

Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee

Andrew Whiten^{1,*}, Nicola McGuigan², Sarah Marshall-Pescini^{1,3}
and Lydia M. Hopper^{1,4}

¹*Centre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group,
School of Psychology, University of St Andrews, St Andrews KY16 9JP, UK*

²*Department of Psychology, Heriot Watt University, Edinburgh EH14 4AS, UK*

³*Department of Biomedical Science and Technology, University of Milan, Milan, Italy*

⁴*Department of Psychology, University of Durham, Durham DH1 3LE, UK*

We describe our recent studies of imitation and cultural transmission in chimpanzees and children, which question late twentieth-century characterizations of children as imitators, but chimpanzees as emulators. As emulation entails learning only about the results of others' actions, it has been thought to curtail any capacity to sustain cultures. Recent chimpanzee diffusion experiments have by contrast documented a significant capacity for copying local behavioural traditions. Additionally, in recent 'ghost' experiments with no model visible, chimpanzees failed to replicate the object movements on which emulation is supposed to focus. We conclude that chimpanzees rely more on imitation and have greater cultural capacities than previously acknowledged. However, we also find that they selectively apply a range of social learning processes that include emulation. Recent studies demonstrating surprisingly unselective 'over-imitation' in children suggest that children's propensity to imitate has been underestimated too. We discuss the implications of these developments for the nature of social learning and culture in the two species. Finally, our new experiments directly address cumulative cultural learning. Initial results demonstrate a relative conservatism and conformity in chimpanzees' learning, contrasting with cumulative cultural learning in young children. This difference may contribute much to the contrast in these species' capacities for cultural evolution.

Keywords: imitation; emulation; social learning; cultural transmission;
cumulative culture; chimpanzees

1. INTRODUCTION

Studies of imitation in children and in our closest primate relatives have now spanned a century (Witmer 1909), including over 60 experimental reports for great apes (Tomasello & Call 1997; Whiten *et al.* 2004) and countless others with children (Hurley & Chater 2005).

The last quarter of the twentieth century saw an upturn in the rigour and intensity of the ape research, stimulated by contentious theoretical and empirical contributions. New experimental studies and critiques of previous research questioned the commonly accepted and intertwined views that research had demonstrated that 'apes ape' (i.e. imitate) and exhibit cultures in the wild (Tomasello *et al.* 1987; Galef 1988, 1992; Tomasello 1990, 1996; Heyes 1993). Later studies employing more discriminating methodologies than before generated a number of influential findings, several of which converged on a subsequently influential

conclusion: that unlike children, apes are not true imitators but rather are 'emulators' (Tomasello 1996). Whereas in imitation an individual learns by copying the actions of another, in emulation they learn instead about the environment—for example, about the results of what others do or about the relevant properties of tools and other objects involved. Tomasello & Call (1997), reviewing experiments by Nagell *et al.* (1993), Whiten *et al.* (1996) and others, concluded that 'It is not likely that either monkeys or apes who have not had extensive human contact imitatively learn the instrumental behaviors of others. What are salient for monkeys and apes in such situations are the tool, the food, and their spatial-temporal-causal relations. This is intelligent problem-solving behaviour, but it is not attempting to reproduce the behavior or behavioral strategies of another animate being' (p. 294). That children imitate, by contrast, was not disputed.

In this paper, we describe more recent experiments that challenge this dichotomous view of the nature of social learning in apes and children. We conclude that the evidence shows instead that both chimpanzees and children possess a 'portfolio' of different social learning mechanisms, including both imitation and emulation, that are deployed selectively in different contexts. This work indicates that copying what others do plays a

* Author for correspondence (a.whiten@st-andrews.ac.uk).

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One contribution of 13 to a Theme Issue 'Evolution, development and intentional control of imitation'.

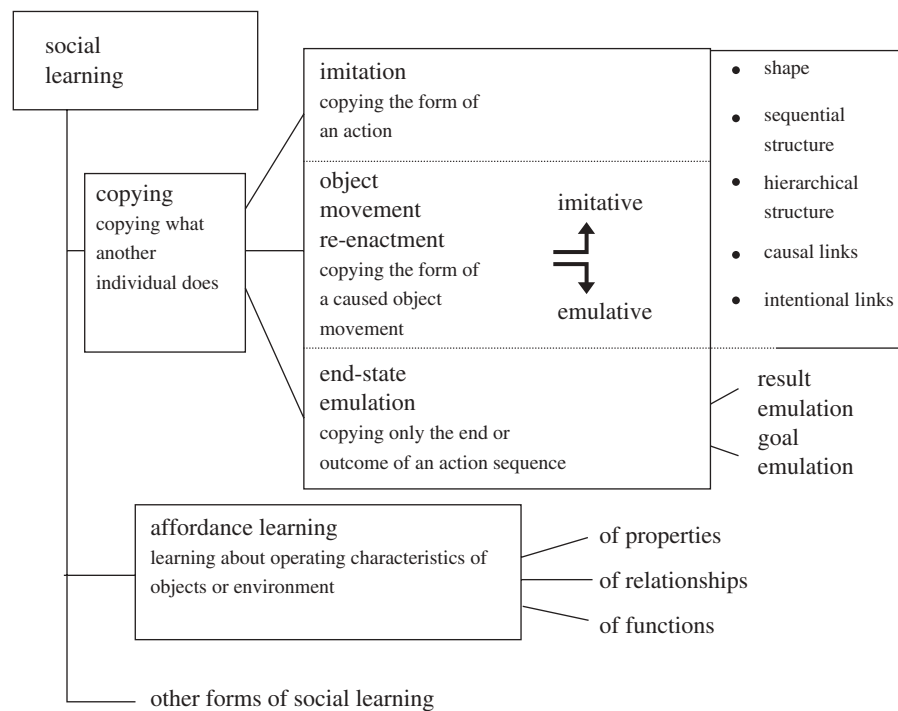


Figure 1. A taxonomy of imitative and emulative learning processes. Here, senses of emulation distributed through the social learning literature are distinguished and fall under the headings of object movement re-enactment, end-state emulation and affordance learning. Simpler forms of social learning, such as stimulus enhancement, are omitted here (see Whiten *et al.* 2004 for a full taxonomy), as are related forms of social influence, such as contagion (see Whiten & Ham 1992). For further explanation, see text, particularly §2b.

more significant role in both species than hitherto appreciated. We acknowledge, and indeed demonstrate, considerable differences in the social learning propensities of the two species, but we are led to conclusions that go beyond characterizing the difference as a simple imitation/emulation dichotomy.

2. DEFINING, DISSECTING AND IDENTIFYING IMITATION AND EMULATION

Imitation and emulation are two processes within larger taxonomies of social learning (Whiten & Ham 1992; Heyes 1994; Whiten *et al.* 2004) but they are our foci here, so we dwell on their definitions. Doing so is important because the two processes are distinguished in several quite different ways in the social learning literature. It is important to recognize a distinction between debates about species differences that hinge on: (i) variations in the way a concept such as imitation is defined versus (ii) for any given definition, the adequacy of relevant empirical evidence in the species of interest. Only such evidence can provide objective, scientific conclusions. Matters of definition, by contrast, cannot be resolved by research. The best we can hope for is some consensus in the terms we use; it would be naive to assume they have some inherently 'correct' meaning. Given the scope for confusion, every study needs to define its key concepts.

(a) Defining and dissecting imitation

Following Whiten & Ham (1992), figure 1 offers a lean definition of imitation as 'copying the form of an action'. We follow this definition here. However,

elsewhere in the social learning literature, additional criteria are set. This means that imitation has in effect been 'dissected' into different subcategories. For example, where the distinction noted above is made, between imitation as 'copying an agent's actions' and emulation as 'learning from the environmental results of what an agent does' (emulation: Tomasello 1996), imitation becomes essentially *bodily* imitation. The authors are free to restrict the scope of imitation in this way, but we note at least two drawbacks in doing so, which can be illustrated by the example of copying somebody's actions with a tool, such as a hammer. The first concern is simply that excluding the movements of the hammer that are being copied from our conception of imitation seems to lose touch with the way the term 'imitation' is applied in everyday life. The second, more important scientific concern is that it remains unclear to what extent copying the 'actions of objects' that people move (e.g. hammering, where the tool becomes an extension of the limb) is a fundamentally different process than copying bodily actions *per se* (see Huber *et al.* 2009). Accordingly, in the present paper, when we discuss evidence for imitation, we may consider this either in the restricted sense of bodily imitation or in the broader sense of 'copying the form of an action' that may go beyond the skin to include tools and other objects. Such issues are analysed in depth by Whiten *et al.* (2004).

An additional criterion for imitation required by some authors is that the action copied be novel, or otherwise improbable (Thorpe 1963). In this case, we are referring to *imitative learning*, rather than imitation in the broader, everyday sense that may include

familiar actions in the copier's own repertoire. That something new is learned is an important requirement where interest focuses on the acquisition of elements of behaviour that constitute a local culture. Accordingly, we also recall this distinction in our analyses of imitation below.

(b) *Dissecting and defining emulation*

Emulation has come to be used to refer to processes even more diverse than is the case for imitation (Byrne 2002), a subject also analysed in greater detail by Whiten *et al.* (2004) than there is scope for here. At first sight, this is confusing, but if the proliferation reflects interesting distinctions, real progress may be made in charting the landscape of social learning. Three main senses of emulation are distinguished in figure 1.

(i) *Object movement re-enactment*

If imitation is limited to bodily movements only, copying how a model makes an object such as a hammer move comes within the domain of emulation. This sense of emulation was called 'object movement re-enactment' (OMR) by Cusance *et al.* (1999), underlining the similarity to copying the form of bodily actions. One can envisage a causal continuum from bodily motions to object movements directly moved by the body (e.g. hammer use) to effects on the environment caused by these (nuts cracked by the hammer). Copying could in principle pick out and re-enact elements anywhere along this causal sequence. Ascription of imitation is most clearly apt at the proximal end of this continuum, whereas the concept of emulation is the clearest more distally. The category of OMR in figure 1 is accordingly annotated to indicate this continuum and the ambiguities it may occasion, relevant in studies described below.

(ii) *End-state emulation*

Emulation was originally distinguished from imitation by Wood (1989), who noted 'instances where children achieve common goals to those modelled, but do so by using idiosyncratic means that were never observed' (p. 72). In figure 1, this is classed within copying, but it is only the end-state(s) of what the model has done that is copied. As Wood suggested, copiers may reach this end in their own way. However, they might happen to choose the same method as the model, which might thus be falsely recorded as imitation.

(iii) *Affordance learning*

A final alternative is that learning is instead about properties of objects or other aspects of the environment, which may help the learner in tackling the task observed without employing imitation. Such 'affordances' of the physical context may include properties of objects such as brittleness, relationships between objects such as containment or functions such as what a tool is good for (Klein & Zentall 2003). Having recognized such affordances, the observer may then exploit them in their own behavioural strategies; these might happen to match the actions of

the model or not, but if they do, it would not be through imitation.

(c) *Chimpanzees as emulators*

The reason that emulation has come to prominence in social learning research and that chimpanzees have been characterized as emulators began with an early study of Tomasello *et al.* (1987). In this experiment, chimpanzees exposed to a model using a stick tool to rake in food were more likely to acquire this behaviour than controls that saw no model, but they did not copy a technique the model had developed to gain food from awkward places. Tomasello *et al.* interpreted this as a failure to imitate. Because control chimpanzees handled the sticks but did not apply them, the authors suggested that the success of the observer chimpanzees depended on more than stimulus enhancement (attracting of attention to the relevant objects); the subjects appeared to have learned by observation that the stick afforded use as a tool. Tomasello (1990) adopted Wood's (1989) term 'emulation' as a label for this. Reviews of several later studies have tended to confirm this picture, with chimpanzees failing to copy details of a model's actions (especially in comparison to children's imitation), and performing instead in ways consistent with emulation (Tomasello & Call 1997; Whiten *et al.* 2004; Call *et al.* 2005). Such low-fidelity copying was suggested to severely constrain the capacity of chimpanzees for the cultural transmission of traditions (Tomasello 1999).

However, few attempts have been made to *directly* test for emulation; instead, emulation has typically been offered as a 'default' explanation when there is little or no evidence of detailed imitative copying. Accordingly, results can often be equally well described as consistent with imitation at a relatively crude level. Thus, in the Tomasello *et al.* experiment outlined earlier, the chimpanzees may have imitated the use of a stick as a rake, but without imitating certain details of the technique. In the two sections that follow, we describe two sets of studies that challenge this characterization of chimpanzees as emulators likely to show little evidence of cultural transmission. First, we describe recent 'diffusion' experiments designed to track cultural transmission, then 'ghost' experiments that directly test for emulation.

3. COPYING FIDELITY IN SOCIAL TRANSMISSION: DIFFUSION EXPERIMENTS

The majority of social learning experiments are restricted to what a single observer learns from watching a single model. However, multiple cultural transmissions are required to sustain traditions. Properly investigating any animal's cultural capacity thus requires a different kind of experiment, in which fidelity of transfer is tracked over repeated transmission events. Just over 30 of these diffusion experiments have now been completed in a variety of taxa including fish and birds (Whiten & Mesoudi 2008), but a corpus of such studies in non-human primates has been built up only in the last few years (Whiten *et al.* 2007). Likewise, only recently has a handful of such studies

been completed with children (Horner *et al.* 2006; Flynn 2008; Flynn & Whiten 2008; McGuigan & Graham in press).

Six controlled diffusion studies have been published for chimpanzees. Whiten *et al.* (2005a) trained a single chimpanzee from one group to use one of the two techniques to extract trapped food from an artificial foraging device (the ‘panpipes’) and trained a chimpanzee from a different group to use an alternative technique. One technique (*lift*) involved using a stick to lift up an obstacle so that trapped food was released to the chimpanzee; in the second technique (*poke*), the tool was instead inserted into an obscured opening, pushing the obstacle until the food fell onto a lower level of the panpipes and rolled out to the chimpanzee. Each chimpanzee was then re-introduced to its 16-strong group and the task made available to all. Each technique spread preferentially in the group in which it was seeded, with a majority matching the technique used by the initial local model.

A further study involved an ‘arbitrary convention’—posting plastic tokens in either of two different receptacles. Again, each method spread in the group in which it was seeded, with the exception of a single chimpanzee that discovered the method used in the other group (Bonnie *et al.* 2007). This and the panpipe study illustrate an ‘open-diffusion’ design, in which who watches whom and who tackles the task next is left open. These approaches were complemented by a ‘transmission chain’ experiment in which transfer was constrained to a linear chain, $A \rightarrow B \rightarrow C \rightarrow D$, etc. Each of the two techniques for opening a foraging box was transmitted along a chain with high fidelity, such that after six transfers, the last individual in each chain was using the same technique seeded at the start (Horner *et al.* 2006).

Further diffusion experiments have examined group-to-group transfer, an essential element of any putative cultures that span hundreds of kilometres (and thus scores of communities) in Africa (Whiten *et al.* 1999; Whiten 2005). For two different artificial foraging tasks, each of the alternative techniques seeded in different groups spread to a second and third group, with high fidelity (Whiten *et al.* 2007; see figure 2). For the most complex task, requiring a sequence of two different operations, the original technique spread across up to 26 chimpanzees in three groups, with none successfully performing the sequence customary in the other three groups.

An important conclusion of this set of studies is that the social learning processes at work are demonstrably adequate to sustain multiple different traditions across different communities, including quite complex variations in foraging techniques. In relation to debates about the limits on imitation in apes and the implications of these limits for culture, this is perhaps a more important conclusion than precisely what terms are agreed apt to describe the underlying learning processes.

That said, we can turn to a more focused analysis of the evidence for imitation in these studies, recalling the two supplementary criteria for imitation favoured by some authors and outlined above: (i) whether the copied pattern is novel and thus truly acquired through

observation and (ii) whether bodily imitation is implicated.

(a) *Are the techniques acquired novel or improbable?*

To experimentalists, the principal way of operationalizing this question is through control conditions; could chimpanzees succeed if no model were available? Such tests were incorporated into all of the experiments outlined above, with variable results that plausibly correspond to the relative simplicity and likely familiarity to the chimpanzees of the elements of action involved. In the studies of Horner *et al.* (2006) and Bonnie *et al.* (2007), the tasks were motorically relatively simple, such as sliding or lifting a door to access food, and some chimpanzees solved the task in the no-model condition. These studies offered robust evidence of cultural transmission yet called on relatively familiar elements of action. In three diffusion studies that employed more challenging tasks (Whiten *et al.* 2005a, 2007), chimpanzees in no-model conditions were not able to solve the task themselves. In different studies as many as 56 chimpanzees have been presented with the panpipes task individually or in small groups, without solving it: the techniques involved are thus to this extent inherently ‘improbable’ (cf. Tennie *et al.* 2009).

In one larger group, a single chimpanzee did succeed by her own efforts, using the poke method (Hopper *et al.* 2007). One solver in 56 chimpanzees does not, however, amount to the technique being ‘within chimpanzees’ repertoire’: to the contrary, a ratio of independent solving as low as 1/56 is consistent with a cultural scenario that includes rare innovators, and a large majority that can only acquire the innovation by copying it or through some other brand of social learning (figure 3).

(b) *Is bodily imitation implicated?*

Most diffusion studies have employed only a single initial model and compared this with a control condition with no model (Whiten & Mesoudi 2008). However, the chimpanzee studies described above all used a two-action design (e.g. poke versus lift in the panpipes) that earlier played an important role in the rising methodological sophistication of dyadic social learning studies (Heyes 1996; Huber *et al.* 2009). Because each of the two different techniques spreads in its respective group, they are by definition being differentially replicated or copied through the group, and in this sense can be described as broadly ‘imitative’. However, if we focus instead on the criterion of bodily imitation, then these results do not demonstrate this, because all the tasks involved object manipulation and it is the movements of these that may be being emulated. The diffusion studies were not designed to distinguish such potential mechanisms; rather, the goal was to examine the extent to which chimpanzees would sustain different traditions, whatever the underlying mechanisms. To discriminate the latter, we conducted supplementary experiments, discussed in §5. Before leaving the diffusion studies, however, we

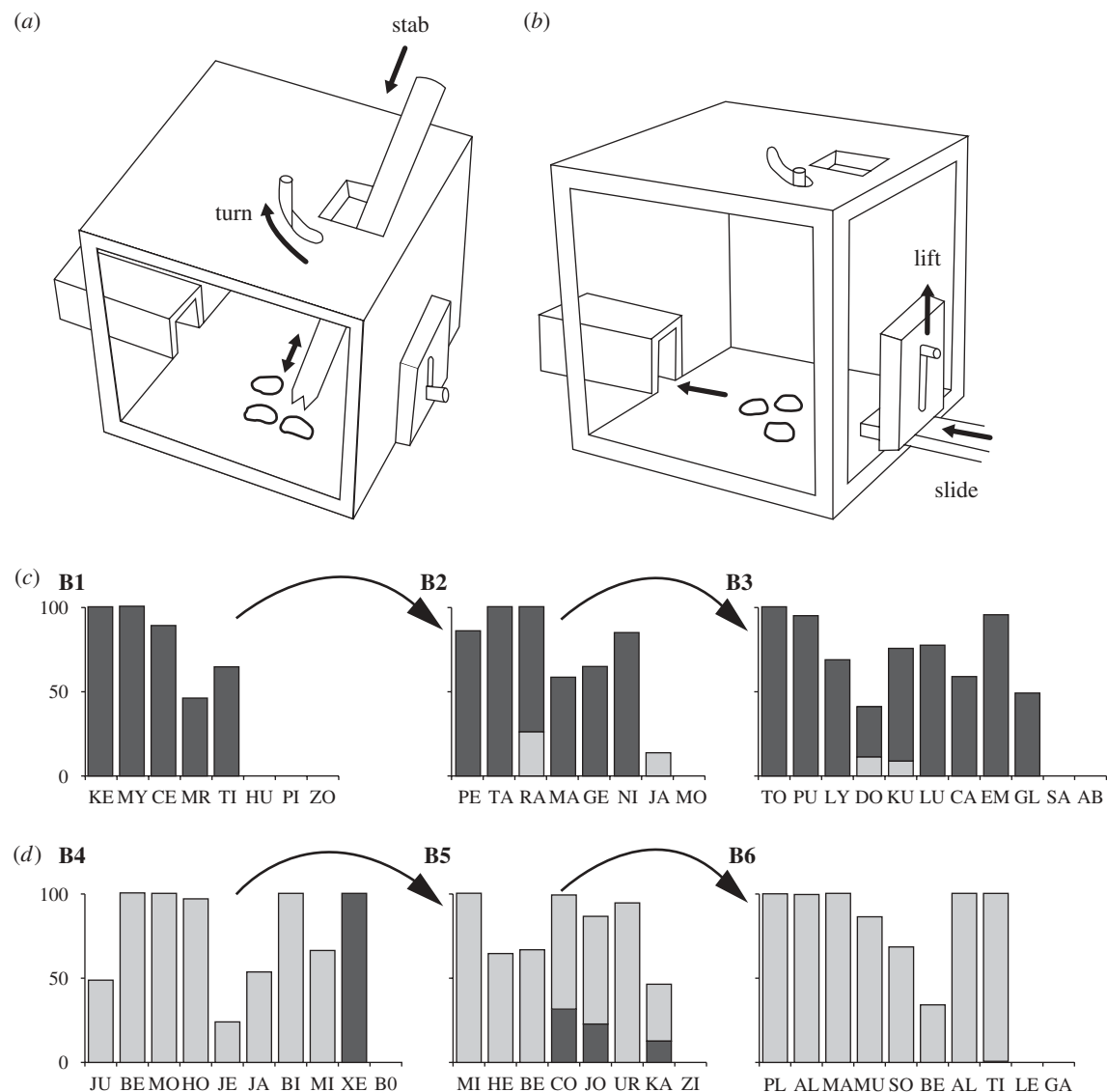


Figure 2. Transmission of alternative foraging techniques within and across groups of chimpanzees (after Whiten *et al.* 2007). (a) Stab technique applied to foraging box, (b) alternative slide technique, (c) spread of stab technique (dark grey bars) within group B1, followed by spread across groups B2 and B3, and (d) spread of slide technique (light grey bars) within and across groups B4–B6. Each group was able to watch the performance of the preceding group through large windows. Fidelity of transmission was high.

consider briefly their broad implications for the scope of cultural transmission in chimpanzees.

4. THE SCOPE FOR CULTURAL TRANSMISSION IN CHIMPANZEES AND OTHER ANIMALS

In a previous paper (Hopper *et al.* 2007), we conceptualized the results of our diffusion experiments in terms of learning thresholds, shown in simple diagrammatic form in figure 3, partly to facilitate engagement with a ‘partner’ paper¹ in the present issue (Tennie *et al.* 2009). In figure 3, two thresholds divide a continuum expressing the degree of challenge that any particular task presents to the species concerned. Below the lower threshold, the task is sufficiently easy that most individuals can acquire it through their own efforts. Above this threshold, individual mastery becomes rarer, but so long as one or more innovators achieve this, others can succeed by learning from them. Above the upper threshold of difficulty, the species simply cannot master the task by

individual effort, nor even by observing a competent model of a different species. Our various tasks map to the three zones in several different ways. The ‘one innovator, 30+ social learners’ of our panpipes studies (Whiten *et al.* 2005a; Hopper *et al.* 2007) serves as one apt illustration of the zone conducive to the emergence of traditions (Zone 2) hypothesized in figure 3.

Tennie *et al.* (2009) conceive of a different kind of zone, a ‘zone of latent solutions’ (ZLS) that they suggest limits the social learning of which chimpanzees are capable. This seems a potentially interesting concept, but unfortunately the authors do not offer a formal definition and the scope of the concept remains elusive. It is not clear how a ZLS will apply to other species including humans and indeed how one would establish its existence, scope and implications. Tennie *et al.* appear to propose that chimpanzee traditions can incorporate only acts that fall within a ZLS where in principle chimpanzees could discover the behaviour themselves, given conducive conditions. But this seems to correspond simply to the conditions

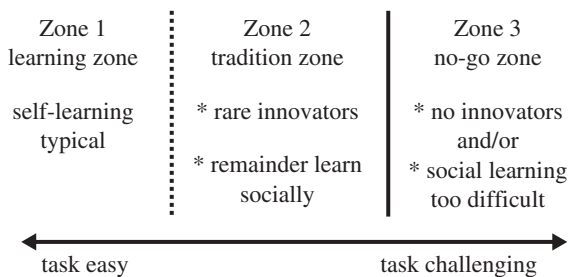


Figure 3. A simple model of tradition and adjacent learning zones. The tradition zone (2) is proposed to lie between two thresholds of task complexity as experienced by the species of interest. Below the first threshold, all or most individuals can master the task by their own efforts. Above the higher threshold, the task is beyond the species' capability. In the part of the tradition zone nearest Zone 3, only rare innovators can master the task but others may acquire it through social learning: such traditions will be relatively robust. In the part of the tradition zone near Zone 1, traditions may be relatively short-lived as more individual-level learning occurs. The transition between Zones 1 and 2 will therefore be graded.

for our 'tradition zone' (figure 3): the acts have to be within the range of at least one chimpanzee that can act as innovator, yet above the lower threshold, or there would be no need for social learning.

Tennie *et al.* offer an experiment they argue to support their ZLS concept but we do not see how it can. Their study incorporates a 'loop technique' that all chimpanzees failed to learn, when demonstrated by a human model. Tennie *et al.* propose that this is consistent with the ZLS hypothesis because if no ape could master the task it is beyond their ZLS and so cannot be socially learned. But the more parsimonious explanation is surely that the task is simply beyond chimpanzees' capability (our Zone 3) as, of course, are so many others (likewise, we suspect that several studies in the social learning literature are not productive because at the opposite end in figure 3, the task is too elementary to require social learning: our diffusion studies have instead focused on discovering the true scope of Zone 2 for the species concerned). It appears to be Tennie *et al.*'s sample of *Homo sapiens* that conforms more clearly to their ZLS model, for one young child showed that they could make a loop without the benefit of a demonstration (so the task is within children's ZLS) and most other children could learn it by observation (our Zone 2). The loop study thus does not appear to speak to the issue of chimpanzees' and humans' very different capacities for cumulative cultural evolution. We return to this topic in §8.

5. TESTING FOR EMULATION THROUGH 'GHOST' EXPERIMENTS

We now shift from diffusion experiments to dyadic experiments to further dissect underlying social learning processes. One way of testing directly whether emulation rather than imitation is involved is the ghost experiment. The handful of existing studies is reviewed in Hopper *et al.* (2008). The underlying

logic is exemplified in Tomasello's (1998) thought that: 'if a mother chimpanzee rolls a log and eats the insects underneath, her child will very likely follow suit . . . (but) the youngster would have learned the same thing if the wind, rather than the mother, had caused the log to roll over and expose the ants' (p. 29).

One can experimentally create this impersonal kind of scenario by replacing the model with some hidden ('ghostly') means of making the objects of interest do what they would if the model were moving them (like the wind in Tomasello's example). Hopper *et al.* (2007) did this using fishing line to discretely pull the obstacle in our panpipes up, releasing the food with no chimpanzee model present. In a second ghost condition, the stick tool was also attached, so that it too moved up as if a ghostly agent were lifting it. If chimpanzees are emulators, it is precisely these aspects of the scene they should attend to and learn from. Hopper *et al.* focused on the lift technique because chimpanzees had hitherto acquired this technique only after watching a chimpanzee performing it.

No chimpanzee learned from the ghost demonstrations. This was a startling result, especially in the case of the 'ghost with tool' presentation, which to a human adult, at least, appears rather clearly to 'give the game away' about what is required. Observer chimpanzees were documented as attending well to the displays, yet they failed to learn from them. Such results question whether chimpanzees are principally or exclusively emulators, rather than imitators. Thorndike (1898) defined imitation as 'learning to do an act from seeing it done' (p. 50). It seems this is exactly what the ghost experiment implies chimpanzees need to do—learn an act from seeing it *done* by a conspecific or other adequate animate model.

However, the story is more complex. A further ghost experiment has revealed subtly different results. In this study, the scenario observed was much simpler, because it was based on the one existing positive result from a ghost experiment with a non-human species—pigeons. In this, Klein & Zentall (2003) had provided one condition in which pigeons watched a conspecific slide a small panel to left or right to gain food, and a ghost condition in which the panel moved with no model present. In an additional condition, the panel likewise moved automatically but a pigeon 'model' was present but merely fed on the food released and did not push the panel. In this study, pigeons showed strong evidence of copying in the active model condition and pushed the door in the direction they had seen it move in the ghost condition. Accordingly, the authors concluded emulation learning was at work. Surprisingly, perhaps, there was no matching in the condition that had included the pigeon alongside the ghost door move.

Hopper *et al.* (2008) replicated this study as closely as feasible with both chimpanzees and children. Three main results are of interest. First, in the chimpanzee model condition, subjects matched the direction of the model's pushing in virtually all trials (on average 99%). Given how easy it is to push the panel either way, one might expect that subjects would explore this, discover that either approach reveals food, and show no side preference. The degree of fidelity to the

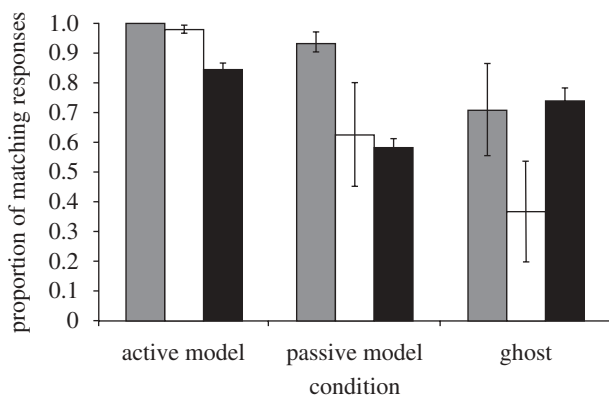


Figure 4. Matching to observed scenarios in full model versus ghost conditions (adapted from Hopper *et al.* 2008). Mean proportion (+s.e.) of matches to direction of door slide witnessed by children (grey bars), chimpanzees (white bars) and pigeons (black bars) in active model, passive 'model' with ghost manipulation and full ghost (no model) conditions. Mean values and s.e. for pigeon data courtesy of Thomas Zentall (2008, personal communication).

model is therefore striking. Children responded with 100 per cent fidelity in this condition (figure 4).

In the ghost condition, both children and chimpanzees initially showed a significant tendency to match the direction of the panel movement. This is the first confirmation of emulation in chimpanzees (or indeed any non-human primate) in a ghost condition. However, in further trials, chimpanzees (but not children) tended to explore pushing in both directions and no longer showed matching to what they had seen. This result is more consistent with the results of the panpipes ghost experiment of Hopper *et al.* (2007) and contrasts quite starkly with the fidelity observed when a chimpanzee had acted as a model, pushing the panel. Our conclusion is that where a task is very simple for a chimpanzee, as in the panel-pushing, emulation may occur, yet be fleeting, and where the task is more complex as in the panpipes, chimpanzees need to be able to see the fuller action display of a model, in order to learn through observation. This seems consistent with the demonstration by Voelkl & Huber (2007) of detailed imitative matching by marmosets in a functional context where such matching made a significant contribution to successful task completion (Huber *et al.* 2009).

The third and final result that deserves mention is that in the condition where the panel moved automatically but the conspecific 'model' was passive, children, unlike both chimpanzees and pigeons, copied almost as faithfully as with the active model (figure 4). Why children did this remains mysterious. Perhaps, it represents a symptom of the extreme cultural conformity of children, to be discussed further below. One cannot strictly describe the response as imitation, insofar as the 'model' child actually did nothing!

The results of these ghost experiments have thus generated several implications for the nature of the imitative and emulative wings of chimpanzees' and children's social learning. In the next two sections, we consider further recent experiments bearing on these processes in chimpanzees and children, respectively.

6. THE NATURE OF IMITATION AND SCOPE OF SOCIAL LEARNING IN CHIMPANZEES

If the ghost experiments speak against the simple notion that chimpanzees are emulators, should we think that in the diffusion experiments they were imitating? In the broad sense, yes—insofar as we showed chimpanzees traditions can *replicate*, spreading with high fidelity (figure 2). However, if the criterion is bodily imitation, the answer is different. Although the ghost experiments underline the importance to chimpanzees of the involvement of an agent, chimpanzees may nevertheless be attending preferentially to events in the neighbourhood of the tool and other objects, rather than limb configurations. Alternatively, they might be copying aspects of the form of the action that include both body parts and external objects. Below we discuss evidence that bears on these different possibilities. We begin, however, with evidence that chimpanzees have the essential capacities for bodily imitative matching.

(a) Bodily imitation

In the 'Do-as-I-do' (DAID) paradigm, the subject first learns to match a training set of bodily actions (e.g. 'touch chin') on the request to 'Do this!'. If this basic routine is clearly grasped, testing proceeds to a battery of relatively novel actions. In both chimpanzees (Custance *et al.* 1995) and an orangutan (Call 2001), a battery of 48 such novel actions showed that these apes could be identified in 'blind coding' as copying a significant number of actions such as touch shoulder/elbow/stomach/thigh/top-of-head; interlink fingers, clap back of hands, lip smack and hug self. Matching with respect to out-of-sight body parts by the chimpanzee subjects was done as well as matching to in-sight parts (Custance *et al.* 1995). These studies demonstrate a capacity for fairly elaborate, if approximate, matching, although they can show only what chimpanzees *can* imitate rather than what they will copy spontaneously.

These results have recently been complemented by remarkable episodes in which, during the course of an experimental study of the social learning of nut-cracking using a stone hammer (Marshall-Pescini & Whiten 2008a), a young chimpanzee watching another nut-cracking made repeated and moderately synchronous matching actions, but involving no nut or hammer.² Such matching or 'mirroring' behaviour is rare (we noted seven such episodes), but graphically demonstrated a spontaneous ability to match the bodily actions of a conspecific.

In some species, a two-action experimental design has been used explicitly to test such matching, with models trained to act on a manipulandum using either of two body parts, such as beak versus foot. In both pigeons (Zentall *et al.* 1996) and marmosets (Voelkl & Huber 2000), significant matching was recorded ('true imitation' in these papers' titles). Relevant ape data have since become available through an experiment designed to answer the more complex question of whether apes imitate 'rationally' (Buttelmann *et al.* 2007). Chimpanzees witnessed human models pressing panels using 'unusual' body

parts: forehead, foot or bottom. The chimpanzees matched the odd body part used in 38 per cent of trials, even after their initial tendency to try a normal body part like the hand had produced the desired effect, such as switching on a light.

There thus seems ample evidence that chimpanzees have a capacity for bodily copying and may apply this in 'rational' imitation. Combining this conclusion with the results of the ghost studies reviewed above, there seems less reason now why the default hypothesis about what mechanism underlies a socially learned tradition such as panpipe 'lifting' versus panpipe 'poking' should assume emulative rather than imitative learning. Indeed, the broader context for considering these alternatives has changed much over recent years. It is not long since it was argued that only humans were capable of true imitation, and not chimpanzees and other animals (Tomasello, 1996). In the intervening years, much evidence for imitation has accumulated for a diversity of animals including birds (Zentall 2004), with particularly detailed copying being implied in species as diverse as dogs, marmosets and archer fish in the studies described by Huber *et al.* (2009) in this issue.

(b) *Imitation/emulation switching*

Another possibility is that chimpanzees will selectively opt to imitate or emulate according to one or several factors that make the choice adaptive. Horner & Whiten (2005) explored this by presenting to both chimpanzees and children a task that a human model dealt with using a mixture of causally relevant and irrelevant actions, some performed on an opaque version of the task and some on a transparent equivalent, where the causal irrelevance of some actions was plain to see. Horner and Whiten predicted that if chimpanzees are able to switch adaptively between different forms of social learning, the opaque version would be tackled by more thorough imitative copying of all actions, the transparent one instead being handled through a more emulative response, omitting visibly irrelevant actions. The irrelevant actions involved stabbing a stick tool into a hole in the test box, which in the transparent version could be seen merely to hit a false ceiling, with no causal connection to the compartment beneath, from which the food reward was later extracted. The young chimpanzees tested did tend to stab the stick in the top hole, significantly more in the opaque than the transparent condition. In this way, they demonstrated context-sensitive, flexible social learning.

More recently, flexibility has been demonstrated in relation to *social* context. In Buttelmann *et al.*'s (2007) study of chimpanzees' imitation of a model that used unusual body parts to press a panel to switch on a display, the model performed under two importantly different conditions: in one, their hands were free, whereas in the second condition, their hands were unavailable (e.g. wrapped inside a blanket) so there was good reason to use their forehead or foot to press the panel. Human infants just 14 months old had earlier demonstrated rational imitation in this paradigm, copying the bizarre actions of the adult in the hands-free condition, but rarely in the

hands-occupied condition (Gergely *et al.* 2002). In an ingenious study in which dogs watched a conspecific either holding a ball in their mouth or not, while using their paw to operate a foraging device, Range *et al.* (2007) demonstrated a parallel effect. Likewise, Buttelmann *et al.* found that the chimpanzees they tested expressed this kind of selectivity, copying the unusual actions in 38 per cent of hands-free trials, versus only 19 per cent in the hands-occupied condition.

The Horner and Whiten, and Buttelmann *et al.* studies illustrate selective and functionally appropriate use of either imitation or emulation in relation to variations in both physical and social contexts. These results are consistent with the portfolio theory of Whiten *et al.* (2004); that chimpanzees possess a portfolio of social learning processes (including imitation, emulation and others) that may be applied selectively according to context.

7. IMITATION AND 'OVER-IMITATION' IN HUMANS

Horner & Whiten (2005) discovered that unlike chimpanzees, which, as noted above, copied less of a model's actions when they appeared causally irrelevant, young children, surprisingly, copied these with high fidelity. These results have been replicated for a larger sample of 3-year-old children by McGuigan *et al.* (2007). Moreover, McGuigan *et al.* extended the study to include 5-year olds, suspecting that as children mature cognitively, the susceptibility to blanket copying would decline. Results were to the contrary: 5-year olds were even more likely than the 3-year olds to copy all they saw, even with the transparent box.

Lyons *et al.* (2007) have replicated these results with a similar task, as well as others that incorporate both causally relevant and irrelevant actions, the latter transparent to view. Lyons *et al.* checked that the children's responses are not merely to please the experimenter, both by allowing the child to complete the task while the experimenter was out of the room (see also Horner & Whiten 2005), and then asking the child to check the reward object had been put in place for the next child. A strong tendency to copy the irrelevant modelled actions remained evident even in this more rushed, 'real-world' context (figure 5). Lyons *et al.* further demonstrated how surprisingly inflexible is young children's conformity, which the authors dubbed over-imitation. Children were exposed to a training programme in which the experimenter extracted reward objects from eight transparent containers, in each case using both relevant and irrelevant actions, and asking the child which actions the experimenter 'had to do' and which were 'silly and unnecessary' (e.g. tapping the side of a container with a feather). Children were effusively praised for correctly identifying irrelevant actions. Nevertheless, these children continued to over-imitate when tested later. With Lyons *et al.*'s version of the Horner and Whiten test box, children copied the irrelevant actions in over 90 per cent of cases versus under 10 per cent in baseline tests.

Lyons *et al.* (2007) even repeated the experiment with explicit instructions to avoid irrelevant acts. Before the usual test trials, each child was reminded of the 'silly

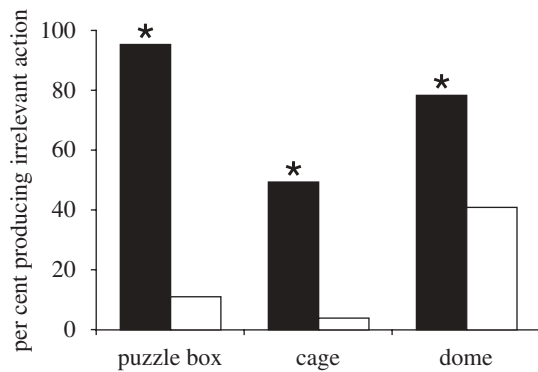


Figure 5. Over-imitation in young children. Percentage of children copying highly visible, causally irrelevant actions of model in three different tasks, compared with baseline performance of comparable actions (after Lyons *et al.* 2007, with permission). See text for discussion. Black bars, observed adult; white bars, baseline. $P < 0.001$.

extra thing' that had not helped earlier, like the feather-tapping, then explicitly told 'I want you to watch really carefully, because when I open this (puzzle object), I might do something that's silly and extra, just like the feather', later adding 'Remember, don't do anything silly and extra, okay? Only do the things you *have* to do'. All such efforts failed to diminish over-imitation in the 3- and 5-year-old children tested.

Whiten *et al.* (2005b) described such effects as over-copying rather than over-imitation (the term of Lyons *et al.* 2007) to acknowledge the fact that for those who define imitation as bodily imitation, there is no evidence here that children's copying is faithful in this respect. Indeed, Lyons *et al.* showed that copying occurred principally in terms not so much of specific actions, as of the transformations of object movements, a closer fit to one or more of the classes of emulation distinguished in §2b and figure 1. Perhaps, then, Lyons *et al.* documented 'over-emulation', following some authors' terminology. However, since other studies have recorded very detailed imitation by human subjects down to the level of the digit used for a task (Custance *et al.* 2006), over-copying offers a more neutral umbrella term pending further investigation of the underlying mechanisms.

Why do such apparently blinkered child responses occur, making performance less efficient (McGuigan *et al.* 2007) than with the more selective chimpanzees (Horner & Whiten 2005)? Whiten *et al.* (2005b) suggested that 'a plausible explanation... is simply that we are such a thorough-going cultural species that it pays children, as a kind of default strategy, to copy willy-nilly much of the behavioral repertoire they see enacted before them. Children have the longest childhoods of any primate, much of which is spent in play, practice and exploration, so there is plenty of opportunity to weed out wrongly assimilated aspects of the actions observed' (p. 280). Given the massive cultural knowledge and skill reservoir of adult humans and the relative ignorance of young children, blanket copying may only occasionally lead children into 'superstitions'—as in experiments where 'silly' components are inserted on purpose. This will later be corrected by childrens' direct interaction with

reality, so it is a 'copy-all, refine/correct-later' strategy, an effect recently confirmed in a diffusion study using the Horner and Whiten boxes by Flynn (2008). Lyons *et al.* (2007) suggest that this strategy enables a child particularly to learn about causal factors that are so often opaque in human skills and tasks, although the automaticity of the system makes it fire even when the circumstances appear transparently inappropriate, as in our experiments.¹

A copy-all, correct-later strategy may be far from limited to childhood. In our ongoing research in this paradigm, we have recently tested adults and found that the trend we earlier documented, of increasing over-copying with age, is extended into adulthood, with adults showing an even higher tendency to act in this way than our 5-year-old sample (unpublished data). Although such apparent irrationality may seem initially surprising, it may again be adaptive in the long run, because adults too can easily be faced with highly novel tasks within which there are causal links invisible to them, at least initially. Interestingly, several papers in the present issue echo this emerging issue of automaticity in human imitation (Brass *et al.* 2009; Catmur *et al.* 2009; Massen & Prinz 2009).

However, the picture of humans as irrational (over-) copiers contrasts with another set of striking findings that have documented what appears to be just the opposite. The work of Gergely *et al.* (2002), in which even 14-month olds avoided copying an adult performing unusual actions when the adult was constrained to act in this way, was described by the authors as 'rational imitation'. Other studies have shown that childrens' copying can be selective, discounting accidents (Carpenter *et al.* 1998) and showing sensitivity to signs of pedagogic engagement (Csibra & Gergely 2006) even in infancy. Just where the boundaries fall (and why) between, on the one hand, 'mindless' or blinkered over-copying and, on the other hand, sophisticated and rational selectivity, in both child and adult, now emerges as an exciting and challenging territory to research more deeply.

8. CUMULATIVE CULTURAL TRANSMISSION: AN EXPERIMENTAL APPROACH

Studies reviewed above, and others, have repeatedly demonstrated high fidelity imitation by children, which contrasts with the rough and patchy copying efforts of chimpanzees. Nevertheless, we have shown that chimpanzees have sufficient copying capacity to sustain traditions incorporating quite complex behavioural techniques. The hypothesis that it is the lack of copying ability that prevents chimpanzees from generating the cumulative cultures so evident in the human case (Boyd & Richerson 1996; Tomasello 1999) now sits less comfortably with these results. What, then, is the true explanation for the massive difference between the two species in cumulative culture (Whiten *et al.* 2003)?

Earlier we critiqued the 'loop' experiment of Tennie *et al.* (2009) that purported to tackle this issue. In our own approach to the topic (Marshall-Pescini & Whiten 2008b), juvenile chimpanzees first learned, through observation of a human model, to slide a

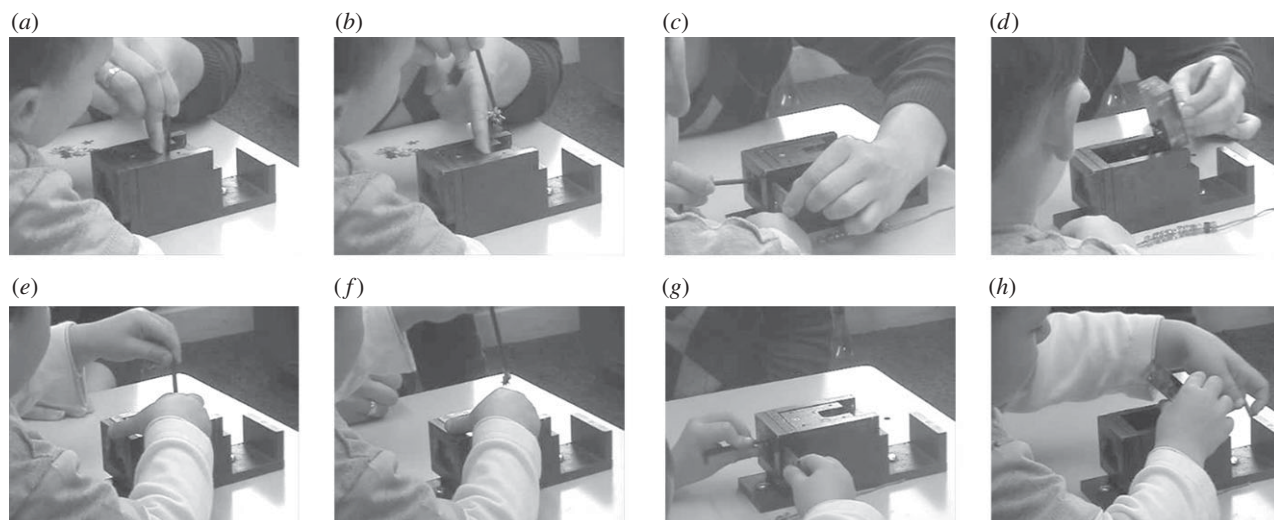


Figure 6. Honey-dip task. (a–d) model; (e–h) child participant. (a) Dip technique: model holds door open with one hand while dipping tool into the box. (b) Retrieval of ‘star’ rewards. (c) Poke technique: model slides the door with left hand while poking bolt with right. (d) Model levers lid open using tool. (e) Child performing ‘dip’ technique. (f) Child retrieving rewards. (g) Child performing ‘poke’ technique. (h) Child levering lid open with tool.

cover that revealed a hidden hole in an artificial foraging box and insert a probe to extract honey. They then saw the same model using the probe to push in an obscured catch so that, by inserting the probe in the dipping hole, the hinged lid could be levered open to gain all the honey inside, plus several nuts.

Instead of adopting this potential step-up in cumulative culture, the chimpanzees stuck to their dipping, gaining only a few licks of honey each time. This was not because the task was too difficult, because some control youngsters that saw no model did explore and discover the more complex technique. We have now tested 3- and 4-year-old children’s responses in a similar test (figure 6: see electronic supplementary material, methods). Despite the fact that the second, more productive method was made slightly more challenging for the children by the addition of a sliding cover over the crucial catch holding the lid closed, eight of 12 children already using the dipping technique evidenced cumulation by upgrading to the second technique and another three children appeared to attempt the beginning of it: only one persisted in dipping (table 1).

These results suggest that although chimpanzees can observationally learn quite complex techniques, these quickly become habitual, restricting what alternative methods can be switched to, even where the benefits appear manifest. Children, by contrast, demonstrated cumulative cultural learning. Hrubesch *et al.* (2008) have since demonstrated a similar result to that we found in chimpanzees, which they described as ‘conservatism’. Chimpanzees failed to upgrade to an improved technique for gaining food discovered by a few members of the group; moreover, practitioners of this technique later prevented from using it failed to copy the simpler method of others, which remained productive. Although the inflexibility of chimpanzees’ social learning in these situations may appear surprising, there is a remarkable consistency in these studies. What appears to be revealed is a social learning propensity that is initially capable of

Table 1. Response of each child in baseline and experimental phases. M, male; F, female (with age in months). (1), probed but used hand to open the lid, with no levering; (2), slid panel open but failed to insert stick tool in hole to push the bolt.

child	baseline	phase 1 dip model	phase 2 probe + lever model
M36	no dip	dip × 3	probe + open (1)
M38	no dip	dip × 3	probe + lever
F39	no dip	dip × 3	attempt (2)
M40	no dip	dip × 3	dip × 3
F42	no dip	dip × 3	attempt (2)
F42	no dip	dip × 3	probe + lever
F44	no dip	dip × 3	probe + lever
M45	dip × 3	—	probe + lever
F47	no dip	dip × 3	probe + lever
F50	no dip	dip × 3	probe + lever
F50	no dip	dip × 3	probe + lever
F55	no dip	dip × 3	attempt (2)

the sophisticated levels of copying described in earlier sections of this paper, but in any one context quickly becomes ‘canalized’ or crystallized, producing a routine resistant to cumulative or other change.

9. CONCLUSIONS

Our results and conclusions bear on each of the three aspects of imitation addressed in this theme issue: evolution, development and control.

On the *evolutionary* question, we have established several points of similarity between chimpanzee and human cultural transmission that indicate the characteristics likely to have existed in our common ancestor of approximately 6 million years ago. These include capacities (i) to sustain multiple-tradition local cultures, (ii) to copy others with sufficient fidelity to transmit culturally variant behavioural techniques within and between communities, and (iii) to call on both imitative and emulative

forms of learning within a portfolio of different social learning processes. Conversely, since the human and chimpanzee lineages diverged, our species has acquired more refined capacities for both higher fidelity imitation and cumulative cultural learning.

Turning to imitative *development*, an intriguing picture is emerging in which children exhibit quite surprising susceptibility to over-copying of others in the face of apparently obvious perceptual evidence of causal irrelevance. These findings appear paradoxical in light of other studies showing sophisticated imitative selectivity. However, we note that the latter findings concern infants and, again perhaps surprisingly, it is in the older and more cognitively mature children (and even adults) that we find more 'blanket' copying. These intriguing, apparent paradoxes should drive further research to resolve them in coming years.

Finally, there is the question of *control* of imitation. As the prior paragraph indicates, one new and interesting set of issues here concerns ontogenetic changes—a lessening of control, towards more 'mindless' blanket copying as children develop. However, in both human infants and apes, other studies are mapping a widening range of conditions in which individuals express selectivity in their social learning strategies. These include social factors such as the intentions of, and constraints on, the model and physical factors such as principles of causality. In addition, our preliminary results suggest that chimpanzees may be restricted in their capacity to modify and upgrade the first approaches to a task they learn, in contexts where children show a readiness to upgrade, facilitating a process of cumulative cultural change.

We conclude by noting that the overview we present in this paper underlines how this theme issue comes at a time of rich discoveries about the evolution, development and control of imitation in both human and non-human species and that, moreover, these three perspectives are becoming linked in exciting and productive ways.

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ENDNOTES

¹Additional comments appraising the studies of Lyons *et al.* (2007) and Tennie *et al.* (2009) are in the electronic supplementary material.

²A video clip of the behaviour of the two chimpanzees accompanies Marshall-Pescini & Whiten (2008b) in electronic supplementary material at <http://dx.doi.org/10.1037/0735-7036.122.2.186.sup>. The observer chimpanzee had already attempted cracking using a hammer stone, but not successfully.

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