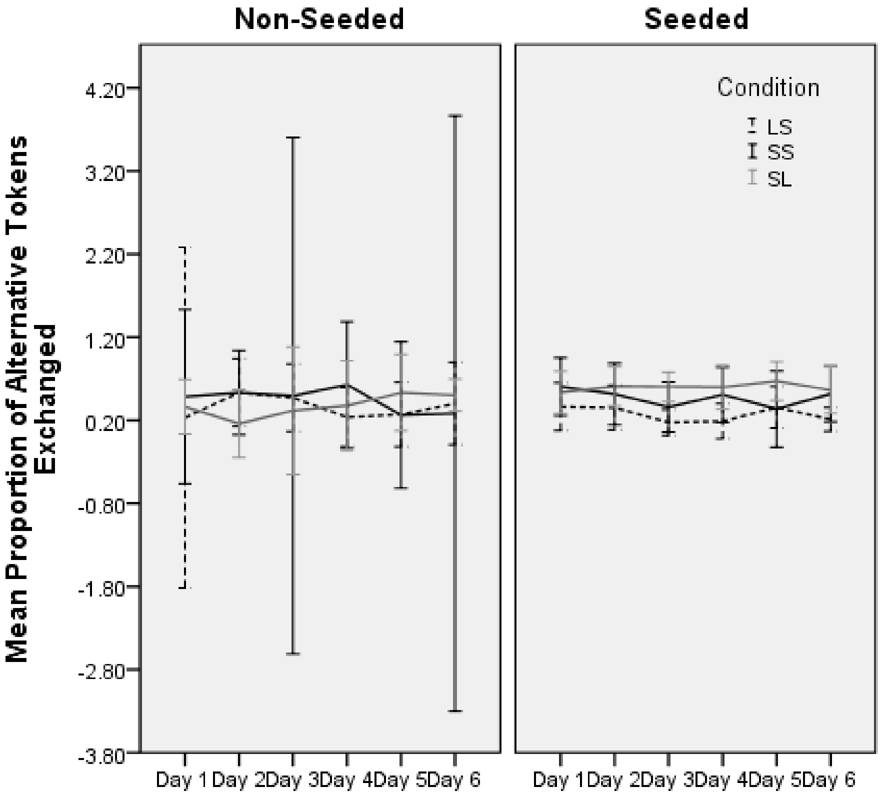

Figure 6. Tokens exchanged according to test day, model and reward condition. Error bars represent 95% confidence intervals.

Asocial Controls. Asocial control individuals exchanged a mean of 63 (*SD* = 10.27) pre-experienced tokens during the personal experience pre-tests. During test sessions, with access to both token types, overall 118 pre-experienced (*M*=23.6, *SD*=17.40) and 45 alternative tokens (*M* =9.00, *SD*=17.97) were exchanged (See Appendix B Table B 1). There was no significant difference observed in the median number of pre-experienced and alternative tokens exchanged per individual (*Z*=-1.095, *N*=5, *p*=.375). However, the number of pre-experienced tokens exchanged exceeded what would be expected by chance alone (binomial, *p*<.001).

Asocial versus Group Open Diffusion Exchanges: SL Condition. Overall, 27.6 % of Asocial, 49% of Non-Seeded and 65% of Seeded (SL) participant exchanges were made with the alternative (Large) token. Alternative token exchange was 2.36 times more likely in Seeded groups than in Asocial controls; 1.78 times more likely in the Non-Seeded group than in Asocial controls; and 1.33 times more likely in Seeded than Non-Seeded groups.

As Asocial controls exchanged proportionally more tokens on average (*M*=32.62) and in total (163) during the first 40 minutes of testing than individuals in the Seeded condition (*M*=7.42, total exchanges = 89 for 2-groups), we compared the first 163 exchanges made overall by individuals in the SL condition according to model condition (SL Asocial/SL Non-Seeded/SL Seeded). Asocial individuals exchanged significantly more of the pre-experienced tokens (*M*=23.60) than Seeded (*M*=8.71; *t*(17)=2.516, *p*=.022, 95% CI mean difference [2.404, 27.367], alphas*=.025) but not Non-Seeded (*M*=18.20; *t*(8)=.543, *p*=.602) individuals. No significant difference was observed in the number of alternative tokens exchanged by Asocial (*M*=9.0) and Seeded (*M*=14.64; *t*(17)=-.591, *p*=.576, alphas*=.025) or by Asocial and Non-Seeded (*M*=13.80; *t*(8)=-.380, *p*=.714) individuals. As shown in Table 3, for the first 163 exchanges, Asocial individuals exchanged more pre-experienced tokens than alternative tokens; and individuals in both Seeded groups exchanged more of the alternative than pre-experienced tokens.

Table 3.

Token Preferences according to Model condition (1^{st} 163 tokens exchanged by group only)

Model Condition	Tokens Exchanged		Token Preference
	Pre-experienced	Alternative	
Asocial	118	45	P
Non-seeded	94	69	-
Seeded (group 1)	67	96	A
Seeded (group 2)	54	109	A

Note: P=Pre-experienced token preference; A = Alternative token preference;
- = No token preference

There was no significant difference in latency to exchange the Large token at the open diffusion stage according to whether groups were seeded with a model (*MD*=18 min 05 sec, *IQR*=48.11) or not (*MD*=19 min 34 sec, *IQR*=161.17; Mann Whitney U-Test: *U*=30.00, *N*=18, p=.805). Asocial control participants' latencies to exchange could not be directly compared to the groups since they did not have to deal with social dynamics when exchanging. There was no significant association between model condition (Asocial/Non-Seeded/Seeded) and the token type first exchanged (FET: *N*=62, *p*=.789).

Participants with no history of participating in inequity aversion tasks exchanged a greater number of pre-experienced tokens in the Asocial condition (*M*=23.60) than those in the Seeded SL condition (*M*=6.60; *t*(13)=2.723, *p*=.017). There was no difference in the number of pre-experienced tokens exchanged by inequity task naïve chimpanzees in the Non-Seeded and Asocial conditions (*t*(6)=-.244, *p*=.815).

Conservatism. Strong conservative behaviour would predict that participants, irrespective of model presence (Seeded/Non-Seeded) and token rewards, would display a preference for the token exchanged in the personal pre-experience stage. Conversely, if an explorative strategy was employed, a preference to exchange the alternate, unseen, token first would be expected in Non-Seeded and Asocial conditions. There was no evidence of either strategy as the token type (pre-experienced/alternative) first exchanged by Non-Seeded and Asocial participants 2 1,24=.000, *p* = 1.000). No preference was observed for first exchanging either the pre-experienced (*N*=29) and alternative tokens (*N*=34) (Seeded/Non-Seeded/Asocial 2 (1,63)=.397, *p*=.529). There was additionally no significant difference in pre-experienced (*MD*=18.00, *IQR*=48.00) and alternative (*MD*=19.00, *IQR*=36) token exchanges made by all participants (reward and model conditions collapsed; Sign Test: *Z*=-.512, *N*=63, *p*=.609).

Token and Food Theft. Overall there were 38 counts of attempted food theft and 31 successful food thefts, as well as 12 successful scrounging events. Excluding groups in the SS conditions (wherein tokens were equally rewarded), attempted (92%) and successful thefts (93%), and scrounging events (100%) were directed towards the Large food, significantly exceeding what would be predicted by chance alone (binomial: *ps*<0.005). To examine whether food (attempted) theft, and scrounging were associated with performance, correlations were conducted between each of these variables and the number of Large tokens exchanged. There was no correlation between either the number of scrounging events per individual (Spearman’s rank coefficient: rho = .223, *N*=40, *p*=.166), the number of attempted (rho = .109, *N*=40, *p*=.502) and successful (rho = .096, *N*=40, *p*=.554) food thefts and the number of Large token exchanged.

During open diffusion sessions chimpanzees also stole conspecifics’ tokens. Overall, 79 such cases were documented, 42 of which were for the alternative token.

Excluding the SS group, there was no preference observed for stealing a token yielding the Large (*N*=35) or Small (*N*=30) rewards (FET: *p*=.620).

Overview of Findings: Chimpanzees. In the Seeded condition, chimpanzees exchanged a greater proportion of alternative tokens in the SL than did individuals in the LS condition. The level of tokens exchanged by Seeded groups was suggestive of a proportional imitation rule (SL>SS>LS), albeit chimpanzees exchanged fewer (SL<1), or more (LS>0), alternative tokens than was predicted for this copying strategy (SL=1, SS=.5, LS=0). Chimpanzees in the SS condition exchanged tokens at random. In contrast, there was no difference in the proportion of exchanges made with the alternative token according to reward condition for Non-Seeded individuals. When considering the SL condition only, social demonstration was important in the development of a preference for the alternative token.

Study 2: Child Method

The child methodology followed that employed with chimpanzees, with the following adjustments, outlined below, to accommodate species' differences.

Participants

Sixty-three 4- to 5-year-old children (*M*=4.87, 38 females) participated. Participants were recruited and tested in their primary schools (UK) in mixed-sex groups (N=7-10, lower group numbers were due to absences, Table 4). Informed consent was provided by participants' parents or guardians.

Table 4.
Child participation according to model and reward conditions

Reward condition	Token Value			Participation (Model Condition)		
	Pre-experienced		Alternative	Asocial	Non-Seeded	Seeded
LS	Large	=>	Small	*X*	1 group	1 group
SS	Small	=>	Small	*X*	1 group	1 group
SL	Small	=>	Large	9 Participants	1 group	1 group

Note: Small = 1 'plain' sticker, Large=4 'smiley' stickers; x=no participants.

Materials and Procedure

Due to ethical considerations of provisioning food to children, stickers constituted the rewards. A single, small, coloured, circular sticker formed the Small reward and four larger, coloured, circular, smiley face stickers the Large reward. Dichotomous preference tests revealed a preference for the four smiley stickers over the single plain sticker (see Appendix C). Black (full length, 28cm) and white (folded in half, 14 cm) pipe cleaners formed the differential tokens for children. No preference was observed for either token type (see Appendix C). Tokens were distributed to the group via two token receptacles spatially separated by 140 cm. White tokens were placed into a white receptacle with a lid and black tokens were placed in a black receptacle with a lid (38cm x 34cm x 8cm). Each receptacle was placed on the floor ca. 220 cm away from the exchange area, with the lid on and the relevant tokens inside at the beginning of tests (see Figure 7). Rewards were contained in two opaque and different coloured opaque cylinders with lids (blue/green: height 17cm).

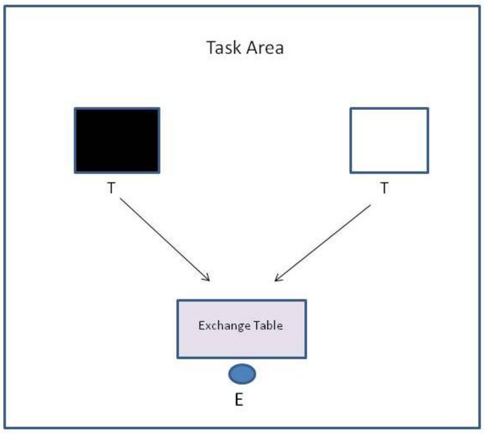

Figure 7. Child experimental set-up. Tokens were dispensed via two receptacles (T locations, white and black) positioned either side/in front of the experimenter (E). Children could retrieve tokens from either token location (T) during testing. To retrieve a reward, tokens had to be transported and exchanged at the central location (E). Rewards were concealed in two opaque cylinders located either side of the experimenter (at location E).

Children experienced the same reward conditions (LS, SS, SL) and model conditions (Asocial, Non-Seeded, Seeded) as chimpanzees (Table 1 above). Pilot tests conducted with a group of 9 children (not incorporated into the present study) indicated the need to reduce test times to maintain motivation levels. The pre-experience phase was run for 20 minutes, followed by 10 minutes of model observation (Seeded-groups only), followed by 30 minutes of open diffusion with access to both tokens. Children received at least a 2 hour break between each phase. Asocial controls were run for 10 minutes (5 minutes pre-experience and 5 minutes access to both token types).

At the beginning of testing, the experimenter gave the following verbal instructions; “I would like to play a sticker game. In the boxes there are tokens and every time you give me a token I will give you stickers. You can look in the boxes now” (pre-experience phase); “I would like to play the sticker game again, but this time it is [model’s name] turn” (model observation phase); “I would like to play the sticker game again. In the boxes there are tokens and every time you give me a token I will give you stickers. You can look in the boxes now” (open diffusion phase). All children were provided with an opaque plastic cup in which stickers could be placed. Children were free to stop participating at any time. For the Seeded groups, one female (medium dominance/popularity/age) from each group served as the model. Dominance and popularity was assessed by two members of staff using ratings (who, in each dyad, would win a contest over a toy [dominance] and who had more friends in their class [popularity] (Flynn & Whiten, 2012). Model training consisted of simply asking the model, away from the rest of the group, to exchange the pre-specified token. Understanding was confirmed by requesting the model to repeat what they had been asked and by asking ‘what token should you exchange?’. Prior to running the OD sessions, this training process was repeated. If models exchanged the incorrect token during later diffusion, no reward was provided. Thus, models were also informed that “if you give me token [X] you will not get sticker(s)”.

Data Scoring and Reliability

Exchange was defined as giving a token to the experimenter, placing it on the exchange desk or holding their plastic cup towards the experimenter with a token inside. An independent coder assessed a subsection of the data (5 minutes per reward condition) for purpose of inter-rater reliability. High agreement was attained (token type exchanged: Kappa coefficient: .848, p<.001).

Results

As with chimpanzees, in this section we consider levels of token exchange during the study phases (pre-experience/model observation/open diffusion). Levels of attention to conspecific exchanges are considered before turning to the level of token exchange according to model and reward conditions.

Pre-Experience Phase. During the pre-experience stage, participants exchanged 12.8 (Mean) tokens (*SD*=6.4). There was no significant difference in the number of tokens exchanged during this stage according to whether the token yielded the Large reward (*M*=13.7) or Small reward (*M*= 12.7; *t*(58)=.556, *p*=.580, 95% CI mean difference [-2.678, 4.743]).

Model Observation: Seeded groups. During the model observation stage, participants attended to 23.1 (Mean) exchanges (*SD*=11.08) with models exchanging, on average, 37 tokens overall (*SD* = 7.34).

Attendance during Open Diffusion. Participants attended to 39.6 (Mean) peer exchanges (*SD*=23.6). There was a significant difference in the proportion of attention given to exchanges depending upon token type (alternative) and reward $2\ 2,51 = 41.179, p$<.001, see Figure 8). Individuals attended to a greater proportion of alternative tokens (alternative/total observed exchanges, alphas*=.0167) in the SL (*MD*=.94, *IQR*=.13) than in SS (*MD*=.64, *IQR*=.09; *U*=5.50, *N*=34, *p*<.001) and LS (*MD*=.38, *IQR*=.19; *U*=.000, *N*=35, *p*<.001) conditions, and in the SS than in the LS condition (*U*=17.00, *N*=33, *p*<.001).

There was a significant difference in the level of attendance to peer exchanges according to token type (reward and model conditions collapsed: Sign Test: -2.970, *N*=51, *p*=.003), such that participants attended more to exchanges of alternative (*MD*=18.00, *IQR*=12.00) than pre-experienced (*MD*=9.00, *IQR*=27.00) tokens. For the groups (Seeded and Non-Seeded) that were exposed to tokens of differential value, attention to conspecific exchanges was significantly lower to those involving Small (*MD*=4, *IQR*=18.00) than Large rewards (*MD*=28, *IQR*=22.00; *Z*=-4.733, *N*=35, p<.001).There was no significant difference in attendance to the alternative token according to whether the group was seeded or not (*t*(26.867)=-1.665, *p*=.108).

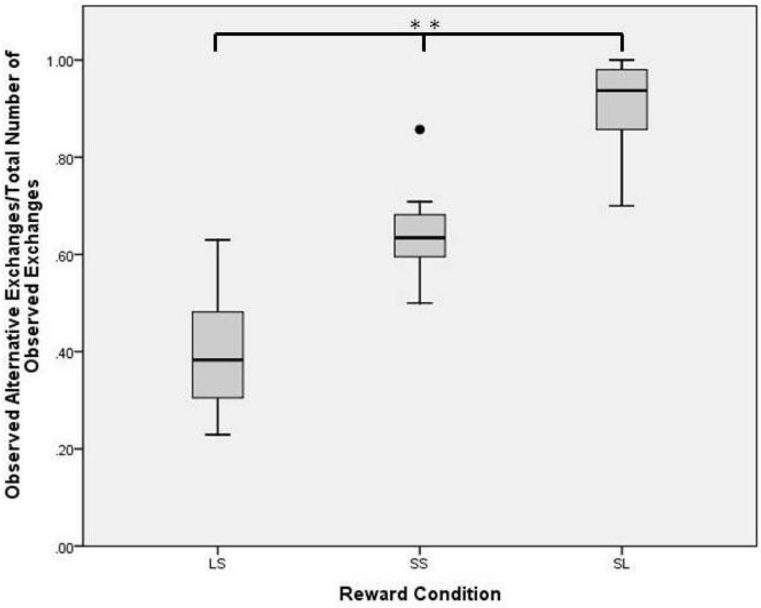

Figure 8. Median proportion of alternative token exchanges attended to (out of total attended exchanges; black horizontal line) as a function of reward condition. Whiskers represent the minimum and maximum attendance (unclassified outliers represented by circles) and boxes represent interquartile ranges.

Token Exchanges in Open Diffusion according to Reward Condition:

Seeded groups. There was a significant difference in the proportion of alternative tokens exchanged by individuals in Seeded groups according to reward condition (K-

2(2,21)=14.38, *p*<.001, Figure 4 above). Individuals in the SL condition (*MD*=1.00, *IQR*=.07) exchanged a greater proportion of alternative tokens (alpha*=.0167) than SS individuals (*MD*=.49, *IQR*=.54; *U*=.00, *N*=14, *p*=.001) and LS condition (*MD*=.54, *IQR*=.22; *U*=.00, *N*=15, *p*<.001). There was no difference in the proportion of alternative tokens exchanged between SS and LS conditions (*U*=20.00, *N*=13, *p*=.945).

Inspection of Figure 4 (see above) indicates SL>LS, SS=LS (employment of the Proportional observation rule). The proportion of alternative tokens exchanged in the SS (*MD*= .49) did not significantly differ from the predicted proportion (.54) given employment of this Proportional observation strategy (One sample Wilcoxon Signed Rank test: *W*=12.00, *N*=6, *p*=.753). The proportion of alternative tokens exchanged in the SL (MD=.97) did not differ from the predicted proportion (1.0) given employment of Proportional observation (*W*=21.00, *N*=8, *p*=.67). There was no difference in the number of alternative and pre-experienced tokens first exchanged by Seeded individuals according to reward condition (FET: *N*= 24, *p*=.810), as first exchanges made with the alternative token were at a high level, irrespective of reward condition (LS: 6/8; SS: 6/7; SL 8/9 alternative 1st exchanges).

Token Exchanges in Open Diffusion according to Reward Condition: Non-Seeded. There was a significant difference in the proportion of alternative tokens exchanged by Non-Seeded groups according to reward condition (K-W: χ^2(2,30)=10.74, *p*=.005). Individuals in the SL condition (*MD*=.94, *IQR*=.11) exchanged a greater proportion of alternative tokens (alphas*=.0167) than SS individuals (*MD*=.73, *IQR*=.45; *U*=18.50, *N*=20, *p*=.014) and LS (*MD*=.28, *IQR*=.56) condition (*U*=8.00, *N*=18, *p*=.003). There was no difference in the proportion of alternative tokens exchanged between SS and LS conditions (*U*=24.00, *N*=18, *p*=.165). There was no significant association between the token type first exchanged and reward condition (FET: *N*=30, *p*=.50).

Individual Token Preferences in Open Diffusion according to Reward Condition: Learning Strategies. Binomials were conducted to determine individual token choices, allowing each participant's overall preference to be identified (see Appendix D Table D2). In the Seeded condition, there was a significant association between reward condition and individual preferences for the alternative token (FET: *N*=21, *p*=.013, phi=.644, Figure 9). A greater proportion of individuals displayed a preference for the alternative token in the SL (7/8) than LS (1/7) condition (FET: *N*=15, *p*=.01, phi=.732; alphas*=.0167). No difference in individual token preference was recorded between the SS (2/6) and SL conditions (*N*=14, *p*=.091), or between SS and LS (*N*=13, *p*=.559).

In Non-Seeded groups, there was again a significant association between reward condition and alternative token preferences (FET: *N*=30, *p*<.001, phi=.813). The proportion of individuals with a preference for the alternative token was significantly higher in the SL (10/10) than in the LS (1/10) (FET: *N*=20, *p*<0.001, phi=.905, alphas*=.0167) and SS (2/10) (FET: *N*=20, *p*=0.001, phi=.816) conditions. There was no difference between SS and LS conditions (FET: *N*=20, *p*=1.000).

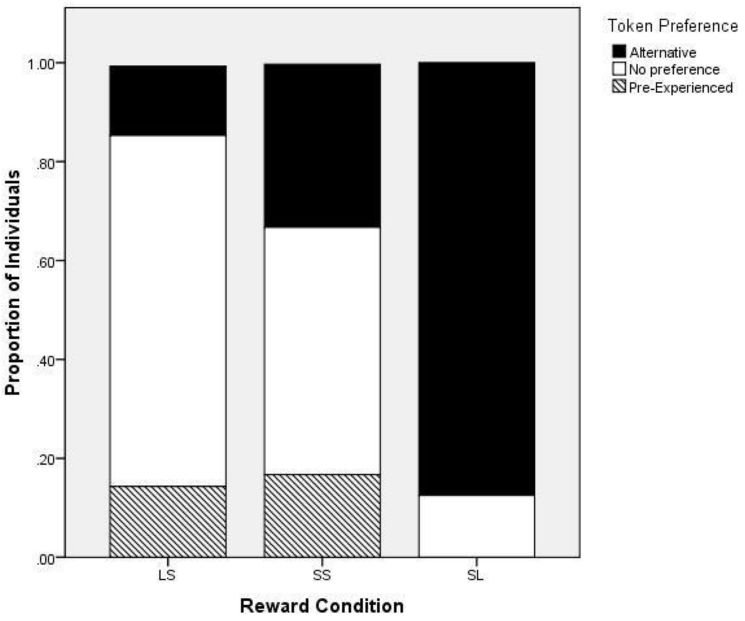

Figure 9. Proportion of individuals within each reward condition displaying token, or no token, preferences (Seeded condition only).

Asocial SL Control. Overall, Asocial controls (*N*=9) exchanged a mean average of 20.6 (*SD* = 3.20, range 15-26) (pre-experience phase). During sessions with access to both token types, exchanges totalled 105 pre-experienced (*M*=11.67, *SD*=8.94), and 90 (*M*=10.00, *SD*=6.98) alternative, tokens. There was no significant difference in the number of pre-experienced (Small) and alternative (Large) tokens exchanged (Wilcoxon: *W*=-.059, *N*=9, *p*=.977). At the participant level, five participants selected tokens at random, two showed a preference for the alternative token and two for the pre-experienced token (see Appendix D Table D1).

Asocial versus Group Exchanges: SL Condition. Asocial controls, overall, exchanged 195 tokens during test sessions (*N*=9 x 5 minute tests), which was approximately comparable to the number of tokens exchanged by Seeded (SL=156) and Non-Seeded groups (SL=163). Individuals in the Seeded condition exchanged significantly fewer pre-experienced tokens (*MD*=.00, *IQR*=1.75) than Asocial controls (*MD*=11.00, *IQR*=18.00; *U*=5.00, *N*=17, *p*=0.002, alphas*=.025);

individuals in the Non-Seeded condition exchanged significantly fewer pre-experienced tokens (*MD*=1.000, *IQR*=2.00) than Asocial controls (*U*=9, *N*=19, *p*=.002). Latency to exchange the alternative token did not significantly differ according to whether the SL group was seeded (*M*=1 min 27 sec, *SD*=1.056) or not (*M*=1 min 30 sec, *SD*=.89; *t*(16) =.058, *p* =.954).

Conservatism. Across reward conditions there was evidence of an explorative strategy, with a predominance of alternative tokens first exchanged ($\mathrm{N}_{\text{Pre-experienced}}$=13, $\mathrm{N}_{\text{Alternative=}}$26) by participants not exposed to a model demonstrating the alternative token (Non-seeded and Asocial collapsed), significantly differing from 2(1,39)=.4.333, *p* = .037). However, this preference was mirrored in participants 2(1,24)=10.667, *p*=.001). There was also a significant difference in the number of token exchanges made by all participants according to token type (reward and model conditions collapsed; Wilcoxon Signed-Rank Test: *W*=-2.867, *p*=.004, *r*=.37), with participants exchanging more of the alternative tokens (*MD*= 12.00, *IQR*=10.00) than the pre-experienced tokens (*MD*=5.00, *IQR*=10.00).

Token and Reward Theft. No token thefts were recorded in children. Neither were there scrounging instances or attempted/successful reward thefts.

Overview of Findings: Children. Individuals in the Seeded condition exchanged a greater proportion of alternative tokens in the SL condition than in the LS condition. There was no difference in the proportion of alternative tokens exchanged by SS and LS individuals. This same pattern of alternative token exchange was evident in individuals in the Non-seeded condition. Asocial control individuals, overall, showed no preference for either token. Seeded and Non-seeded individuals exchanged proportionally fewer of the pre-experienced tokens than Asocial control individuals.

Cross Species Comparison. The proportion of alternative tokens exchanged by individuals according to reward condition and proportions of individuals who displayed alternative token preferences according to species are displayed in Table 5 (below; Seeded condition).

Table 5.
Evidence for payoff biased learning according to species

	Pan	Payoff Strategy	Homo	Payoff Strategy
No. of Alternative exchanges/Total exchanges	SL>SS>LS	Suggestive of PI (SL>SS>LS)	SL>LS; SS=LS	PO
No. of individuals switching	SL>LS; SS=LS	Inconclusive	SL>LS; SS=LS	Inconclusive

Note: PI=Proportional Imitation; PO = Proportional Observation

Overall, children's exchanges comprised of a greater proportion of alternative tokens than observed in chimpanzees (*U*=2605.50, *N*=126, *p*=0.002). Similarly, the proportions of alternative exchanges (out of total observed exchanges) attended to were greater in children than chimpanzees (*U*=2164.50, *N*=112, *p*<0.001). SL Seeded children (*MD*=1.00, *IQR*=.05) exchanged a significantly (alphas*=.0167) greater proportion of alternative tokens than did chimpanzees (SL Seeded: *MD*=.727, *IQR*=.56; *U*=91.50, *N*=21, *p*=0.001, Figure 4 above). No species differences were observed in the proportion of alternative tokens exchanged in the Seeded SS condition (*U*=37.00, *N*=19, *p*=.898) or Seeded LS condition (*U*=76, *N*=20, *p*=.031).

Non-Seeded SL children (*MD*=.939, *IQR*=.11) exchanged a significantly (alphas*=.0167) greater proportion of alternative tokens than did chimpanzees (*MD*=.373, *IQR*=.57; *U*=70.00, *N*=17, *p*<0.001, Figure 4 above). No species differences were observed in the proportion of alternative tokens exchanged in the Non-Seeded LS condition (*U*=26.50, *N*=17, *p*=.417) or in the Non-seeded SS condition (*U*=28.00, *N*=15, *p*=.768).

Mean token exchanges were higher in chimpanzees than in children, reflecting different task exposure durations for chimpanzees (6 hours OD) and children (30 minutes). Children on average exchanged 19 tokens (reward condition collapsed), compared to 75 exchanges made by chimpanzees.

Discussion

In this study we examined whether chimpanzees and 4- to 5-year old children, strategically copied demonstrator token preferences depending on the size of the reward. We found a similar pattern of token preferences for both species in a condition in which a model demonstrated a token exchange. Specifically, the proportion of individuals switching to an alternative token was greater when the alternative token yielded a larger rather than a smaller reward. We now discuss these points in further detail.

Was there evidence for social learning?

An assessment of payoff biased copying rules first requires an assessment of whether social learning was at play. We found clear evidence of the role of social learning in reward optimization in both chimpanzees and children. Asocial controls showed either no token preference (children) or a preference for the pre-experienced token (chimpanzees). This was despite the previously unseen-alternative token yielding a greater return (SL condition); a result of independent interest given the assumption that in the absence of social influence the frequency of differential method use should be proportional to their payoffs and opportunity to perform them (Kendal, Custance, Kendal, Vale, Stoinski et al., 2010). That is, once alternative behaviours are learned, individuals are predicted to perform the ‘best’ behaviour in their repertoire (Rendell, Boyd, Cownden, Enquist, Eriksson, Feldman et al., 2010; Rendell, Boyd, Enquist, Feldman, Fogarty & Laland, 2011). In the SL condition, individuals showed a clear preference for the alternative token in Seeded-groups (both species) and for children in the Non-Seeded group. A direct comparison between Seeded and Asocial control individuals, for both species, indicated that social learning, in the early stages of the open diffusion, was essential for reducing the number of pre-experienced tokens exchanged (SL condition). Thus, social as opposed to asocial information allowed rapid avoidance of a previously learned, but inefficient, response. These data firmly suggest that opportunities to observe other individuals, whether requiring the additional observation phase (chimpanzees) or not (children), were required to increase resource gain.

In chimpanzees, no effect of reward condition was recorded in the Non-Seeded condition, suggesting that in the absence of a demonstrator, the proportion of alternative exchanges was not determined by token payoffs. This was despite only two of 19 individuals failing to exchange at least one of the alternative tokens and despite clear food preferences observed for the higher reward. Seeded chimpanzee groups, conversely, showed differential exchange patterns according to reward conditions, again highlighting that social learning played a key role in their resource maximization. Specifically, Seeded chimpanzees exchanged proportionally more of the alternative token when it was paired with the large payoff (SL condition), than when it was paired with the small payoff (and the pre-experienced token yielded the large reward; LS condition). This suggests that observation of the trained demonstrator facilitated reward maximization in the LS and SL conditions by avoidance of, and encouragement of, switching to the socially demonstrated alternative, respectively. This contrasts with the findings of Hopper and colleagues (2011) who found chimpanzees copied demonstrator token preferences irrespective of their reward value.

In children, high levels of alternative token exchange (94%) occurred in SL groups whether they were seeded or not. While this could be taken to imply that social learning was not required for children to switch to the Large token, finding that both Seeded and Non-Seeded groups displayed a preference for the alternative token while Asocial individuals did not, speaks against this interpretation. Furthermore, as with chimpanzees, direct comparison of token exchanges according to model condition showed that Asocial individuals exchanged significantly more of the pre-experienced tokens. Again, this highlights that opportunities for social learning enabled avoidance of the previously learned, but inefficient, behavioural response.

A potential explanation for species differences according to model condition (groups only) may be due to a strong emphasis upon social learning in children, such that the influence of the trained model was relatively minor compared to the opportunity to observe other fellow naïve individuals exchange tokens for different rewards. Furthermore, the simplicity of the presented task may have rendered high levels of social information prior to switching to higher value tokens unnecessary for children; observation of initial peer exchanges may have been sufficient for children to subsequently maximise token payoffs in the SL condition. This contrasts with chimpanzees, who required additional social information acquisition opportunities to maximise their reward gain. An alternative explanation could be that an interplay of both a ‘copy the dominant’ and ‘payoff biased’ strategies was important for chimpanzees to maximise rewards, and in the absence of a medium-high ranking model who demonstrated a token preference, sensitivity to reward payoffs was reduced (Non-Seeded groups). The ability to communicate verbally could also have facilitated child performances. Children, in a group setting, made statements such as “If you get the white one then you get that box?” and “If we have black do we get big ones [stickers] like these ones, the long ones?” (see Appendix E Table E1 for child verbal responses), conveying important task information to their peers. Lastly, children were biased towards first exchanging the alternative token, thus adopting a novel solution (Wood, Kendal, & Flynn, 2013). This initial bias may have enabled Non-Seeded groups to observe any differential reward contingencies from the outset. This, in turn, could have lessened the requirement for the observation phase, enhancing similarity across Seeded and Non-Seeded groups.

Were Payoff Biased Copying Strategies Used?

Our main question concerned the specific payoff copying rule underpinning species’ token exchanges. Initial predictions were made concerning the proportion of individuals switching to the alternative token according to the payoff biased copying rule. The number of chimpanzees and children who switched to (showed a significant preference for) the alternative token was greater in the SL than LS condition only (with SS equal to SL and LS). For chimpanzees, the proportion of alternative tokens exchanged was also greater in the SL than LS Seeded condition

(SL>LS). Inspection of the mean proportion of alternative exchanges made by seeded chimpanzees pointed towards employment of the Proportional imitation rule (SL>SS>LS), albeit chimpanzees exchanged less (SL<1), or more (LS>0), of the alternative token than was predicted for this copying strategy (SL=1, SS=.5, LS=0).

Comparing the proportions of alternative tokens exchanged (and not the proportion of individuals) in children, according to reward condition (SS, LS, SL; Seeded and Non-Seeded), indicated the use of a Proportional observation rule (Schlag, 1998, 1999) in which copying is dependent upon demonstrators' payoffs only. Specifically, the proportion of alternative tokens exchanged was significantly higher in the SL condition compared to the SS and LS conditions, with no difference between SS and LS conditions (where the alternative tokens=Small rewards; see Table 2). Thus, as has been shown in adult humans (Morgan, Rendell, Ehn, Hoppitt & Laland, 2011), we find support that children, too, copied according to the demonstrators' payoffs, rather than in proportion to reward satisfaction (Proportional reservation) or relative payoff to self and other (Proportional imitation).

We do not suggest that children are incapable of payoff biased transmission rules such as Proportional imitation. Rather, the comparable proportions of alternative exchanges in SS and LS conditions may reflect children's bias towards social learning even at the expense of behavioural efficiency (here quantified by gained payoff). Various studies have shown that children are adept social learners, who readily and faithfully reproduce observed behaviour (Flynn & Whiten, 2008; Horner & Whiten, 2005; Lyons, Young & Keil, 2007), to the extent of copying inefficient (task irrelevant) actions (Horner & Whiten, 2005; Lyons et al., 2007). This contrasts with social learning in chimpanzees, who tend to copy less faithfully (Tennie, Call & Tomasello, 2006; Tomasello, Savage-Rumbaugh, & Kruger, 1993;

Whiten et al., 1996). Finding that children, overall, showed higher levels of exchange with the alternative token than chimpanzees is perhaps suggestive of pronounced social information use in 4- and 5-year old children. Children displayed an exploratory in which they predominantly exchanged the unseen, alternative token, first, and thus naïve individuals demonstrated the alternative token from the outset. This exploratory strategy coupled with pronounced social information use could explain children's use of Proportional observation over alternative payoff biased strategies. Further indication that children are adept social learners was provided by species differences in the levels of token exchanges. In the Seeded SL condition, children exchanged proportionally more of the alternative, Large, token, than chimpanzees, this occurred despite children's comparatively short task exposure. This suggests that children were quicker to adopt a payoff rule than chimpanzees. This bias towards Proportional observation from the task outset supports previous research showing that humans may possess a bias towards success biased copying rules (Mesoudi, 2011).

Schlag's (1998, 1999) copying strategies predict that copying occurs in proportion to how much better payoffs are. Future tests of these strategies require greater variation in rewards to track whether copying is directly proportional to differences in payoff to self and others. For example, the incorporation of rewards that vary on a wider scale (1vs4, 1vs5, 1vs 8 etc.), with larger sample sizes, would prove beneficial. It is also worth noting that the necessary inclusion of rewards that varied in both quality and quantity in the present study creates difficulty in assessing the current results in terms of copying strategies. That is, quality alterations made it particularly hard to assess proportional copying according to *how much* better a reward value is, due to likely individual differences in preference magnitude, despite clear preference for the Large reward.

In this study we considered a form of success biased copying in which fixed payoffs resulted directly from exchange of two tokens. Outside experimentally controlled settings such as those used in the present study, success information is unlikely to be so direct and clear cut (McElreath et al., 2008). Rather, indirect cues to success reliant upon cumulative success (e.g. social dominance) or payoffs based on trait combinations are likely to be used. Multifarious components contributing to payoffs create difficulty in isolating specific traits/behaviours responsible for better payoffs. While past research hints at the use of general success and model based learning (Horner et al., 2010), future consideration should be given to whether, and which (other than direct and unchanging payoffs) success-general cues are used by species in more naturalistic settings.

Are Children and Chimpanzees Conservative Learners?

Chimpanzees have been described as conservative learners, either ‘satisficing’ upon reward gain (Marshall-Pescini & Whiten, 2008) or initial solution, once proficient, inhibiting subsequent learning flexibility (Hrubesch, Preuschoft, & van Schaik, 2009). Such conservative behaviour has been proposed as a potential route to constraining cultural progression (Marshall-Pescini & Whiten, 2008). In the present study, we found no evidence of conservative behaviour, which would be expected to constrain chimpanzees’ capability to switch to the alternative token irrespective of rewards. Rather, we report that chimpanzees selectively copied according to the dividends of the behavioural options. This supports a recent large-scale comparative study conducted in chimpanzees and children, which also failed to lend support for conservative learning in chimpanzees (Dean et al., 2012). However, our chimpanzee Asocial controls did retain a preference for the previously learned response (pre-experienced token) while our child equivalents did not. This hints that children, in the absence of social information, were slightly more exploratory than chimpanzees. Interestingly, Dean and colleagues also found no support that scrounging either facilitates (Caldwell & Whiten, 2003) or constrains (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997) social learning, a result again reflected by the present findings. Specifically, we found no relation between reward scrounging, thefts and attempted thefts and task performance. Scrounging events and (attempted) thefts were clearly directed towards the large-medium value food, confirming chimpanzees' food preferences. However, it should be noted that scrounging may be biased towards the Large rewards since their greater numerosity would have served to increase the likelihood of fallen food (available for scrounging).

Concluding Remarks and Future Directions

The identification of transmission biases in various species serves to further our understanding of evolved adaptations for social information (McElreath et al., 2008). In this study we report clear evidence for selective payoff biased transmission in both chimpanzees and children. Our results point toward chimpanzee's employment of the Proportional imitation, and children's employment of the Proportional observation, rule. Our results add to the growing corpus of literature showing that chimpanzees (and children) acquire information socially (Hopper et al., 2011; Hopper et al., 2007; Horner & Whiten, 2004, 2005) and selectively (Biro et al., 2003; Kendal et al., submitted; Wood, Kendal & Flynn, 2012). This ability to flexibly isolate whether it was beneficial to copy others, or not, represents an important adaptive response that can protect one from copying maladaptive and unreliable information (Laland, 2004). Our findings also have implications for cumulative culture; specifically, this presence of payoff biased social learning in chimpanzees hints that limitations on cultural ratcheting (or lack thereof, Tennie et al., 2009) may not relate to an inability to socially adopt behaviours that pay.

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Chapter V

Robust retention and transfer of tool construction in chimpanzees: implications for cultural stability

The previous two chapters concerned two forms of success biased copying; public information use and payoff biased transmission. This chapter investigates the long-term memory capabilities of chimpanzees. This research, as it builds upon a previously published paper in the same journal (Price, Lambeth, Schapiro & Whiten, 2009), is submitted to *Proceedings of the Royal Society: Biological Sciences* with the following authorship:

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Abstract

Whether long-term memory places constraints on the preservation of cultural behaviours in chimpanzees has yet to be investigated. In the present, longitudinal, study we investigated whether complex tool behaviours used to gain an out-of-reach reward, and learned either socially or asocially, were retained over ca. 3.6 years. Chimpanzees retained specific tool manufacture styles with improved efficiency, flexibly creating tools dependent on need. Additionally, complex tool behaviours were transferred to a perceptually different task situation. Accordingly, we report some of the first evidence for appreciable long-term memory and improvements in the utility of complex tool manufacture in chimpanzees; important for cultural stability and the prevention of cultural regression.

Introduction

Chimpanzees (*Pan troglodytes*) show a broad, regionally variable range of behaviour which is thought to be cultural (Whiten, Goodall, McGrew, Nishida, Reynolds & Sugiyama, 1999), an inference supported by controlled experiments (Whiten, Horner & de Waal, 2005). Many of these cultural behaviours involve differential tool use (Whiten et al., 1999); chimpanzees use tools for insect and prosimian predation, honey collection and nut cracking (McGrew, 2010a; Pruetz & Bertolani, 2007). These extractive and percussive tasks can require elaborate tool kits, comprised of tool sets (the sequential use of multiple tools), composite tools (concurrent use of two or more tools) and compound tools (tool parts combined to create one unit) (McGrew, 2010b). Despite the empirical evidence for these complex forms of tool use (McGrew, 2010b), there is little indication that they have become more complex over generations, nor resulted in artefacts impossible for individuals to recreate within a single generation (cumulative culture); a hallmark of human culture (Tennie, Call & Tomasello, 2009).

The reasons behind the difference in chimpanzees' and humans' cultural complexity are much debated (Dean, Vale, Kendal, Flynn & Laland, in press). Chief among the requirements identified for cumulative culture are innovation, required for modification and progress, and complex social learning mechanisms like imitation and teaching, that allow faithful behavioural propagation and prevent cultural regression (Dean, Kendal, Schapiro, Thierry & Laland, 2012). One important, yet overlooked, psychological attribute required for cumulative culture is memory (Vale, Flynn, & Kendal, 2012); long-term memory (LTM) allows behavioural preservation in populations, and provides protection from cultural loss by negating the need for repetitious learning events. While studies have investigated the autobiographical and working memory capabilities of chimpanzees (Inoue & Matsuzawa, 2007; Martin-

Ordas, Berntsen, & Call, 2013), whether cultural behaviours are retained after substantial time delays warrants empirical attention.

In the current study, we assessed whether chimpanzees retained complex tool use behaviours learned asocially and socially, over the course of years in which practice was not possible. Specifically, we retested, following a substantial delay (ca. 3.6 years; Price, Lambeth, Schapiro, & Whiten, 2009), chimpanzees who in 2008 had created elongated tools via either of two alternative methods (*combination* of two tools versus *extension* of a single tool) to obtain an out-of-reach reward. In the original study, Price and colleagues (Price et al., 2009), exposed chimpanzees to graded degrees of social demonstrations via video; namely, (i) combine-and-retrieve reward in which the demonstrator was depicted combining two provisioned tool elements to create a single elongated tool to subsequently rake in a reward; (ii) retrieve-reward only in which the demonstrator raked in a reward with a provisioned, already combined, tool; (iii) reward consumption only in which the demonstrator was depicted eating a reward only (no tool interaction or provisioning); (iv) no-video control where subjects received no video demonstrations and, (v) tool extension-and-retrieval in which the demonstrator created an elongated tool by extending the internal rod contained in a single tool (extension method). Note that in all demonstrations the same male model served as the demonstrator. Observation of detailed tool combinatory information was found to facilitate complex tool manufacture, yet unlike asocially learned approaches, it led to persistent combined tool manufacture even when rewards could be retrieved with a single, unmodified, tool (Price et al., 2009).

The present study extended these findings, addressing two important questions: (i) whether the same chimpanzees, successful at creating an elongated tool to retrieve a reward in Price et al. (2009), would retain their specific method of complex tool manufacture (Retention Task) for ca. 3.6 years; and (ii) whether the original social information received would have an enduring inhibitory influence on the flexibility of tool construction and use according to reward distance (Distance Flexibility). Additionally, because of its potential importance in innovation, cumulative culture and adaptation to changing/new environments (Boesch, 1995), we investigated whether chimpanzees transferred tool use knowledge to a new but analogous task. We, therefore, presented chimpanzees with a perceptibly different, yet functionally similar Transfer task, and to assess the impact of causal visual feedback we presented opaque and transparent forms. Our ultimate aim was to assess chimpanzees' capabilities that have important implications for cultural stability and progression.

Method

Subjects

Thirty-one chimpanzees (*M* age = 32 yrs., range 20-48; 12 males), housed at the Michale E. Keeling Center for Comparative Medicine and Research (KCCMR) in Bastrop, TX USA, participated in this study that was completed over 2011-12. The KCCMR is fully accredited by the AAALAC-I. Chimpanzees were group housed with access to enriched indoor-outdoor enclosures with climbing facilities. Eleven of these subjects had successfully created an elongated tool and retrieved an out-of-reach reward in 2008 using the combine or extension method (Price et al., 2009). Twenty 2008 task-naive chimpanzees provided baseline data; termed 'control' or 'naïve' subjects according to study participation (Table 1). No food or water deprivation occurred. Subjects progressed from a Retention study to a Transfer-Opaque study, then a Transfer-Transparent study.

Table 1.

Chimpanzee Study Participation and Terminology

Terms	Description	Price et al. study	Retention study	Transfer-Opaque study	Transfer-Transparent study
'experienced subjects'	Created an elongated tool to retrieve a grape in 2008 (*N*=11). Participated in Price et al. and all three studies here	✓	✓	✓	✓
'control subjects'	Baseline for the experienced subjects. Participated in all three studies but not in the Price et al. study (*N*=10)	x	✓	✓	✓
'naïve subjects'	Baseline who participated in the Transfer-Transparent study only (*N*=10)	x	x	x	✓
'experienced combiners'	*Subclass* of 'experienced subjects' who created a tool using the combine method (*N*=10). Excludes subjects who used the extension method to retrieve a grape in 2008 (*N*=1)	✓	✓	✓	✓
'combine method'	Creation of an elongated tool by insertion of a tool into the opening of a second tool component	NA	NA	NA	NA
'extension method'	Creation of an elongated tool by pulling an internal rod from a single tool	NA	NA	NA	NA

Retention Study

Materials

The raking platform was the same platform originally used by Price and colleagues (Price et al., 2009). The platform was constructed out of acrylonitrile-butadiene-styrene (50cm x 55, Figure 1) and attached to a wheeled cart (122cm L x 31 H x 74 W). Grapes were placed either close to (13cm from the platform edge) or distant from (49 cm from the platform edge, against a 13-cm-high wall) subjects. Two available tool elements could be ‘combined’ (Table 1) through insertion of a 28 cm rod into the opening of a second tool component (a 39-cm-long hollow polycarbonate tube). An alternative tool ‘extension’ method (Table 1) involved twisting and pulling a nylon rod that protruded 3 cm out of the hollow polycarbonate tube. Close grapes could be accessed with a single, unmodified tool, while distant grape retrieval required an elongated tool. Trials were recorded on a Sony Handycam DCR-SR58E.

Procedure

Subjects were tested individually and voluntarily in their indoor compartments (ca. 2.4 m x 2.4 x 1.8^3). The raking platform was positioned in front of the subject, flush against the enclosure mesh. Test sessions lasted 20 minutes or until all 8 grapes were retrieved (4 close and 4 distant grape placements, presented in a pseudo-randomized order such that one distance would not reoccur in succession more than three times, with the location of grape placement on the first trial counterbalanced across subjects). A maximum of three sessions were conducted per subject. Trials began after grape placement by the experimenter (GV) and presentation of the tool elements. After each successful grape retrieval, subjects returned the tool elements to the experimenter (who dismantled them), cued by a trained ‘give’ gesture. Animals voluntarily participated in the procedures and their return for multiple trials suggests that the procedures were enriching/stimulating for them.

Transfer Studies

Materials

The transfer boxes (40.6cm L x 21.6 H x 30.5 W) consisted of either a black or transparent polycarbonate box, attached to a wheeled cart (59.7cm L X 63.5 H x 45.7 W). Inside were two mechanisms (close and distant), which when pushed using a tool, would release grapes (Figure 1). A single, unmodified tool could be inserted into an opening in the front of the box to release the close mechanism. To release the distant mechanism two tools had to be applied, either through combining them or using a serial method of inserting the smaller of the two tools first, followed by the larger tool. The two tools provided measured 23.2cm (diameter 1.9cm) and 28.5cm (diameter 2.8cm) (coloured red and yellow respectively). Grapes were baited in two transparent feeding tubes above the box and, upon release, rolled onto a tray beneath the box. The grapes were visible to chimpanzees in both Transfer studies.

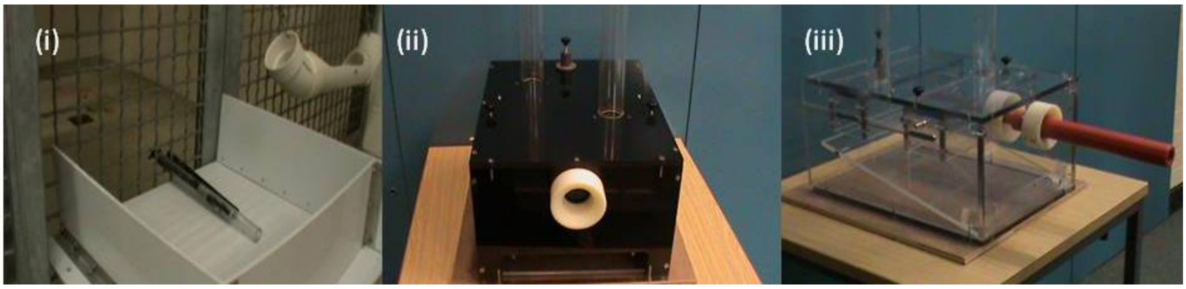

Figure 1. (i) Retention raking platform with tool elements; (ii) Transfer-Opaque task; (iii) Transfer-Transparent task with combined tool inserted.

Procedure

For the Transfer-Opaque study, three grapes, rather than one, constituted the reward. Each feeder tube was baited individually depending upon trial type (close or distant). To encourage initial task participation, all subjects were presented with the close distance first, followed by a distant trial, with the last 6 trials randomized. In the Transfer-Transparent study, grape quantities were increased (3 for each close, and 15 for each distant, trial), to enhance motivation (trial distances were randomized with first trial distance counterbalanced across subjects). For both transfer studies, a maximum of three 20 minute sessions were conducted, with termination if rewards were retrieved on all 8 trials (4 close and 4 distant).

Video Coding

Video sessions were coded using the scheme of Price et al (2009). Subjects were assigned tool interaction scores according to the level of tool manipulation performed, relating to the complete combine and extension methods (Retention: maximum score 14, Appendix F Table F1) or a modified scheme (Transfer, Appendix G Table G1; maximum score 22). Six sessions from each study were coded by an independent coder, with high reliability across raters' tool interaction scores (Kappa Coefficients: Retention=. 928; Transfer-Opaque = .921; Transfer-Transparent = .875). Due to the ordinal nature of the data and normality violations, non-parametric two-tailed statistical analyses are reported.

Results

Retention Study

Experienced subjects' (Price et al., 2009) highest tool use scores were predicted by their scores attained in the original study (combine method: r_s =. 74, N=11, p=.009; extension method: r_s =. 63, N=11, p=.038). Only one of the experienced combiners (N=10) failed to construct a combined tool. Note that in 2008, none of our experienced subjects were exposed to the extension-and-retrieve demonstration (see Appendix H Table H1). Latencies to retrieve a grape using a constructed, combined, tool were lower in the retention study than in 2008

(Wilcoxon signed-rank test: *W*=.00, *N*=7, *p*=.018, see Figure 2; note: the participant who failed to construct a combined tool and a female, due to lack of task participation during the 1st two 20 minute sessions, were excluded from the analysis). All three subjects who previously created an elongated tool using the extension method did so again in the current study, although one did so in-between trials prior to returning the tools to the experimenter. A further female (experienced combiners) discovered the extension method.

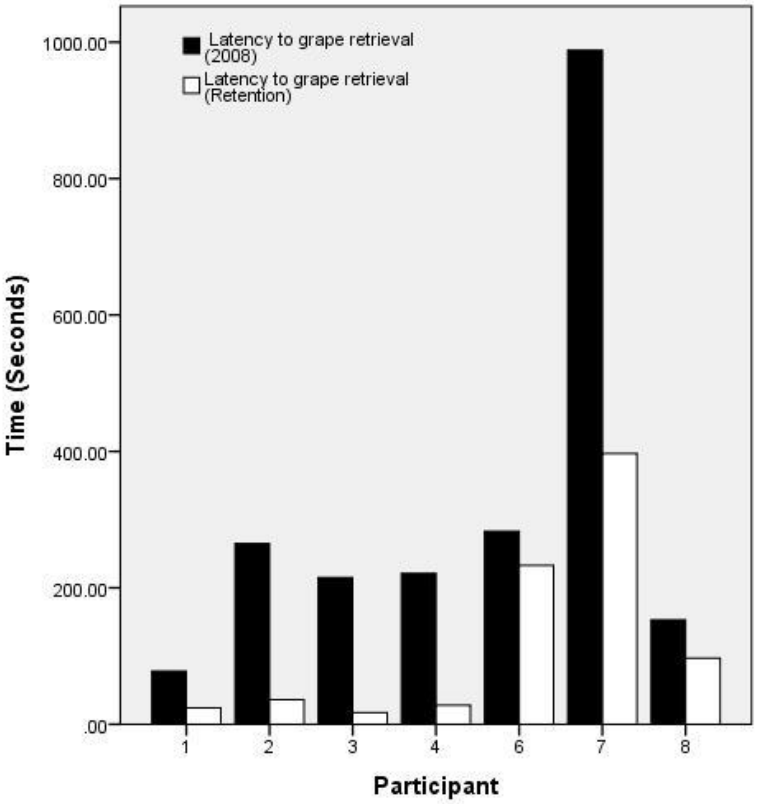

Figure 2. Latencies to retrieve a grape using a constructed, combined, tool in Price et al. (2008) and in the Retention study.

Experienced subjects (*N*=11) attained higher scores on the combine method scale (*MD*=14.00) than controls (*MD*=2.00, *U*=3.50, *N*=21, *p*<.001, Figure 3). Only one control subject (*N*=10) constructed a combined tool and they failed to retrieve a grape. There was no significant difference in the highest score attained by experienced (*MD*=6.00) and control (*MD*=4.50) subjects on the extension method (U=44, N=21, p=.452).

Overall, experienced subjects achieved high success, with the majority of subjects (N=8 achieving 100% success) retrieving all eight grapes, contrasting with only 5 control subjects retrieving only some close grapes with an unmodified tool (range: 1-3 grapes). Unlike the experienced subjects, no control subject successfully created an elongated tool (by combination or extension) to retrieve a distant grape.

Is this an enduring effect of social information?

No significant difference was observed in the highest combine score achieved as a function of the social information exposure in 2008 i.e., (i) combine-and-retrieve reward (ii) retrieve-reward only (iii) reward consumption only (iv) no-video control (note: none of the current participants were exposed to the extend and retrieve social information condition in 2008; K-W test: $x^2(3)=2.40$, $p>.05$, adjusted critical value for k=4 with our sample sizes per condition =6.364 at α=.05, see Meyer & Seaman, 2013). This is as expected since 9 of the 10 subjects who combined in 2008 successfully combined in the current study.

Scores for tool extension did differ according to the original form of exposure to social information concerning the combine method (adjusted critical value for k=4 with our sample sizes per condition =6.364 at α=.05, see Meyer & Seaman, 2013) (K-W test: $x^2(3)=6.59$, $p<.05$). Mean rank performance on the tool extension scale was lowest for those exposed to the combine-and-retrieve demonstrations (4.00, N=5), followed by retrieve-reward only (5.33, N=3), video control (reward consumption only) (9.00, N=1), with those exposed to no demonstration ranking highest (10.50, N=2). Post hoc comparisons were not appropriate due to low subject numbers per condition. Following Price et al., we thus grouped subjects according to original exposure to the full combine-and-retrieve demonstration (*N*=5) or not (*N*=6). There was a non-significant trend in the data suggesting that subjects exposed to the combine-and-retrieve demonstration (in Price et al., 2009) showed lower scores (*MD*=3.00) on the tool extension method than those not exposed to the combine process (*MD*=10.50; *U*=5.00, *N*=11, *p*=.065).

Assessing Flexibility in Tool Manufacture

Unlike Price et al.(2009) , we found no difference between the number of combined tools (combine scores $\geq$ 11) created for the close grape placement by those who were originally exposed to combine-and-retrieve video footage (*N*=4) and experienced combiners exposed to the other forms of demonstration or no video (*U*=9.50, *N*=10, *p*=.657).

More combined tools (score $\geq$ 11) were manufactured by experienced subjects during distant (*MD*=4.50) than close grape trials (*MD*=1.00; *W*=-2.55, *N*=10, *p*=.008). Overall, experienced subjects created18 combined tools during close (12 grape retrievals), and forty-two during distant (33 grape retrievals), trials.

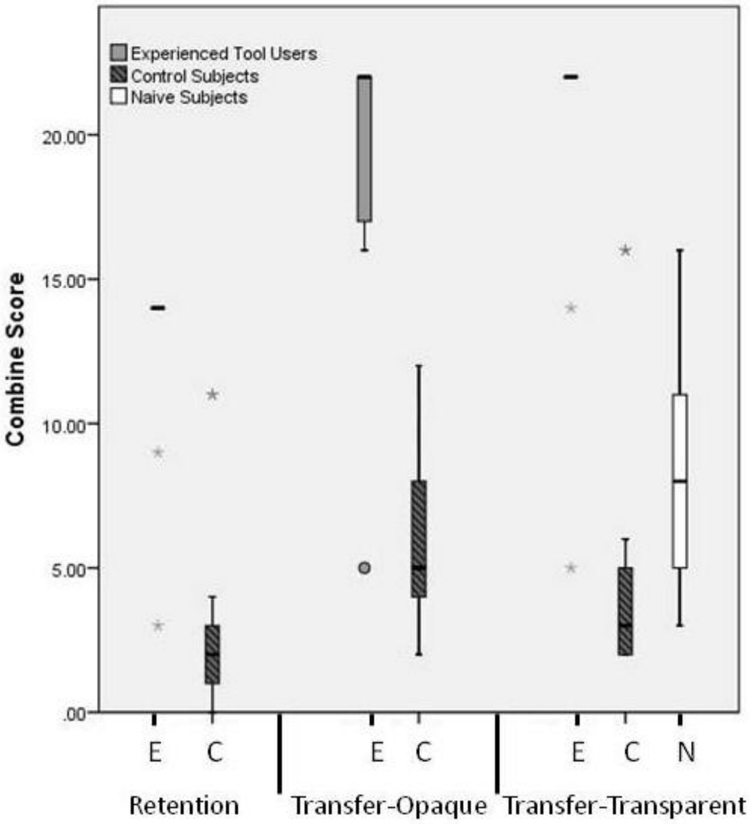

Figure 3. Median combine scores (black horizontal line) and interquartile ranges (boxes) according to study and participant experience. Whiskers represent the minimum and maximum combine scores (unclassified outliers represented by circles or extreme cases by asterisks). E = experienced tool users; C = control subjects; N = naïve subjects. Note that all but two experienced subjects achieve the maximum score of 14 in the Retention test.

Transfer Studies

Subjects were exposed to transfer tests to determine whether prior tool use experience would generalize to a new task. One female subject (experienced with tool extension) failed to participate for procedural reasons.

Transference of skills to a new causally opaque task?

Experienced combiners' combine scores in the transfer tests were significantly correlated with combine scores attained in the Retention study ($r_s=.64$, $N=10$, $p=.045$). Experienced combiners scored higher on the manipulative performance scale (*MD* = 22.00) than control subjects, one of whom combined previously (*MD* = 5.00: *U*=5.50, *N*=20, *p*=.001); they also completed more trials in terms of retrieving grapes (*MD*=5.50, *SD*=3.11; possible 8 trials) than control subjects (*MD*= .00, *SD*=.42, *U*=7.00, *N*=20, *p*<.001). Only two of 10 control subjects successfully gained grapes, and this was by inserting unmodified tools. Note, that all first trials were close grape placements and thus as the majority of controls failed to progress from the first trial the need for combined tools was limited.

Seven of the 10 experienced combiners combined tools to gain grapes and a further two combined but failed to gain distant grapes. The remaining subject was the same individual who failed to combine tools during the Retention study. Two experienced combiners also discovered the alternative, serial method; one using it to gain three, and the other, two of the four distant grapes.

There was no difference in the number of combine actions performed (scores$\geq$5, Appendix G Table G1) or combined tools created (scores$\geq$16) for the close grape placements according to the original social information exposure in Price et al.'s study (full combine and retrieve footage versus all other variants of social information; combine actions: *U*=12.00, *N*=10, *p*=.916; combined tools: *U*=9.50, *N*=10, *p*=.530).

Investigating Transference of skills to a new transparent task

Eight of the 10 experienced combiners combined tools to release grapes from the baited feeder tubes. Four of the experienced combiners used the alternative, serial method, (two had discovered the method with the Opaque task). Two naïve (of 10) and one control (of 10; see Table 1) subjects successfully combined tools, but failed to release the grapes. Two control subjects also discovered the serial tool method, one of whom released grapes during a close trial.

There was a significant effect of experience on the manipulative performance scores attained ($\chi^2(2)=18.01$, $p<.001$) and on the number of reward retrievals (8 trials possible per subject, $N=30$; $\chi^2(2)=19.29$, $p<.001$). Post-hoc paired comparisons (M-U tests, Bonferroni adjustment applied $\alpha = .017$) revealed that experienced combiners scored significantly higher on the combine scale ($MD=22.00$) than naïve subjects ($MD=8.00$; $U=9.50$, N=20, $p=.001$) and control subjects ($MD=3.00$; $U=4.00$, $N=20$, $p<.001$). Naïve subjects had significantly higher combine scale scores ($MD=8.00$) than control subjects ($MD=3.00$; $U=19.00$, $N=20$, $p=.017$). This was not due to the level of participation, as indicated by the number of total tool manipulations per subject, which did not differ significantly across naïve and control groups ($U=29.50$, $N=20$, $p=.126$). Experienced combiners retrieved rewards on significantly more trials ($MD=8$) than naïve ($MD=0.00$): $U=6$, $N=20$, $p<.001$) or control subjects ($MD=.00$: $U=7$, $N=20$, $p<.001$; Bonferroni adjustment applied $\alpha = .017$).

Performance Across Studies

Experienced combiners retrieved a similar number of grapes across all three studies (Retention/Transfer-Opaque/Transfer-Transparent; Friedman Test: $\chi^2(10, 2)=4.52$, $p=.095$). In the transfer studies, task transparency influenced the number of combined tools created by experienced combiners according to grape distance (Chi Square: $\chi^2(1, 226)=15.34$, $p<.001$, phi=.26); experienced combiners combined more tools during close ($N=102$) than distant ($N=57$) trials with the Opaque task (Binomial: $p<.001$), but more combined tools were created during distant ($N=43$) than close ($N=24$) trials with the Transparent task (Binomial: $p=.027$). No improvement was recorded in the number of rewards retrieved by control subjects across the Transfer-Opaque and Transfer-Transparent studies.

Discussion

Chimpanzees retained the ability, over ca. 3.6 years without practice, to create elongated tools. Over this period, the efficiency of this behaviour, in terms of flexible manufacture according to how far rewards were out-of-reach, improved. This shows considerable retention and an enhanced understanding of tool manufacture. Furthermore, those chimpanzees competent at making the tools were able to apply this skill to new tools and task situations and did so flexibly when provided task-relevant visual information (Transfer-Transparent study). Chimpanzees, therefore, exhibited appreciable long-term memory for complex tool behaviours that was not context dependent (cf. Martin-Ordas et al., 2013).

Retention of tool use techniques

The majority of chimpanzees persisted with their original method or methods of tool creation. Those experienced with the extension method of elongated tool manufacture produced such tools during retest. Similarly, all but one chimpanzee who previously created combined tools, retained this capability. Such high levels of retention indicate that the mechanism underpinning initial learning of tool manufacture (asocial or social) was not important for retention; rather, once a method was mastered, chimpanzees retained this specific capability.

Interestingly, two subjects who created elongated tools using the extension method in 2008, did so again, despite their lack of success at retrieving grapes with this tool over three years previously. Assuming individuals were not re-discovering the extension method during the Retention test, this suggests that reinforcement of the response (tool manufacture) via reward was unnecessary for its retention. There was minimal evidence (one control among 10) of asocial learning of tool combining. This subject failed to use the compound tool to retrieve a reward, indicating limited causal understanding of manufactured tool function (Price et al., 2009).

We found no enduring effect of the type of social information subjects were exposed to in relation to functional application several years later. Rather, the inhibition of flexible tool use, originally reported in subjects exposed to full combine-and-retrieve demonstrations compared to those not exposed to full demonstrations (Price et al., 2009), appeared to have diminished over time. In 2008, our experienced subjects were provided one opportunity to retrieve a distant reward, followed by a post session of varying grape distances two weeks later (Price et al., 2009). The effect of social information was, therefore, potent enough to override efficient tool use after a delay of two weeks, but not ca. 3.6 years. The absence of further combinatory demonstrations could have extinguished any associative rules or conservative tool use that may have limited behavioural efficiency (Hopper, Lambeth, Schapiro & Brosnan, 2011; Hrubesch, Preuschoft & van Schaik, 2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009). This hints at the potential benefit of a hiatus in social demonstration and/or practice, upon cultural evolution of skills. It would be of interest to investigate whether exposure to full combine demonstrations would again disrupt flexible tool use according to grape distance.

Intriguingly, an enduring effect of social information was recorded with regard to the degree of proficiency attained using the extension method. Specifically, experienced chimpanzees not exposed to full combine-and-retrieve demonstrations tended to score higher on the tool extension scale than those who were originally exposed. This may reflect a reduction in full exploration of task options due to canalization of behaviour resulting from observation of a specific tool-use technique (Flynn & Whiten, 2008).

Many animal studies have typically concentrated on retention abilities following relatively short delays (≤24 hr. intervals). To our knowledge only one long-term (autobiographical) memory study in chimpanzees has been conducted, finding retention of knowledge regarding a task-functionally-appropriate tool after a similar hiatus to the present study (Martin-Ordas et al., 2013). Specifically, cued recall was reported wherein reinstatement of the same test area, experimenter and experimental set-up allowed experienced chimpanzees to identify the task appropriate tool they had used 3 years previously (Martin-Ordas et al., 2013). In the current study, we add to these findings by reporting evidence for retention not only of tool use, but also specific, socially learned methods of tool manufacture even in less cued environments (different experimenter and often different test areas). The current findings, coupled with those reported by Martin-Ordas and colleagues (Martin-Ordas et al., 2013) are suggestive that, at least for some motor tasks, time delays before retest could be significantly increased. Furthermore, one female in the present study retained her specific method of tool manufacture (extension) after receiving one grape trial only in 2008 (due to lack of participation in the post session). This indicates that, even after one trial learning, information may be retained for extended periods.

Transfer of Tool use

Our secondary aim was to establish whether chimpanzees would transfer tool knowledge to a new task situation, and evaluate the impact of visual causal information on levels of tool combining. The majority of experienced combiners were able to combine novel tools to solve perceptually different, but functionally similar, tasks. This contrasts with subjects who failed to combine tools to release out-of-reach rewards, irrespective of exposure to the raking task (controls) or no exposure (naïve subjects).

Experienced chimpanzees were markedly persistent in their attempts to use combined tools for close grape trials in the Transfer-Opaque study, despite high levels of unsuccessful attempts (see also Hrubesch et al., 2009). Rather than suggesting a breakdown in functional tool flexibility, it is likely that the restricted task-relevant visual information in this condition limited understanding. By contrast, flexible action appropriate to context was enhanced with the transparent task that allowed visual accesses to inner box mechanisms. Due to the order of study presentation, it is difficult to ascertain whether this improvement was due to practice effects or newly acquired causal information. Our result is, however, reminiscent of chimpanzees disregarding observed task-irrelevant actions in their copying of techniques applied to a transparent task boxes that revealed relevant causal information (Horner & Whiten, 2005).

The degree to which causal reasoning, trial and error learning, insight or response transfer to similar stimuli, underpins complex tool use, remains contentious (Hihara, Obayashi, Tanaka, & Iriki, 2003). In terms of serial tool use (transfer tasks), our results suggest that generalisation is not essential, as two control subjects, without combining experience, discovered this method during the transfer tests. It is perhaps most parsimonious to consider that serial tool use occurred through iterated behaviour; that is, upon one tool insertion not releasing the grapes, this action was repeated by inserting a second tool. However, insight learning cannot be ruled out.

Overall, chimpanzees displayed proficient complex tool use, retaining specific methods of tool manufacture after a long delay, and transferring these skills to a new context, with efficiency (generally flexible tool construction according to reward distance). The retention of complex tool behaviour, despite an interim absence of raw materials to manufacture tools or resources requiring their use, is important for the long-term maintenance of cultural variants, especially in terms of preventing cultural regression. In chimpanzees, a corollary in the wild may be where tool use is required to access rare or infrequently available resources (e.g. seasonally available Coula nuts, Tai Forest: Luncz, Mundry, & Boesch, 2012), and so practice is impossible for extended periods. Similarly, transferring skills to new contexts may aid innovation capabilities and allow adaptation to new or changing environments (Boesch, 1995). Finally, the findings indicate that limitations in long-term memory and transfer of skills to novel contexts may not be the factor that constrains cumulative culture in chimpanzees.

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Chapter VI

General Discussion

In this series of studies three, previously undocumented, cognitive or socio-cognitive capabilities in chimpanzees (*Pan troglodytes*) that have implications for cultural progression and stability were investigated. First, the findings demonstrated that chimpanzees, and children (*Homo sapiens*), possess the ability to optimize resource selections using public information. Second, payoff biased social learning, present in both chimpanzees and children, facilitated the maximization of reward gain. Third, chimpanzees were capable of retaining complex tool manufacture, with improved efficiency of use, following a substantial hiatus of ca. 3.6 years. Each will now be discussed in turn, before considering future research directions.

Success copying I: Public information use

Public information constitutes a form of social information that conveys insights into the quality of a resource that can aid decisions of habitat selection, where to and with whom to breed, predator avoidance, and selection of feeding locations (Nocera, Forbes, & Giraldeau, 2006; Valone, 1989). In chapter III public information use was documented in chimpanzees and 5-year old children, who, after observing demonstrations via video of a conspecific gaining rewards at a fast and slow rate, subsequently selected the resource rich site during a ‘social foraging’ task.

Finding public information use in two primate species, coupled with such findings in other species (fishes: Coolen, van Bergen, Day & Laland, 2003; Coolen, Ward, Hart & Laland, 2005; invertebrates: Laidre, 2013; birds: Smith, Benkman, & Coffey, 1999 ; Templeton & Giraldeau, 1996), lends support for the prediction that public information is widespread in nature, promoting greater accuracy in environmental assessments in a diverse range of species (Valone & Templeton, 2002). The current findings indicate that, within the specific experimental context, chimpanzees and children were capable of collecting social information to enable an adaptive response in terms of selecting the better quality resource. This ability to discern resource quality using social information constitutes an important attribute for many species since it can reduce uncertainty and improve the efficiency of decisions concerning feeding site selections (Galef & Giraldeau, 2001; Valone & Templeton, 2002). It is noteworthy, however, that public information use is only adaptive when used selectively, as payoff returns reduce as the number of social information collectors (scroungers) increase (the 'producer-scrounger' game: Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991). The identification of public information in a phylogentically diverse range of species ranging from invertebrates to birds, and now ape species, hints that public information constitutes a relatively simple form of information for many animals to exploit. Indeed, the acquisition and use of public information requires only simple cues and underpinning social learning processes such as local enhancement (Webster & Laland, 2012), relative foraging commotion or movement (Laidre, 2013) and quantity discrimination such as number of offspring during breeding site selection (Parejo, White, Clobert, Dreiss, & Danchin, 2007).

Public information, however, may also be important for other, perhaps more complex, forms of social learning. The discernment of others' relative successes using public information may be an important foundation for payoff biased social learning, in which an appraisal of others' (and sometimes one's own) payoffs are key to updating behaviour adaptively (Kendal, Rendell, Pike & Laland, 2009). This is because observation of the resource itself is not always possible (e.g., food occluded by the forager's hand) and thus other cues (e.g., consumption rate) are required to supplement perceptual information to assess payoff magnitudes. Therefore, for species capable of socially learning more efficient behaviours that yield greater payoffs, public information should permit payoff biased transmission under a broader range of conditions than using personal information alone, i.e. when personal information allowing payoff quantification is restricted. To the extent that payoff biased copying can facilitate cumulative culture by allowing (rare) beneficial modifications to rapidly spread (Baldini, 2012; McElreath, Bell, Efferson, Lubell, Richerson & Waring, 2008) and by protecting against the propagation of low paying (and hence, often, suboptimal) behaviours, public information use may also have implications for cultural ratcheting (Tomasello, 1994). Specifically, payoff biased copying can provide one means for cumulative culture to increase in cultural complexity and efficiency as social learners incorporate only advantageous, high paying, innovations into their repertoire through, for example, 'copy if better' social learning rules (Laland, 2004).

Future research is needed to disentangle the relation between public information and payoff biased social learning, perhaps through investigation of whether payoff biased social learning can occur in species that do not use public information. For example, payoff biases could be investigated in three spined sticklebacks (*Gasterosteus aculeatus*) who consistently fail to use public information. One limitation of such an approach is that it is unclear whether three spined sticklebacks are incapable of using public information or are just not motivated to use public information (Coolen et al., 2003). While research investigating payoff biased transmission across species is sparse, current findings including those in this thesis (Chapter III and Chapter IV), are suggestive that species who employ payoff biased social learning strategies (Nine-spined sticklebacks, *Pungitius pungitius*: Kendal et al., 2009; Pike, Kendal, Rendell & Laland, 2010), also use public information (Nine-spined sticklebacks: Coolen et al., 2003; Homo sapiens: Morgan, Rendell, Ehn, Hoppitt & Laland, 2012). Similarly, Norway rats (*Rattus norvegicus*) who employ a 'copy when dissatisfied' (Galef, Dudley & Whiskin, 2008) rule, also use public information (Galef & Whiskin, 1999). However, I do not wish to suggest that all species using public information employ payoff biased social transmission, but that public information may be a necessary skill for payoff copying.

Experiment 1 (Chapter III) considered whether public information was sourced and used in a 'foraging' context in which personal information was not available (Coolen et al., 2003; Kendal, Coolen, & Laland, 2004). Considering that a reliance on social information should increase when personal information is difficult to source (Boyd & Richerson, 1988), it would be of value for further research to establish whether public information use persists in situations where prior personal, conflicting or alternative information has been sourced. This is especially so given that many nonhuman species often weight personal information over alternative social information (guppies: Kendal et al., 2004; starlings: Templeton & Giraldeau, 1996; sticklebacks: van Bergen, Coolen & Laland, 2004), whereas, children switch between personal and socially sourced task solutions (Wood, Kendal & Flynn, 2013) and will copy demonstrated behaviour, even when more efficient solutions exist, with greater fidelity than chimpanzees (Nagell, Olguin, & Tomasello, 1993). Differential strategies in this regard may also have implications for species' extent of cumulative culture. For example, species that weight personal information heavily and only fall back on social information under specific circumstances (e.g. copy when personal information is costly), should possess up-to-date and reliable information. However, a heavy reliance on personal information can also be at the expense of propagating (beneficial) innovations and, thus, cultural progression. Overreliance on social information, as often seen in children (Lyons, Damrosh, Lin, Macris & Keil, 2011; Lyons, Young & Keil, 2007), by contrast allows inefficient behaviour to propagate (Horner & Whiten, 2005; Lyons et al., 2007), but can also promote behavioural flexibility by encouraging learning of multiple solutions from others, and allows (faithful) transmission of culture. Furthermore, if individuals intentionally select and perform the *best* behaviour in their repertoire, thus enabling others to copy this behaviour, social information use should allow the propagation of beneficial modifications (Rendell, Boyd, Cownden, Enquist, Eriksson, Feldman, 2010; Rendell, Boyd, Richerson & Henrich, 2011).

In summary, in the first of the presented series of experiments, chimpanzees and 5-year old children, similar to multiple other species, attended to the cues inadvertently provided by conspecifics acquiring resources at different rates (Coolen et al., 2003; reviewed in: Dall, Giraldeau, Olsson, McNamara & Stephens, 2005; Danchin, Giraldeau, Valone & Wagner, 2004; Valone & Templeton, 2002). This result extends current phylogenetic listings of public information use to ape species, sheds new light on the type of information that can benefit primate foraging activity and provides further evidence for the utility of video demonstrations for social learning studies (Hopper, Lambeth & Schapiro, 2012). This ability to use public information may also play a role in cultural evolution. Danchin and colleagues (2004), in particular, have postulated that public information may yield cultural, group typical, behaviour; for example, as seen in the reversal of mate preferences in fish subjected to conspecifics mating with non-preferred males for extended periods (Dugatkin, 2000). Similarly, the reproductive successes of others can lead to change in annual breeding site selection (via public information use); a form of traditional change where groups congregate in better habitats through social information use, thought to have consequences for the evolution of coloniality (Danchin, Boulinier, & Massot, 1998). In line with this, it may be conjectured that through organisms converging on successful behavioural solutions, the selective use of public information may benefit cultural evolution by moving cultural change in the direction of incorporating behaviours that are beneficial.

Success copying II: Payoff Biased Social Learning Strategies

In Experiment 2 (Chapter IV), evidence for sensitivity to payoffs underpinned by selective social learning was reported in chimpanzees and 4- to 5-year old children. Specifically, the proportion of individuals who ceased use of a personally-learned token, switching to the alternative socially demonstrated token was greater in a condition where the alternative token provided a higher payoff than the personally-learned token (SL: personal token =small reward, socially demonstrated token=large reward), than when the opposite was the case (LS: seeded groups, both species). Turning to the proportion of alternative tokens exchanged (not the proportion of individuals who did so) the data were suggestive that children made use of a proportional observation rule whereby they copied according to demonstrator’s payoffs (Schlag, 1998, 1999). In contrast, the data were suggestive that chimpanzees used a proportional imitation rule whereby copying depends upon rewards to self and other (Schlag, 1998, 1999). The referral to proportional *imitation* here is for consistency with past terminology (Kendal, Rendell, Pike & Laland, 2009; Morgan, Rendell, Ehn, Hoppitt & Laland, 2012; Schlag, 1998, 1999) rather than to infer that chimpanzees employed imitation.

Multiple transmission biases have been reported in animal species, particularly in fish (Kendal, Coolen, Laland, 2009; Kendal et al., 2004; Laland & Williams, 1997; van Bergen et al., 2004) and children (Birch et al., 2008; Brosseau-Liard & Birch, 2010; Wood, Kendal & Flynn, 2012). Our findings showed that chimpanzees and children were capable of employing payoff biased transmission, adding to previous findings showing indirect model based (Birch et al., 2008; Brosseau-Liard & Birch, 2010; Horner et al., 2010; Wood et al., 2012) and state dependent (Kendal et al., 2004; Laland & Williams, 1997; van Bergen et al., 2004) social learning in animals. Payoff biased learning, which constitutes a more direct form of copying than other model based biases (e.g. age, success and dominance dependent copying), can facilitate cumulative culture by preventing maladaptive or neutral trait hitchhiking that can otherwise occur from model based social learning biases (Boyd & Richerson, 1985). Indeed, copying strategies dependent upon payoff to other (PO) and self (PI), have been shown to outcompete more general success biased copying that can allow sub-optimum trait copying (Schlag, 1998, 1999). Accordingly, payoff based learning, like public information use, allows incorporation of beneficial behaviours into species' repertoires and culture, with the potential to give rise to group typical behavioural traditions with important fitness consequences (e.g. increasing survival chances through greater energetic returns).

A proportional observation rule, as reported in children in this thesis, has recently been reported in human adults (Morgan et al., 2012). Participants were provided a 'pitch modulation task' and provided with both a rank based on their own performance and the performance rank of another participant, whom they could copy. Overall, a demonstrator's rank influenced participants' copying decisions such that low scoring demonstrators were not copied (PO). Morgan and colleagues (2012) also reported that copying high ranked demonstrators was dependent upon participant's personal task success. Thus, some evidence was found for a proportional imitation rule (in which copying depends upon payoff to other relative to self). The authors interpreted these results as evidence for a proportional observation (PO) rule and a conditional proportional imitation rule (PI) as high performing demonstrators were copied, but those subjects who acquired particularly low performance ranks (the 'conditional' context) showed especially high levels of copying successful demonstrators (Morgan et al., 2012). In Experiment 2 (Chapter IV), children's copying (as shown by the proportion of alternative tokens exchanged) was dependent upon the demonstrator's payoff only (PO); random token exchange was observed in the SS and LS condition, in which demonstrators' payoffs yielded low rewards, whereas high levels of copying was observed in the SL condition, in which demonstrators' payoffs were high. This is consistent with PO for which pre-experienced token values should be ignored, with copying proportional to the demonstrators' payoff only (S**S**=L**S**, but SL>LS). One potential explanation as to why random token exchange occurred in the LS seeded condition (children), where maximal reward gain occurs by 'sticking' to the personally learned token option, is children's high propensity to copy others (Flynn & Whiten, 2008; Horner & Whiten, 2005; Lyons et al., 2007), even inefficient (Horner & Whiten, 2005; Lyons et al., 2007), actions. An alternative strategy of attending to relative rewards to self and other (PI) would predict exchange of tokens in the LS condition should not have been at random but limited to the higher paying pre-experienced token. This PI strategy was reflected in the overall pattern of results in chimpanzees; they showed reliance on asocial information when presented with a demonstrator who exchanged a token for a lower reward than their existing token (LS), and used social information only when the demonstrators' reward was better than their own (SL). Meanwhile, individuals in the SS group selected at random. These findings point toward copying dependent upon reward to self *and* other (PI). Larger samples of both species would prove fruitful for disentangling the specific payoff biased rule employed, particularly in chimpanzees, by increasing statistical power.

Chimpanzees appeared to require more extended social learning opportunities than children. Chimpanzees showed differential patterns of token exchange according to reward condition in the seeded condition, but not in the non-seeded condition (in which they were not exposed to the additional model observation phase: affording less social learning opportunity). In contrast, for children there was no difference in exchanges between groups that were seeded, or not, with a trained demonstrator. Potentially, the task employed was too simple to require lengthy engagement in social learning for children. It is, however, noteworthy that social learning was involved in children's reward maximization, given that asocial controls, collectively, selected tokens at random. Thus, access to naïve peers (in the non-seeded condition) was necessary for children to exchange tokens in accordance to their payoffs. Nevertheless, future research would benefit from conducting asocial controls for all reward conditions rather than just for the SL condition, at least for children. This is especially so given that the respective roles of asocial and social learning could not be assessed in children exposed to the LS and SS conditions, due the absence of asocial controls and the similarity of response between seeded and non-seeded groups.

To sustain motivation levels, children received 30 minutes open diffusion compared to six hours open diffusion with chimpanzees. Yet children in the SL condition exchanged proportionally more of the alternative, Large-Medium Value token, than did chimpanzees. This suggests that children were quicker to adopt a payoff rule than chimpanzees. Similarly, finding 94% of children's exchanges were made with the alternative token (in both seeded and non-seeded groups SL condition) shows rapid and consistent token switching to the high paying token. This suggests that humans possess a bias towards proportional observation, as evident through this strategy's employment from the outset of experimental tasks (Mesoudi, 2011). Future research should consider whether extended task exposure in children may alter the payoff biased rule employed, for example, whether they copy according to, not only demonstrator's payoffs (PO), but the difference in payoff to self and other (PI).

It has been suggested that once a solution has been learned, it can interfere with subsequent flexible learning of alternative solutions (Boyd & Richerson, 1985). The results of Experiment 2 highlighted that conservative learning was not present in children nor chimpanzees. Specifically, both species were able to switch to the alternative, demonstrated behaviour when coupled with higher reward values than the previously learned behavioural option. Children have recently been shown to incorporate both personally discovered and socially demonstrated behaviours when they yield the same payoff, indicating behavioural flexibility (Wood, Kendal & Flynn,, 2013). We add to this finding by showing that when socially demonstrated payoffs are better than personally learned solutions, children reproduce the socially demonstrated behaviour only. Past findings have indicated that chimpanzees stick to previously learned behaviours upon presentation with alternative solutions

(Hrubesch, Preuschoft & van Schaik, 2009; Marshall-Pescini & Whiten, 2008). These findings have recently been challenged (Amici, Aureli, & Call, 2008; Dean et al., 2012; Manrique, Völter, & Call, 2013). Manrique and colleagues, for example, presented chimpanzees with a puzzle box with three variant behavioural solutions, successively blocking a solution after discovery. Chimpanzees were reported to switch techniques after a previously used one became obsolete, evidencing behavioural flexibility (see also Lehner, Burkart, & van Schaik, 2011for similar findings in orangutans). The findings of Experiment 2, further suggest that chimpanzees can switch behaviour even when the previously learned behaviour remains available. This, along with other recent findings (Dean et al., 2012; Manrique et al., 2013), indicate that chimpanzees are less conservative than previously thought (Marshall-Pescini & Whiten, 2008). The capacity to switch behavioural responses (socially and asocially learned) has implications for cultural evolution in changing environments wherein behaviours can become redundant (Boyd & Richerson, 1985; Mesoudi, 2011). It is worth noting, however, that in Experiment 2 the chimpanzees only had to switch to an alternative behavioural option (differential token) without modifying the underlying behavioural response (exchange behaviour). It would be beneficial for future research to further examine whether behavioural flexibility persists when novel behaviours are more complex than previously learned in a situation where both the novel and learned behaviours can be practiced.

Future research should consider varying task difficulty, especially for children of a similar age to those tested in Experiment 2. Increasing task complexity, and in particular increasing the variance in payoffs, should promote further insight into whether children are capable of the PI rule or whether they attend to demonstrators payoffs only (PO). Specifically, it would be of interest to introduce a form of 'bi-modal fitness' landscape in which two local, differently rewarded, optimums exist based on different combinations of responses (see Mesoudi and O'Brien, 2008a; b for multimodal landscapes). For example, multiple differential tokens could be introduced with different combinations at their exchange yielding different payoffs (for example, single yellow token exchange=1 reward; simultaneous exchange of yellow and black tokens = 4 rewards; simultaneous exchange of yellow and black followed by green = 5 rewards, stepping up to a first locally adaptive optimum). Individuals could be trained on single token exchange (e.g. yellow token =1reward) prior to introducing two demonstrators per seeded group, one who models part of the behaviour optimum 1, the other modelling part of optimum 2 (e.g. using different shaped, coloured tokens/different exchange location, for different rewards). This would then allow room for innovation and 'hill climbing' (incremental change via asocial or social learning of a solution towards the local optimum); both of which are relevant to cultural evolution. Furthermore, through inclusion of two demonstrators, model based biases and their interplay with payoff biased rules could also be assessed by varying demonstrators' characteristics (e.g. do learners copy dominants' less rewarding behaviour [local optimum 1] over subordinates' more rewarding behaviour [optimum 2]). Such an experimental set up contrasts that of Experiment 2, which employed a simple, dichotomous, choice task (see also McElreath et al. 2008), and may not approximate the complex social environments experienced by children (Mesoudi, 2011), or chimpanzees.

Enhancing task difficulty, in addition to improving ecological validity, may also impact upon the use of payoff biased rule. Specifically, any masking effect of the imitation of causally irrelevant actions (Lyons et al., 2011; Lyons et al., 2007), if present in children, may not come into effect when required to copy more complex response sequences and this may result in more evidence for use of a PI strategy. Increasing task difficulty could alternatively increase the level of social learning (through ‘copy when asocial learning is costly’, ‘copy when uncertain’ strategies: Boyd & Richerson, 1985; Kendal, Coolen & Laland, 2009; van Bergen et al., 2004) with little attention paid to differential payoffs.

In summary, the findings of Experiment 2, (i) lend support for the current corpus of evidence for social learning in chimpanzees (Biro & Carvalho, 2011; Bonnie, Horner, Whiten & de Waal, 2007; Hopper, Spiteri, Lambeth, Schapiro, Horner & Whiten, 2007; Horner & Whiten, 2005) and children (Flynn & Whiten, 2008; Horner & Whiten, 2005; Lyons et al., 2007), (ii) extend current literature by showing use of payoff biased learning rules, important for cultural evolution (Mesoudi, 2011), in two primate species, and (iii) suggest that chimpanzees are not conservative learners (Gruber, Muller, Reynolds, Wrangham & Zuberbuhler, 2011; Manrique et al., 2013). Coupled together and contrary to past predictions, it may be expected that the limited, arguably absent (Dean et al., in press), capabilities of chimpanzees for cumulative culture may not be restricted by an inability to selectively copy others according to the payoffs garnered for different behavioural options. Instead, it may be postulated that other cognitive and social attributes may be responsible for limiting cultural progression. For example, less readily engaging in complex social learning mechanisms (e.g. teaching), limited prosociality and the lack of verbal/written language are likely important in this regard (Carruthers, 2013; Dean et al., 2012; Fogarty, Strimling & Laland, 2011; Lewis & Laland, 2012; Tomasello, Kruger & Ratner, 1993). More precisely, it is likely that a heightened capacity in humans for these, and other, factors and the interplay between them, including social learning strategies and payoff biases, are responsible for the human cultural explosion.

III: The retention of complex tool manufacture behaviour

In the third series of experiments in this thesis (Chapter V), chimpanzees' capacity to retain complex tool manufacture styles (tool combining or extension) over the course of ca. 3.6 years was investigated. Chimpanzees were found to retain tool manufacture styles (combine and/or extend) and to improve the flexibility with which elongated tools were made according to need (distant grapes). Such functional improvement in tool creation may reflect improved causal reasoning, discussed below, or a reduction in the canalisation towards (socially) learned information. Tool modification by combining tool components is a complex tool behaviour for chimpanzees, one that is rare in the wild being restricted to anvil-stabilizer couplings (Bossou), and the compression of multiple leaves to create water absorbent leaf sponges (Matsuzawa, 1991; McGrew, 2010). Similarly, elongated tool creation through the extension method is a complex tool manipulation, especially considering chimpanzees tend to create tools by deconstructive rather than constructive tool modification, e.g. material length reduction to make probes (McGrew, 2010).

The retention of socially learned information following an imposed delay has previously been documented in children and chimpanzees. Nine-month old children, for example, can reproduce parts of modelled demonstrations following a 1 month delay (Carver & Bauer, 1999) and at twenty months can reproduce temporally ordered demonstrated acts following a delay of two years (Bauer, Wenner, Dropik, Wewerka, & Howe, 2000). Chimpanzees have been shown to reproduce demonstrated object manipulations following a short,10 minute, delay, with copying accuracy improving with age (Bjorklund & Bering, 2003). Similar capabilities have also been reported following a 48 hour delay (Tomasello, Savage-Rumbaugh & Kruger, 1993) and have been shown to generalise to similar objects (Bjorklund et al., 2002). These findings provide support for the high levels of tool retention and transfer of skill to a similar task reported in Chapter V (see also Martin-Ordas, Berntsen & Call, 2013).

It is noteworthy that the specific learning mechanism underlying chimpanzees' original tool manufacture acquisition in 2008 (Price et al., 2009), cannot be definitively identified. In the original study, chimpanzees were exposed to various degrees of social demonstration relating to the tool combine or extension method of elongated tool creation; namely, combine-and-retrieve reward, retrieve-reward only (with already combined tool), video control (reward consumption only), no-video control and tool extension-and-retrieval. Overall, those exposed to the combine-and-retrieve reward demonstration combined significantly more than those not exposed to combinatory actions. The authors interpreted this as a potent effect of social learning (Price et al., 2009). However, three chimpanzees, in the video and no video controls, asocially learned to create elongated tools to retrieve rewards, and three also did so after exposure to the retrieve-reward only demonstration (perhaps by emulation or asocial learning). Hence, while social learning facilitated tool combining activity, asocial learning also played a role. Thus, Experiment 3 showed deferred retention of both social and asocial information (cf. Bjorklund & Bering, 2003). Finding high levels of specific tool manufacture retention in all but one chimpanzee, nevertheless, indicated that the initial learning mechanism underpinning learning (e.g. combine-and-retrieve, *allowing* imitation; retrieve-reward only, *allowing* emulation; no-video control, asocial learning) was not important for cued recall.

Chimpanzees possess notable memory capabilities; they can remember hidden food locations after ca.12 days (Menzel, 1999) and display impressive working memory for spatial-numeral arrangements presented on touch screens (Inoue & Matsuzawa, 2007). Until recently, the long-term memory capabilities of chimpanzees had largely been neglected. In addition to Experiment 3, one exception, to my knowledge, was provided by Martin-Ordas and colleagues (2013), who recently documented the retention of tool use knowledge in chimpanzees and orangutans. Testing autobiographical memory, subjects were retested on a tool use task following a 3 year delay. During the initial tests, subjects were exposed to an experimenter hiding two different tools in two locations; only one of which was functionally appropriate for a subsequent raking task (task appropriate tool allowing reward retrieval). During retest, presentation of the same experimental apparatus, test area and experimenter but omitting visual access to the tool hiding event, 10 of 11 experienced subjects searched for tools in the correct target locations. Moreover, in general, those that first found the task appropriate tool, ceased further tool searching behaviour, while those who did not searched the second location (without use of the task inappropriate tool). These results contrasted control subjects, who, without past task knowledge, failed to search in either tool location (Martin-Ordas et al., 2013). Coupled together with the results of Experiment 3 in this thesis, these data strongly suggest that chimpanzees possess, along with noteworthy working memory (Inoue & Matsuzawa, 2007), considerable long-term memory for past tool use behaviours, tool manufacture and experimental apparatus, lasting the course of years. This indicates that the tendency to test memory over relatively short periods (Bjorklund & Bering, 2003; Sayers & Menzel, 2012; Tomasello et al., 1993) may have significantly underestimated chimpanzee's memory capabilities. It may be postulated that long-term memory capabilities are essential for chimpanzees to locate and access infrequently available resources (e.g. seasonally available Coula nuts, Tai Forest: Luncz, Mundry & Boesch, 2012) for which food extraction/percussive behaviours may not be practiced for extended periods. Accordingly, long-term memory may serve to, (i) maintain the size of chimpanzees cultural repertoires, (ii) aid survival when faced with seasonal variability in food resources (by recall of food extraction/processing techniques when resources are in season, reducing the time required to access food should behaviour have to be relearned each fruiting season), (iii) enable the transmission of skills to other individuals (by maintaining behaviours long enough that they may be demonstrated to juveniles and conspecifics), and (iv) allow individuals to track and remember potential models with a past history of successful behaviour.

The ability of chimpanzees to transfer a tool manufacture skill to a novel context was also examined. The transferral of knowledge to new situations is important for both innovation and adaption to changing or new environments (Boesch, 1995). Skill transfer has also been conjectured to rely on inferential causal reasoning (cause and effect learning, isolating the precondition for the effect) and analogical causal reasoning (generalizing this knowledge of cause and effect to similar, analogous situations: Vaesen, 2012). Causal reasoning and knowledge generalisation has been investigated using variants of the trap-tube task; insertion of tool at the correct end of a tube to push out, or rake in, a reward without it falling into a trap. Chimpanzees' task performances, however, seem to vary across individuals with little evidence of immediate task comprehension (Limongelli, Boysen, & Visalberghi, 1995) and with limited evidence for knowledge transfer (Martin-Ordas & Call, 2009; Martin-Ordas, Call, & Colmenares, 2008). Conversely, experienced combiners reported in this thesis readily transferred tool combining skills across similar tasks. This finding is all the more pertinent given that chimpanzees more readily rake in rewards (as in the retention study) as opposed to pushing-displacing rewards via a probe action (as in the transfer studies) (Martin-Ordas et al., 2008; Mulcahy & Call, 2006).

It is worth noting that, after tool combination practice during the retention study, chimpanzees could have, upon presentation of the new task, simply repeated combine actions without causal understanding of why they did so. There is, however, reason to doubt this interpretation. First, four experienced combiners discovered the novel, serial method, of tool use during the transfer tests. This speaks against repetitious tool acts, irrespective of context. Second, enhanced performance was observed upon presentation of the transparent, as opposed to opaque, task. This, coupled with documentation of improved performance upon presenting chimpanzees with transparent task conditions (Horner & Whiten, 2005; Volter & Call, 2012), suggests improved functional understanding of the task occurred by visual access to the inner box mechanisms. Such enhanced performance across transfer studies, however, could occur through practice effects. Yet, naïve controls (who did not participate in the transfer-opaque and retention studies) performed better than controls (participating in all studies) when exposed to the transfer-transparent task. This hints that additional practice with the transfer task (when in the opaque version) did not enhance individuals' task performances with the transparent task. Future research would benefit from counterbalancing task presentation order across participants to isolate: (i) whether complex tool manufacture was transferable in the absence of presenting the original raking task first, and (ii) whether improved flexibility of tool manufacture in the transfer-transparent task was, as hinted by the data, due to additional visual access to the inner workings of the box.

Culture has been shown to influence memory (Bartlett, 1932). Normative influence (or normative conformity) from communicating with others, for example, can alter one's memory for event details resulting in erroneous or modified memory recall (Petterson & Paterson, 2012). Cross cultural differences have also been documented in the specificity of autobiographical memory (Dritschel, Kao, Astell, Neufeind, & Lai, 2011; Humphries & Jobson, 2012), memory for one's own body movements (Haun & Rapold, 2009) and visual-spatial memory (Kearins, 1981). The relation between culture and memory, however, is not uni-directional. It is well known that the limit of working memory imposes a constraint on the amount of information processed (Miller, 1956). We might, therefore, expect working memory constraints to limit the specificity or level of match between observed and reproduced cultural traits, especially after brief or single demonstrations. Similarly, implicit or semantic memory, manifested in expectations, may influence the content of information culturally transmitted (direct transmission bias) (Boyer, 2009). Finally, in species, for whom certain behaviours may not be continually practiced, we may expect that long-term memory is likely to play an important role in behavioural and cultural maintenance. That is, in the absence of repeated visual demonstrations of behaviours, learned behaviour patterns may become lost unless encoded and retained in an organism's memory. A well-known example of cultural loss was documented in the Polar Inuit, who, in the 19th Century were reported to lack much of the cultural technologies (e.g. kayaks and bows and arrows) observed in surrounding populations (discussed in Boyd, Richerson, & Henrich, 2011). This loss was thought to be due to an illness causing the death of many elder, knowledgeable individuals. Long term memory should be considered an essential facet of culture, one that can help protect against cultural distortion and entropy through storage. Here, valuable insight into the long-term memory capabilities of chimpanzees was provided; one of a range of memory processes that may influence cultural transmission and culture (Boyer, 2009).

Future Directions

While I have mentioned potential future studies in previous chapters, I now add to this. Chimpanzees and children used social information adaptively. Yet social information use depends on a multitude of factors. Context and knowledge states, such as ‘copy when uncertain’, ‘copy when personal information is costly’ (reviewed in Kendal, Coolen, Laland, 2009), are not the only determinants of the type of information used. Individual differences have been identified in decisions to use personal or social information (Morand-Ferron, Wu, & Giraldeau, 2011). Female zebra finches’ reliance on social information, for instance, has been shown to correlate across mating and foraging tasks and was negatively correlated with their personal sampling ability (Rosa, Nguyen, & Dubois, 2012). With this in mind, a future avenue for primate social information studies is to isolate potential individual differences in the reliance on social and personal information using a battery of tasks (see for example Herrmann, Hernandez-Lloreda, Call, Hare & Tomasello, 2010). Individual information biases could be established by providing subjects with personal information regarding a resource location (patch sampling) and social information of an alternative resource location (conspecific sampling), prior to a dichotomous decision of the two patches, and comparing this to resource selections of subjects who receive no prior personal information (Kendal et al., 2004). This base method lends itself to alternative contexts, and, for example, could be applied to a similar tool use task to the retention study by providing different tool options personally and socially sampled. Comparisons across task contexts and measurements of individual levels of personal information use (level of task exploration and the extent to which foraging sites are sampled) would then allow individual preferences for information type to be identified (Rosa et al., 2012). Once personal biases are identified, consideration could be given to the factors that overcome personal preferences of information source (e.g. particularly persuasive model biases/task circumstances such as the difficulty with which information is collected), as well as personality correlates (internal characteristics associated with personal and social information weighting). For example, one could ask: (i) do risk-taking individuals rely upon personal sampling and neophobic individuals social information? (ii) Does high sociability predict reliance on social, over personal, information? (iii) Are adept social learners also better innovators and which information do they weight more heavily (Reader & Laland, 2002b; Wisdom & Goldstone, 2010)? This identification of individual variation in preferred information source (personal or social) will have important implications for studies investigating social learning and social learning strategies. For example, evidence for a Propotional Imitation strategy could have been hidden in Experiment 2, if some children simply weighted social information above personal knowledge and thus copied peer responses (token selections) even when they yielded worse rewards.

Throughout this thesis there has been a running theme of ‘cumulative culture’. Following the identification of payoff and success copying allowing improvements in efficiency, the next logical step is to adapt these methods to determine whether payoff copying motivates species to step up their behavioural complexity. This could easily be determined, again, using the token exchange paradigm by the addition of a more complex behaviour yielding higher payoffs than unmodified token exchange. Building on chimpanzees capability to combine tool elements (Experiment 3), combining a token and token cap (behaviour demonstrated by a trained model and yields a large reward) versus unmodified token exchange (yields small reward), is one such possibility. A comparison of group performance and asocial controls would then allow a determination of whether payoff biased copying lends itself to improvements in behavioural complexity. This study was in fact conducted with the chimpanzees at the KCCMR, albeit the data has not been formally analysed yet.

Concluding remarks

In this thesis, three cognitive or socio-cognitive attributes, considered important to a species' extent of culture, and cultural progression (cumulative culture), were investigated. For cultural evolution, a key process is cultural transmission. The specific means employed to transmit culture can have important consequences at the population level (Boyd & Richerson, 1985; Mesoudi & O'Brien, 2008). For example, transmission biases, and indeed copying mechanism, can have large scale implications (cultural micro- and macro-evolution: Mesoudi, 2006) such as whether organisms are likely to converge on optimum behaviours and even whether learned (non-genetic) knowledge can be passed on to the next generation (organisms capable of social learning) or not (purely asocial learning organisms).

Evidence for success-biased social information use was documented in chimpanzees and children, showing comparable use of public information across species. Building upon this, chimpanzees and children were shown to use a more direct transmission bias (payoff biased copying) to, in general, selectively perform behaviours which maximized behavioural payoffs. This is adaptive since both species acted on social information when it was beneficial to do so; albeit children did not maximise reward gain when presented with a demonstrator who's behaviour yielded rewards worse than their own. These findings, in general, are in line with predictions of flexible use of asocial and social information through employment of transmission biases (Boyd & Richerson, 1985; Laland, 2004). Thus, in line with the definition of cumulative culture (Dean et al., in press; Tennie et al., 2009; Tomasello, 1990), this would enable individuals to improve behavioural efficiency in terms of improved returns. Note, however, that the essential feature of cumulative culture is that improved efficiency and cultural complexity moves beyond what individuals, without social information, can invent in their lifetimes. Thus, while this thesis indicates that success and payoff biased copying may move culture towards improvements (reward gain), the experiments nonetheless do not show improvement in this cumulative manner. Finally, chimpanzees were shown to retain detailed tool manufacture and use over extended periods and transferred this capability to a new context. Such long term memory is useful for maintaining cultural behaviours that may not be practiced for extended periods due to seasonal change, preventing cultural entropy. Generalising knowledge, in addition to behavioural flexibility, may also prove beneficial when undergoing environmental change, allowing adaptation to one's surroundings (Boyd & Richerson, 1985). The lack of behavioural conservatism (Experiment 2), combined with discriminate use of social learning (Experiment 2), enhanced flexibility of tool creation according to need over time (Experiment 3) and generalisation of knowledge to a novel task (Experiment 3) all have important implications for adapting to environmental change.

From these findings, we may speculate that long-term memory retention in chimpanzees, coupled with public information use, may allow chimpanzees to remember resource rich patches that they may not have sampled themselves (e.g. due to resource monopolisation by conspecifics); such a skill is useful for seasonally available resources. Similarly, payoff biased learning coupled with long-term memory may allow chimpanzees to employ better methods as practiced by others (and as identified by greater payoffs) after significant delays and to track successful models. This should promote transmission and memory, and thus retention and practice, of effective over suboptimum behaviour, proving beneficial for future social learners who can then copy these effective behaviours. It would be of interest for future research to investigate the interplay between retention of previously learned skills and payoff biased copying, for example, at what point would prior personal information become so outdated that all social information is copied (irrespective of reward value)? Similarly, when presented with two opposing demonstrations, one yielding better rewards, would species retain information regarding the better behaviour, as opposed to the poorer behaviour, for greater periods of time? Finally, one might ask whether species switch from a retained behaviour, such as tool combining, upon social demonstration of more efficient solutions such as use of an already combined tool to gain an out-of-reach reward.

Overall, the findings of this thesis suggest that the limited, arguably absent, capability of cumulative culture in chimpanzees may not, be attributed to their lack of ‘copy if better’ social leaning strategies, as supposed by Laland (2004). Similarly, chimpanzees possess requisite long-term memory to retain behaviour patterns in their repertoire long enough for social transmission to conspecifics (preventing cultural slippage) as the occasion arises (e.g. processing of rarely encountered resources). These findings suggest that, to the extent that cultural ratcheting is absent in this species, other attributes or an interplay between attributes, must be involved. The work presented in this thesis, indicates that chimpanzees show impressive long term memory abilities, can use public information to identify abundant resources and, evaluate payoffs to other and self to direct social learning towards maximising resource gain.

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Appendices

Appendix A. Reward, colour and motivation tests in chimpanzees (Chapter IV)

Reward Preferences. Dichotomous food preferences were initially run to identify preferred food quantities. Preference tests involved baiting two feeder tubes with food, differing in quantity, (alternating the side on which the large quantity was placed) and then presenting them simultaneously to chimpanzees, allowing a forced choice. Pilot tests with 1vs4 grapes (*N*=5) and 1vs8 (*N*=6) grapes failed to provide consistent preferences. Dichotomous preference tests with food differing in both quality and quantity (1 carrot piece versus 4 apple pieces) did yield consistent preferences (for apple), defined as selection of one food type on 8 or more of the 10 trials (Hopper et al., 2011) in all but one participant. As this individual was an asocial control, food preference tests were run with a different food item (1 carrot piece versus 4 green pepper pieces) and yielded a consistent preference (for pepper). This alternative food was used in subsequent tests for this individual. All preference tests were run on different days to the main study.

Exchanging for carrot. A pilot test was conducted with individuals not participating in the main study (*N*=7) to ensure that chimpanzees were sufficiently motivated to exchange a token for the less preferred reward (carrot). The test consisted of dispensing multiple tokens into chimpanzees' outdoor enclosure. An experimenter stood in a location approximately 3.96 metres away from the area in which the tokens were dispensed, with the right arm extended towards the chimpanzees enclosure (palm-up beg gesture). All chimpanzees exchanged tokens for single carrot pieces (range 4-21, across a 20 minute period). Thus carrot was considered sufficiently motivating for token exchange.

Token-Colour preferences. Preference tests were also conducted to determine whether individuals displayed a bias towards one of the two token colours. Yellow and black comparisons have been employed in past research, finding no unlearned bias towards either colour (Horner, Carter, Suchak, & de Waal, 2011). The experimenter held one token in each hand, arms outstretched towards the participant, allowing a forced choice to be made by gesture (de Waal, Leimgruber, & Greenberg, 2008). A preference was considered present if one token type was selected on 8 (or more) of 10 trials (de Waal et al., 2008; Horner et al., 2011). No participant displayed a token preference and overall the yellow token was selected on 429 of 830 trials (binomial: p=.349). No rewards were provisioned during token preference tests and all token preference tests were conducted on different days to experimental tests, often over multiple days/sessions where participant motivation was low.

Appendix B. Chimpanzee token preferences (IV).

Table B1.
Chimpanzee token preferences (Asocial control)

Pt	No. Pre-experienced Tokens	No. of Alternative Tokens	Total Exchanges	P-Value (Binomial Test)	Preference
1	30	0	30	p < 0.001	P
2	18	0	18	p < 0.001	P
3	50	0	50	p < 0.001	P
4	4	4	8	N.S	-
5	16	41	57	p=0.001	A

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference (tokens selected at random).

Table B2.
Chimpanzee token preferences according to reward- model condition

Pt	Model Condition	Pre-experienced (No. Exchanged)	Alternative (No. Exchanged)	P-value (Binomial)	Preference
1	LS Non-seeded	330	23	p<0.001	P
2	LS Non-seeded	108	57	p<0.001	P
3	LS Non-seeded	1	13	p<0.05	A
4	LS Non-seeded	56	28	p<0.05	P
5	LS Non-seeded	69	31	p<0.001	P
6	LS Non-seeded	0	3	N.S	-
7	LS Non-seeded	14	14	N.S	-
8	SS Non-seeded	178	175	N.S	-
9	SS Non-seeded	136	54	p<0.001	P
10	SS Non-seeded	0	1	N.S	-
11	SS Non-seeded	0	2	N.S	-
12	SS Non-seeded	21	5	p<0.05	P
13	SL Non-seeded	80	135	p<0.001	A
14	SL Non-seeded	81	53	p<0.05	P
15	SL Non-seeded	3	0	N.S	-
16	SL Non-seeded	3	4	N.S	-
17	SL Non-seeded	18	5	p<0.05	A
18	SL Non-seeded	37	22	N.S	-
19	SL Non-seeded	3	0	N.S	-

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

Table B2.

Continued

Pt	Model Condition	Pre-experienced (No. Exchanged)	Alternative (No. Exchanged)	P-value (Binomial)	Preference
20	LS Seeded	158	37	p<0.001	P
21	LS Seeded	158	55	p<0.001	P
22	LS Seeded	16	17	N.S	-
23	LS Seeded	0	1	N.S	-
24	LS Seeded	35	49	N.S	-
25	LS Seeded	27	38	N.S	-
26	LS Seeded	366	42	p<0.001	P
27	LS Seeded	18	0	p<0.001	P
28	LS Seeded	93	13	p<0.001	P
29	LS Seeded	12	2	p<0.05	P
30	LS Seeded	4	0	N.S	-
31	LS Seeded	30	1	p<0.001	P
32	SS Seeded	184	16	p<0.001	P
33	SS Seeded	24	36	N.S	-
34	SS Seeded	54	65	N.S	-
35	SS Seeded	16	1	p<0.001	P
36	SS Seeded	0	1	N.S	-
37	SS Seeded	4	19	p<0.05	A
38	SS Seeded	2	0	N.S	-
39	SS Seeded	12	1	N.S	-
40	SS Seeded	6	23	p<0.05	A
41	SS Seeded	19	22	N.S	-
42	SS Seeded	18	2	p<0.001	P
43	SS Seeded	4	87	p<0.001	A
44	SS Seeded	1	16	p<0.001	A
45	SL Seeded	47	33	N.S	-
46	SL Seeded	8	0	p<0.05	P
47	SL Seeded	18	156	p<0.001	A
48	SL Seeded	24	13	N.S	-
49	SL Seeded	4	42	p<0.001	A
50	SL Seeded	1	33	p<0.001	A
51	SL Seeded	0	59	p<0.001	A
52	SL Seeded	52	19	p<0.001	P
53	SL Seeded	9	27	p<0.001	A

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

Table B2.

Continued

Pt	Model Condition	Pre-experienced (No. Exchanged)	Alternative (No. Exchanged)	P-value (Binomial)	Preference
54	SL Seeded	3	20	p<0.001	A
55	SL Seeded	76	36	p<0.001	P
56	SL Seeded	31	74	p<0.001	A
57	SL Seeded	22	32	N.S	-
58	SL Seeded	3	19	p<0.001	A

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

Appendix C. Reward and token preferences in children (in reference to Chapter IV)

Reward Preferences. Due to ethical considerations of provisioning food to children, stickers constituted the rewards. A single, small, coloured, circular sticker formed the Small reward and four larger, coloured, circular, smiley face stickers the Large reward. Dichotomous preference tests were run with each participant. All individuals selected the smiley stickers over the single plain sticker in 8 or more trials (*N*=10).

Token Preferences. Black (full length, 28cm) and white (folded in half, 14cm) pipe cleaners formed the differential tokens for children. Note, white was used instead of yellow since children show colour biases (Boyatzis & Varghese, 1994). No token preferences were observed (5 trials per individual, 149 of 315 selections were for the black token, *p*=.367). No rewards were provisioned during token preference tests.

Appendix D. Individual token preferences in children (Chapter IV)

Table D1.

Exchanges made by Asocial controls (SL condition: Child)

Pt	**No. Pre-experienced Tokens**	**No. of Alternative Tokens**	**Total Exchanges**	**P-Value (Binomial Test)**	**Preference**
1	25	0	25	p < 0.001	P
2	11	9	20	p = .824	-
3	19	18	37	p = 1.000	-
4	5	16	21	p = .027	A
5	1	18	19	p < 0.001	A
6	1	6	7	p = .125	-
7	9	13	22	p = .523	-
8	11	10	21	p= 1.000	-
9	23	0	23	p < 0.001	P

Note: A = Preference for the Alternative token; P = Preference for the Pre-experience token; - = No Preference

Table D2.

Child token preferences according to reward-model conditions

Pt	**Model Condition**	**Pre-experienced (No. Exchanged)**	**Alternative (No. Exchanged)**	**P-value (Binomial)**	**Preference**
1	LS Non-seeded	7	10	N.S	-
2	LS Non-seeded	26	0	p<0.001	P
3	LS Non-seeded	11	2	p<0.05	P
4	LS Non-seeded	24	1	p<0.001	P
5	LS Non-seeded	0	7	p<0.05	A
6	LS Non-seeded	7	10	N.S	-
7	LS Non-seeded	9	13	N.S	-
8	LS Non-seeded	10	7	N.S	-
9	LS Non-seeded	20	1	p<0.001	P
10	LS Non-seeded	11	0	p=.001	P
11	SS Non-Seeded	0	17	p<0.001	A
12	SS Non-Seeded	1	6	N.S	-

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

TableD2.

Continued

Pt	Model Condition	Pre-experienced (No. Exchanged)	Alternative (No. Exchanged)	P-value (Binomial)	Preference
13	SS Non-Seeded	6	14	N.S	-
14	SS Non-Seeded	10	10	N.S	-
15	SS Non-Seeded	14	7	N.S	-
16	SS Non-Seeded	1	7	N.S	-
17	SS Non-Seeded	4	13	p<0.05	A
18	SS Non-Seeded	13	2	p<0.05	P
19	SS Non-Seeded	0	4	N.S	-
20	SS Non-Seeded	5	5	N.S	-
21	SL Non-seeded	0	16	p<0.001	A
22	SL Non-seeded	1	15	p=.001	A
23	SL Non-seeded	2	14	p<0.05	A
24	SL Non-seeded	1	16	p<0.001	A
25	SL Non-seeded	3	14	p<0.05	A
26	SL Non-seeded	1	12	p<0.05	A
27	SL Non-seeded	0	16	p<0.001	A
28	SL Non-seeded	0	17	p<0.001	A
29	SL Non-seeded	2	18	p<0.001	A
30	SL Non-seeded	0	15	p<0.001	A
31	LS Seeded	11	8	N.S	-
32	LS Seeded	9	8	N.S	-
33	LS Seeded	2	16	p=0.001	A
35	LS Seeded	4	7	N.S	-
36	LS Seeded	7	16	p<0.05	-
37	LS Seeded	17	25	N.S	-
38	LS Seeded	26	7	p=0.001	P
39	SS Seeded	15	12	N.S	-
41	SS Seeded	5	22	p<0.05	A
42	SS Seeded	8	9	N.S	-
43	SS Seeded	2	22	p<0.001	A
44	SS Seeded	9	3	N.S	-

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

TableD2.

Continued

Pt	**Model Condition**	**Pre-experienced (No. Exchanged)**	**Alternative (No. Exchanged)**	**P-value (Binomial)**	**Preference**
45	SS Seeded	15	3	p<0.05	P
46	SL Seeded	3	36	p<0.001	A
48	SL Seeded	1	16	p<0.001	A
49	SL Seeded	2	23	p<0.001	A
50	SL Seeded	0	8	p<0.05	A
51	SL Seeded	1	18	p<0.001	A
52	SL Seeded	0	2	N.S	-
53	SL Seeded	0	38	p<0.001	A
54	SL Seeded	0	21	p<0.001	A

Note: A= preference for the alternative token; P= preference for the pre-experienced token; - = no preference

Appendix E. Child responses (Chapter IV)

Table E 1.

Child verbal responses according to condition

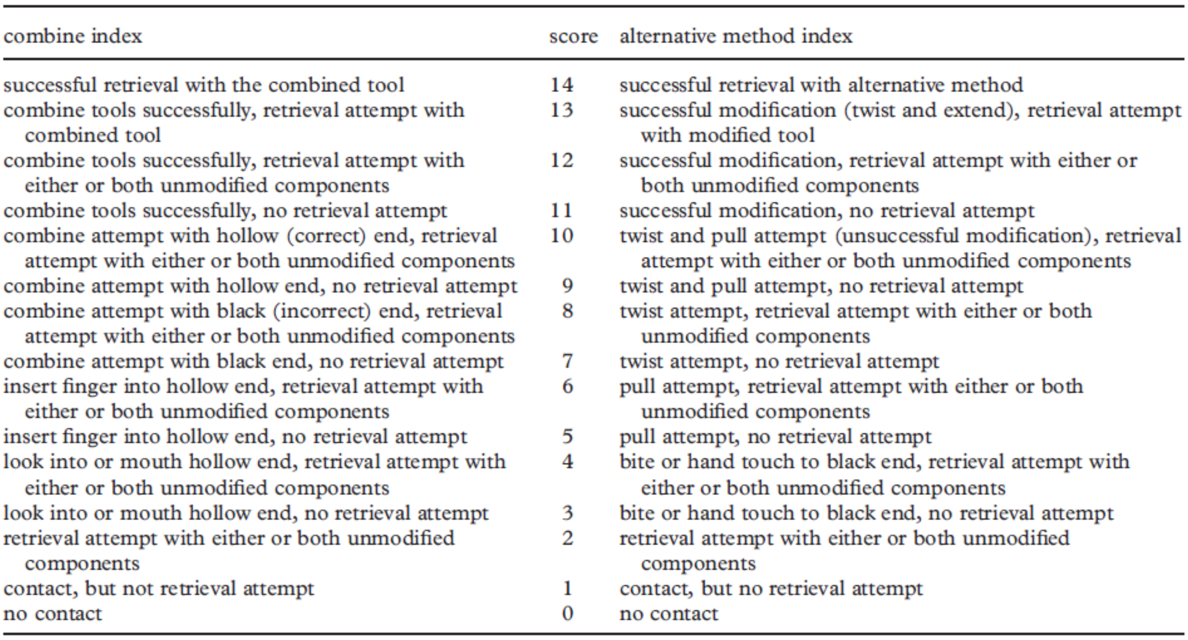
Condition	Verbal Responses
LS Non-Seeded	If you get the white one then you get that box?
	Oooo, yeah
	Yes, I'm getting the smiley faces
	If we have black do we get big ones like these ones, the long ones?
	Yes (in answer)
	I got black, black
	It's that one actually
	No you don't because you picked white (in answer)
	Why do we all need stickers?
	Is it done yet?
	How long do we have left?
	Are we getting smiley face stickers today?
SS Non-Seeded	We haven't got any smiley stickers today?
	Are we going to get the smiley stickers?
	Another red
	Are we going to have a go tomorrow?
	I've got a black one.
	I've got a white one, I got 3 reds and I got 2 greens
	I'm going to mix my juice, I'm going to mix my juice
	[participant name] got the together stickers
SL Non-Seeded	I got 5 this time
	I didn't get red stickers yet
	Are you videoing us
	And when you get black you get that one, yes I got pic
	I can beat you are your black, because the white team beats the black team
	Orange
	Why are we doing this?
	Why are we doing this?
	Pretend I was a black snake
	I'm a white
	Why is the sticker different?
	Yours is white
	Mine is still pink
	Why don't you just see in there?
	Why are we doing this again, I'm going to tell my mummy and daddy I've got loads
	That one is uninteresting, that means he has no friends.
	There are loads of white tokens, why are there loads of white tokens, I might just go get blue
	Black, black
	I keep getting white because I want loads of stickers
	This time I won't get that, ever ever again

Table E1.
Continued

Condition	Verbal Responses
SL Non-Seeded (Cont'd)	We always get loads [participant name] pushed in Everyone is getting white
LS Seeded	Where’s the white ones go? Is it the black one is that one, so the white ones that one (touches the white token sticker box) Hey where’s my one?
SS Seeded	We look at X-box, X-box, X-box better than wii Is that, is that (points to black box), full now? Do you have white stickers? Do you have any white stickers? Are there any stickers in there? Oh, I know what you're doing, you’re keeping them in order so if you get a white you do that tub and if you get black you do that side When will we ever stop playing this? After this go can we stop? Can we stop playing this game? I like this game On my next turn I'm going to find out what’s in that box
SL Seeded	I always want the black ones

Appendix F. Coding Scale (Chapter V)

Table F1. Combine and alternative method indices and scores (from Price et al. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society Series B; Biological Sciences,* 276(1671), 3377-3383). Reproduced with authors' permissions.



combine index	score	alternative method index
successful retrieval with the combined tool	14	successful retrieval with alternative method
combine tools successfully, retrieval attempt with combined tool	13	successful modification (twist and extend), retrieval attempt with modified tool
combine tools successfully, retrieval attempt with either or both unmodified components	12	successful modification, retrieval attempt with either or both unmodified components
combine tools successfully, no retrieval attempt	11	successful modification, no retrieval attempt
combine attempt with hollow (correct) end, retrieval attempt with either or both unmodified components	10	twist and pull attempt (unsuccessful modification), retrieval attempt with either or both unmodified components
combine attempt with hollow end, no retrieval attempt	9	twist and pull attempt, no retrieval attempt
combine attempt with black (incorrect) end, retrieval attempt with either or both unmodified components	8	twist attempt, retrieval attempt with either or both unmodified components
combine attempt with black end, no retrieval attempt	7	twist attempt, no retrieval attempt
insert finger into hollow end, retrieval attempt with either or both unmodified components	6	pull attempt, retrieval attempt with either or both unmodified components
insert finger into hollow end, no retrieval attempt	5	pull attempt, no retrieval attempt
look into or mouth hollow end, retrieval attempt with either or both unmodified components	4	bite or hand touch to black end, retrieval attempt with either or both unmodified components
look into or mouth hollow end, no retrieval attempt	3	bite or hand touch to black end, no retrieval attempt
retrieval attempt with either or both unmodified components	2	retrieval attempt with either or both unmodified components
contact, but not retrieval attempt	1	contact, but no retrieval attempt
no contact	0	no contact

Table G1.

Transfer Manipulative Performance Scale

Tool Manipulation (Description)	Code
Successful combine and grape retrieval (holds yellow tool end inserting red)	22
Successful combine and grape retrieval (holds red tool end inserting yellow)	21
Successful combine, attempt to gain grapes by inserting red tool and holding yellow	20
Successful combine, attempt to gain grapes by inserting yellow tool first	19
Successful combine, retrieval of grapes with either unmodified tool (note which tool in description)	18
Successful combine, attempt to gain grapes with unmodified component	17
Successful combine, no attempt on grapes	16
Serial Method to gain grapes (one tool is inserted before the other, essentially combining the tools once one is inside the box. Note which tool inserted first i.e. yellow/red)	15
Serial method and attempt to gain grapes (note which tool inserted into box first)	14
Attempt to combine but tools do not insert correctly to combine into a single tool, followed by grape retrieval with unmodified tool (state colour of tool)	13
Attempt to combine and attempt to retrieve grapes	12
Attempt to combine, no retrieval attempt	11
Insert finger into hollow end of yellow tool and retrieve grapes with the tool	10
Insert finger into hollow end of yellow tool and retrieval attempt	9
Insert finger into hollow end of yellow tool and no grape attempt	8
Look or mouth hollow end of yellow tool before retrieving grapes with the mouthed/looked at tool	7
Look or mouth yellow tool end(s) before attempt on grapes with the mouthed/visually inspected tool	6
Look or mouth yellow tool hollow end and no grape attempt	5
Successful retrieval of grapes with single tool (note tool colour)	4
Retrieval attempt with one tool (note tool colour)	3
Contact but no attempt	2
No contact	1
No task approach	0

Appendix H. Retention and transfer study results

Table H1.

Subjects' highest attained scores according to study

Experience	Subject	Original Level of Social Information Seen 2008	Combine Score (2008)	Extension Score (2008)	Combine Score (Retention)	Extension Score (Retention)	Transfer-Opaque Score	No. of times Serial Method was used (Transfer-opaque)	Transfer-Transparent Score	No. of times Serial Method was used (Transfer-
E	Nowi	Combine	14	6	14	2	22	0	22	1
E	Joey	Combine	14	2	14	0	22	0	22	0
E	Keno	Combine	14	6	9	6	5	0	14	1
E	Coco	Combine	14	3	14	3	22	0	22	0
E	Kaya	Combine	14	4	14	8	16	2	22	3
E	Kiht	Partial	14	12	14	3(14 between trials)	17	0	5	0
E	Kelley	Partial	14	6	14	3	22	3	22	5
E	Simba	Partial	14	10	14	10	22	0	22	0
E	Jane	VideoControl	14	6	14	11	22	0	22	0
E	Judumi	No Video	14	12	14	14	22	0	22	3
E	Chechekul	No Video	10	14	3	14	-	-	-	-
C	Kobi	x	-	-	3	5	12	0	5	0
C	Miloni	x	-	-	0	5	5	0	2	0
C	Patti	x	-	-	1	1	3	0	2	0
C	Peghia	x	-	-	4	3	5	0	5	0
C	Quincy	x	-	-	11	7	12	0	16	1
C	Sabrina	x	-	-	2	7	5	0	2	0
C	Sammy	x	-	-	1	3	2	0	2	0
C	shahee	x	-	-	2	2	4	0	2	0
C	Ursula	x	-	-	2	10	8	0	6	0
C	Zippy	x	-	-	2	4	6	0	4	1
N	Ajax	x	-	-	-	-	-	-	8	0
N	Akimel	x	-	-	-	-	-	-	16	0
N	Bahn	x	-	-	-	-	-	-	5	0
N	Dahpi	x	-	-	-	-	-	-	5	0
N	Hannah	x	-	-	-	-	-	-	8	0
N	Mahi	x	-	-	-	-	-	-	3	0
N	Martha	x	-	-	-	-	-	-	8	0
N	Maxi	x	-	-	-	-	-	-	16	0
N	Oki	x	-	-	-	-	-	-	11	0
N	Pashthil	x	-	-	-	-	-	-	5	0

Note: For 2008 and Retention Scale, fully elongated tool manufacture ≥ 11; elongated tool to retrieve grapes =14. For Transfer Scale full combine 16 ≥ ; 14 & 15 = Serial Method. E='experienced tool users'; C='Control subjects'; N='Naïve subjects'. - = Non participation/no score
x = subjects did not participate in the 2008 study