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Experimental Approaches to the Study of Culture in Primates

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Introduction

The topic of culture in nonhumans has received a lot of attention in recent years, and perhaps this is not surprising. The idea that other animals - apes, monkeys, and maybe even rats and fish - may show a semblance of a trait that we consider to be so fundamentally human, is both exciting and controversial. Dialogue between enthusiastic advocates of animal culture on the one hand, and wary sceptics on the other, has therefore generated a fruitful intellectual atmosphere, and spawned a broad, rich, scientific literature on the topic.

In this chapter I hope to illustrate how this atmosphere has been particularly influential in generating innovative and informative experimental approaches to the study of culture, due to the need for controlled (and hence less ambiguous) observations. The consequence of this has been that the experimental literature on culture in nonhumans now has much to offer research on human culture, and exposes gaps in our current knowledge within this area. Although there is a literature on experimental approaches to human culture, it is far from extensive, and studies are somewhat scattered. I will therefore also review some of the experimental research that has been carried out on human culture, drawing comparisons with the animal research.

This chapter will focus specifically on the topic of primate culture in discussing the nonhuman research. There are two main reasons for this narrowing of focus. The first of these is that experimental research on primate culture has necessitated a somewhat more ingenious and creative approach than research on other animals, such as fish and rats (this is an issue that will be returned to later), as practical and ethical issues restrict what can be done. Since these constraints certainly apply to work with humans as well, then it is likely that these approaches might prove to be particularly useful in researching human culture. The second reason for the primate bias in this chapter is simply that, as our closest evolutionary relatives, primates can reasonably be expected to share with humans a greater number of attributes than any other phyletic group. Therefore, whatever form “culture” takes in these species, it is liable to show more similarities with human culture than other animals’ behaviour would. Again, this serves to increase the chances that we may be able to usefully extrapolate some of what we have learned from animals, to enhance our understanding of humans.

Observational Approaches to the Study of Culture in Nonhuman Primates

Those who study animals typically define “culture” as behaviour that is specific to a group, which is transmitted via some form of social learning (see

Caldwell & Whiten, 2006, for a more detailed discussion of this point). Observational approaches to studying culture in primates have therefore focussed firstly on identifying group-specific behaviours. In order to be cultural though, any between-group variation, or within-group similarity, must have arisen as a result of social learning. So researchers must also attempt to rule out competing explanations, such as genetic differences between the groups, or different environmental conditions.

Such observational approaches have provided abundant data on behavioural traditions in primates. Researchers have been able to compare data from different field sites in order to show striking variation between groups. One of the first systematic studies of this type was carried out by Whiten et al. (1999). Data from the seven longest-running chimpanzee field sites was pooled in order to determine whether there were differences in behaviour across sites. Research directors from each of the study sites were presented with a list of 65 behaviours, each of which was suspected to show variation across sites. The research directors reported which of these behaviours they had observed in their study population, and with what frequency. Of the original list of behaviours, a total of 39 were identified as being either customary (the behaviour occurred in all or most individuals of at least one age-sex class) or habitual (the behaviour occurred repeatedly in several individuals) at one or more of the sites, whilst being absent from at least one other, with no apparent ecological reason for the absence. Whiten et al. (1999) concluded that these behaviours were therefore likely to be culturally transmitted. The list included a range of activities, including tool-use behaviours (such as termite fishing and nut cracking), social gestures (such as the grooming “hand-clasp”), and behaviours with a hygienic function (such as the “leaf-napkin”).

Since the publication of Whiten et al.’s (1999) article, similar surveys have been carried out for other primate species, with similar findings. Van Schaik et al. (2003) surveyed orangutan field sites, also identifying a list of behaviours that were customary or habitual at certain sites, whilst being absent from others. Striking behavioural variation between groups of white-faced capuchin monkeys has also now been identified, in both their social behaviours (Perry et al., 2003) and foraging behaviours (Panger et al., 2002).

However, there are limits to what can be learned from purely observational data. Some authors have argued, for instance, that it is simply not possible to claim that group-specific behaviours are cultural, due to the fact that there is always a certain amount of doubt about whether they have been socially transmitted (e.g. see Laland & Hoppitt, 2003; Galef, 2003). Researchers can do their best to rule out the likely competing explanations, but these can never be completely eliminated as possibilities. Galef (2003) in particular has argued that the group-specific behaviours observed in chimpanzees are likely to be the result of differential reinforcement contingencies, arising as a result of different environmental conditions. In other words, the variation in behaviour is purely attributable to individual trial-and-error learning, made possible by different surroundings (see also Galef, 1995). This is a difficult point to defend against, since there are always likely to be subtle differences between environments, which may not be immediately obvious as sources of variation in behaviour, but which could nonetheless have such an effect. Galef (2004) and Laland and Janik (2006) have drawn attention to the two contrasting methods of “ant-dipping” behaviour observed at different chimpanzee field sites. Whilst chimpanzees from the Tai forest use a simple technique involving a short stick, chimpanzees from Gombe use a more complex bimanual technique employing a longer stick. However, chimpanzees from Bossou alternate between the two, depending on the species of ant

(Humble & Matsuzawa, 2002). Galef (2004) asserted that such a finding is not consistent with a hypothesis of traditional behaviour, and Laland and Janik (2006) have suggested that the Tai and Gombe variants may well have been shaped by the local conditions at each site.

Over recent years, field research on culture in primates has utilised increasingly more sophisticated methods, which make it less and less likely that explanations other than social transmission could account for the patterns of behaviour observed. Caldwell and Whiten (2006) have discussed how approaches which either focus specifically on social behaviours, or those which use social contact as a variable in analyses (Panger et al., 2002; Van Schaik et al., 2003) are extremely difficult to refute as examples of cultural behaviours. However, in order to directly test hypotheses about whether the behaviour of other individuals affects the likelihood of adopting a behaviour oneself, experimental manipulations are necessary.

Laland and Hoppitt (2003) have argued that to date the best evidence of cultural behaviour in nonhumans comes from fish. Laland and Hoppitt (2003) cite Helfman and Schultz's (1984) work on reef fish, *Haemulon flavolineatum*. Helfman and Schultz (1984) were able to carry out a direct manipulation of the fishes' social environment, independent of their physical environment. They introduced a fish population to an area where another population already existed, finding that the introduced fish subsequently showed the same preferences for schooling sites and migration routes as the pre-existing members of the population. However, a further naïve population were later introduced to the same site, but this time, all other fish had been removed from this site. What they found this time was that the fish developed entirely novel preferences for schooling sites and migration routes. This direct manipulation of the presence or absence of experienced individuals had the power to demonstrate that the social environment was far more influential than the physical environment in determining the preferences of newcomers.

However, as Laland and Hoppitt (2003) acknowledge, such manipulations would be unfeasible with primates, for a variety of reasons. Moving large numbers of primates from their natural environment for the purposes of carrying out an experiment into social learning would not be ethical, as well as being likely to be logistically a lot more complicated than moving populations of fish.

Experimental Approaches to the Study of Culture in Nonhuman Primates

Nonetheless, experiments in which the social experiences of primates are actively manipulated have become commonplace within the literature on social learning, although these have not taken the form of translocation experiments, such as that carried out by Helfman and Schultz (1984). Researchers have instead been able to carry out experiments with captive primates, in zoos and laboratories, in order to investigate the effects of observing the actions of experienced conspecifics. To a limited extent, field experiments have also been possible with wild primate populations (e.g. see Galef, 2004, in which such an approach is strongly advocated). This section will review the various approaches to investigating culture in nonhuman primates experimentally.

Dyadic Experimental Designs

In dyadic experimental designs, a naïve observer animal is exposed to another, experienced, individual performing a particular behaviour. The earliest examples of

such experiments involved a simple comparison between an experimental condition (in which subjects are exposed to a demonstration), and a baseline condition (in which no such experience is provided). Studies using such a design typically find that subjects that have been exposed to the demonstration are subsequently more likely to perform the behaviour themselves, or do so more quickly, than those in the control group. Warden and Jackson (1935) and Tomasello et al. (1987) carried out experiments of this type, with rhesus macaques and chimpanzees respectively.

These experiments certainly show that the behaviour of other individuals can affect the likelihood that behaviour being adopted by a naïve individual. However, a more powerful experimental design involves contrasting the effects of different demonstrations. If social learning mechanisms have the power to sustain divergent cultures in separate social groups, we would expect that alternative versions of a demonstration would generate contrasting behaviours in different experimental groups.

Primatology has therefore made good use of a methodology developed initially to test for imitation in budgerigars (Dawson & Foss, 1965). Dawson and Foss (1965) devised a “two-action” method. Two-action designs involve two alternative demonstrations on the same object, with each producing the same end result. In Dawson and Foss’s (1965) study, naïve budgerigars observed a trained conspecific accessing a hidden food reward by removing a lid with either their beak or their feet. Dawson and Foss (1965) then recorded the actions that the observer budgerigars carried out on the same apparatus. They found evidence that observers were influenced by the particular demonstration they had seen, in terms of their preferred method of accessing the food reward.

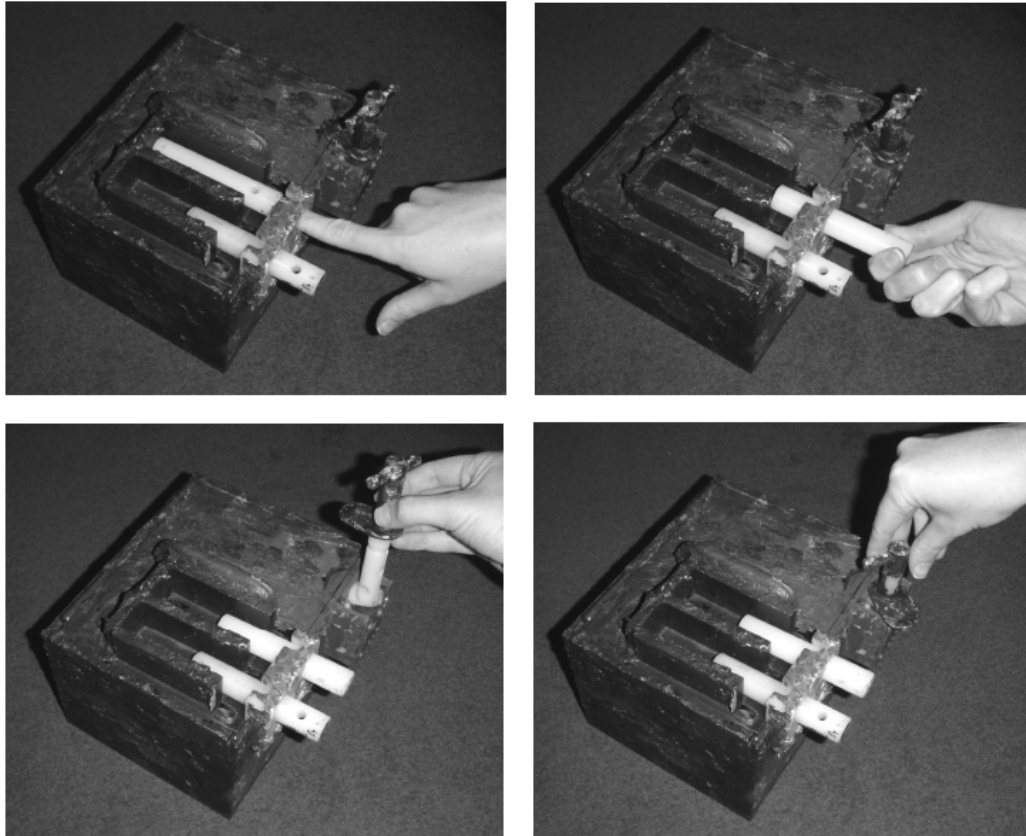
Andrew Whiten and Deborah Custance (Whiten et al., 1996) applied the two-action method in order to test for imitation in chimpanzees, using a piece of apparatus that they referred to as an “artificial fruit” (see Figure 1). The artificial fruit did not physically resemble a fruit, but it was designed to represent a logical analogue of foraging behaviour. It was simply a box with a hinged lid, and various latches that held the lid closed. When the artificial fruit was presented to animals in experiments, it was always presented with a food reward contained inside. In order to access the food reward, the latches therefore had to be released in order to free the lid. This resembled the kind of processing that nonhuman primates sometimes have to carry out on foods within their natural diet (such as nuts, or some fruits), in order to access an edible centre.

Embracing the logic of the two-action design, the artificial fruit had been designed such that there was more than one possible method of removing the latches. Sliding bolts could be either poked through from front to rear, or pulled or twisted out from rear to front. Another latch could be either rotated to free the lid, or lifted out altogether (see Figure 1). The chimpanzees were exposed to a human demonstrator performing one or other of the alternative actions on each of the latches, and were then presented with the artificial fruit themselves. The subjects that had seen twisting of the bolts produced more twisting-like actions, and those that had seen poking produced more poking-like actions.

The artificial fruit had deliberately been designed in such a way that it could be used to test for imitation in a variety of species, and since the original chimpanzee study, the method has also been used with gorillas (Stoinski et al., 2001), orangutans (Custance et al., 2001; Stoinski & Whiten, 2003), capuchins (Custance et al., 1999) and marmosets (Caldwell & Whiten, 2004), as well as parrots (Huber et al., 2001) and adult humans (Horowitz, 2003). The logic of the two-action design was also used in

Voelkl and Huber's (Voelkl & Huber, 2000) study on imitation in marmosets, although in this case a photographic canister was used, which was opened by a monkey using either their hand or their mouth.

Figure 1. An artificial fruit. The bolts can be poked through (top left) or twisted out (top right), and the handle can be lifted out (bottom left) or turned (bottom right).



Group Diffusion Experiments

The problem with some experimental tests of social learning in primates is that they may not accurately simulate the conditions under which learning occurs in the animals' natural environment. Although we can readily demonstrate that primates *can* learn by observation, a question still remains about whether this kind of learning could result in the sort of group-specific behaviours that we observe in the field. Galef (1995) and Heyes (1993) have both argued that social learning will interact with individual learning in such a way that groups will inevitably converge on behaviours that result in the greatest reinforcement compared with alternatives. Between-group variation in behaviour is therefore unlikely to be supported by social learning. Heyes (1993) cites Galef et al.'s (1986) replication of Dawson and Foss's (1965) study on budgerigars: subjects that observed conspecifics accessing hidden food using either their beak or their foot tended to match the demonstrated technique for only the first two trials post-demonstration. In later trials, the difference between the groups disappeared.

However, other approaches to investigating social learning in primates have used designs in which whole groups are tested, rather than individuals. Behaviour is

also typically recorded over longer periods of time in these studies. Since the aim of such approaches is essentially to induce a tradition within a group, they therefore provide a more accurate indication of whether group-specific behaviours can be supported by social learning.

A number of experiments of this type have been targeted towards documenting the spread of a novel behaviour within a single social group (e.g. Tonooka et al., 1997; Huffman & Hirata, 2004). The problem with these designs is that it is difficult to establish the role of social learning, in the absence of a comparison group. Ideally more than one group would be compared, with each having been exposed to a different behaviour. In this way it would be possible to determine whether contrasting cultures could actually be generated. Whiten et al. (2005) did exactly this, combining the two-action method with a group diffusion design. Two demonstrator chimpanzees, one from each of two social groups, were trained to perform a tool-use task, each using a different method from the other. The demonstrator chimpanzees were then introduced back into their groups, along with the apparatus on which they had been trained. Each performed the version that they had learned, and subsequently, there was a clear tendency for their group members to use the same method. The variation between the two groups was maintained over several days of testing, during which the apparatus was available to the chimpanzees for a total of 36 hours. This study effectively showed that social learning in primates does have the capacity to support behavioural variation, as the researchers showed that these alternatives were maintained over time within the two social groups.

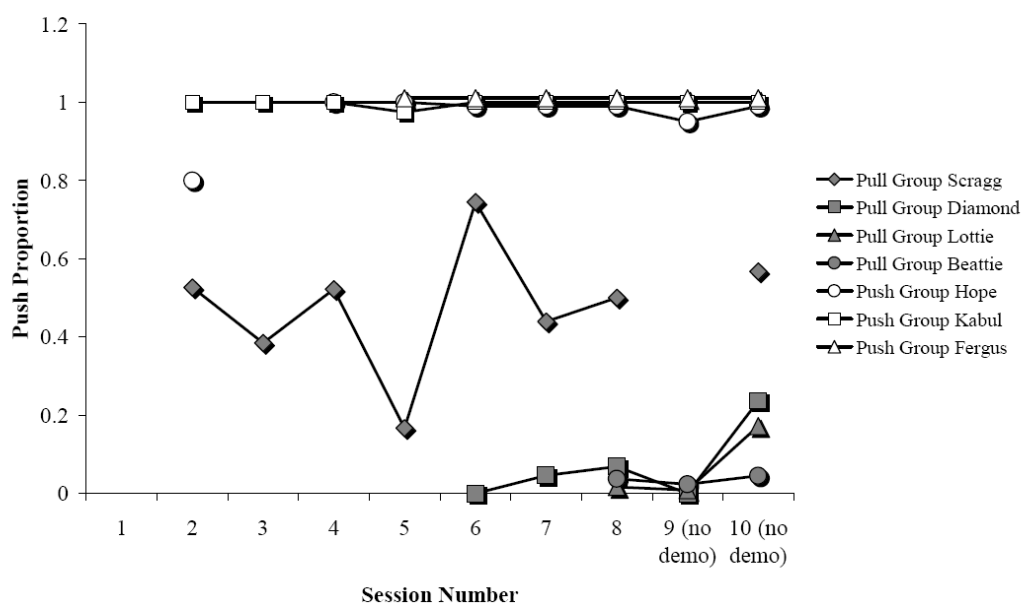
Curiously, in a direct attempt to replicate Whiten et al.'s (2005) study, Hopper et al. (2007) found that two groups of chimpanzees showed a preference for the same method, even though one group had been exposed experimentally to the alternative. They attribute this to differences in the previous experiences of the two populations in question. The chimpanzees studied by Hopper et al. (2007) had extensive experience of enrichment devices which made use of a similar action to the one which was eventually preferred by all members of this population.

Price and Caldwell (2007) carried out a similar experiment with a zoo population of colobus monkeys. Their two-action task involved a box with a clear flap which could be either pushed or pulled to access a food reward inside. The population consisted of two separately housed groups of this species, so these two groups could be exposed to contrasting versions of the demonstration. The demonstration was in this case provided using video footage of another monkey performing the behaviour. The video presentation, whilst sacrificing some ecological validity, allowed for a high level of control over the demonstration, which can potentially be something of a problem in these naturalistic group designs. Price and Caldwell (2007) found that, whilst the demonstration footage was playing, subjects showed a high degree of matching to the demonstration (up to 100% matching for some subjects). Furthermore, the variation between the groups was sustained even after the footage was no longer playing. There was still a statistically significant difference in the behaviour of the groups five days after the final presentation of the demonstration footage. Figure 2 displays the data from this study.

Interestingly, the pull group continued to prefer their demonstrated technique, despite this possibly being a less efficient method. For the subjects tested, the pull technique involved a bimanual manipulation of the apparatus, with the monkeys pulling the flap with one hand, whilst reaching in for the food reward with the other. Pushing, by contrast, was achieved with a single hand. It seems then that pullers may therefore have been disadvantaged by their technique, yet three of the four monkeys

in the pull group continued to pull significantly more than push through all of the sessions. One particular individual, Scragg (see Figure 2), used both techniques roughly equally, and therefore had ample opportunity to learn about the relative effectiveness of the two techniques. However, even this individual continued to make use of the pull technique right up to the final test session.

Figure 2. Redrawn from Price and Caldwell (2007). Proportion of pushes to pulls for each subject, for all sessions. Demonstration clips were shown during sessions 1-8, which were each held on successive days. Session 9 was held 24 hours after the demonstration footage had last been shown, and session 10, five days later.



It is particularly interesting to note that in similar test for social learning in monkeys, which used a dyadic rather than a group design, subjects rapidly converged on one preferred method (Bugnyar & Huber, 1997). Bugnyar and Huber (1997) used a push/pull task similar to that used by Price and Caldwell (2007), but found that the initial preference of observers of the pull demonstration disappeared over the course of five test trials, with all subjects converging on the push alternative.

There are clear differences between the two studies, which make it difficult to draw any strong conclusions about the reasons for the contrasting outcomes. Bugnyar and Huber (1997) tested marmosets, a small New World monkey, and Price and Caldwell (2007) tested colobus monkeys, a larger Old World monkey, and there are clear behavioural and morphological differences between the two species. Furthermore, there are minor differences in experimental method other than the use of a dyadic versus a group design (and of course a similar contrast in outcome was found between Hopper et al. (2007) and Whiten et al. (2005) cited earlier, despite virtually identical methods, which suggests that such differences in outcome may sometimes be attributable to extremely minor variations in procedure or population). Nonetheless, Price and Caldwell's (2007) findings raise the intriguing possibility that testing for social learning in groups may increase the time taken for behavioural variants to

extinguish, compared with testing isolated individuals. The actions of group members may function as repeat demonstrations, influencing individuals to persist with a particular behaviour, and counteracting the effects of their own experience through trial-and-error. This is currently an extremely speculative suggestion. In order to test this, one would have to compare conditions in which subjects were tested either individually or in a social group, in order to find out in which of these conditions the socially learned variants corrupted more rapidly. However, research along these lines may provide crucial insights into how between-group variation can be supported by social learning, despite the influence of trial-and-error learning.

Transmission Chain Experiments

The strength of group diffusion designs lies in their close simulation of natural learning conditions. However, the corresponding disadvantage of this is that little control is possible, following the initial introduction of a behaviour into the group or groups. In transmission chain designs, far greater control is possible, in terms of manipulating certain variables that may affect learning. Another benefit of this approach is that it may provide a better analogue of intergenerational learning, as this is in effect what such designs attempt to simulate.

Transmission chain designs involve the systematic replacement of individuals in controlled laboratory groups such that one-time learners become the demonstrators for later subjects. These approaches have been used to good effect with rats (Galef & Allen, 1995; Laland & Plotkin, 1990), birds (Curio et al., 1978) and fish (Laland & Williams, 1997; Laland & Williams, 1998), as well as nonhuman primates. The first example of this approach being applied to animals was Menzel et al.'s (1972) study of chimpanzees' responses to novel objects. Menzel et al. (1972) were interested to discover whether neophobic responses could be overcome by observing conspecifics interacting with novel objects, and if so, whether this could potentially lead to traditions of avoiding or approaching particular objects. Menzel et al.'s (1972) study population consisted of 19 chimpanzees. At any one time, a total of three of these chimpanzees were housed together in the same enclosure and tested together with the target objects. However, every two months he would replace the longest-standing member of this trio with a new individual from the population. So, by the time the fourth trio was created (consisting of the fourth, fifth and sixth members), the original founder members of the group (i.e. the first, second and third) had been completely replaced. Menzel et al. (1972) found that the first and second trios avoided both of the test objects, but one member of the third trio habituated to one object and began interacting with it, and one member of the fifth trio likewise habituated to the other test object. Subsequent trios would then interact with these objects, continuing the "play" tradition, even once the originator had left the group. Menzel et al. (1972) concluded that the ways in which the chimpanzees responded to the objects was characteristic of the group, rather than being idiosyncratic.

Horner et al. (2007) used a transmission chain design with a two-action task, in an attempt to create two contrasting cultures in chimpanzees. Initially, two individuals were trained to obtain food from a foraging device, each using a different method. These trained chimpanzees provided the demonstration for the next individuals in the chains. Then, the responses of the observers were used as the subsequent demonstration for the next individual, and so on. One version was passed along a chain of five chimpanzees, and the other along a chain of six. In both cases, transmission was virtually perfect, with ten of the eleven subjects exclusively using their chain's original method. This finding strongly supports the idea that contrasting

behavioural traditions can be sustained through social learning, over multiple generations.

Experimental Approaches to the Study of Culture in Humans

So, to date, experimental research on culture in nonhuman primates has made use of a variety of methodologies, and the results raise intriguing issues of broad-ranging consequence regarding how, when and why particular behaviours may be sustained within groups by social learning. In this particular field, therefore, there is much that can be learned from the literature on nonhuman primates, in terms of augmenting our understanding of our own species.

In the current scientific literature, there are a great deal of examples of experimental tests of social learning in humans, but the vast majority of these make use of simple dyadic designs (too many to review here). Few have exploited designs involving naturalistic groups, or transmission chains. This is quite surprising, given how informative such approaches could potentially be. Interestingly, the studies of this type that do exist are fairly scattered throughout the literature. This dispersal is apparent in terms of where such research has been published, as examples can be found in a variety of specialist journals from a number of different disciplines. It is also apparent in terms of when it was published; such approaches have been used for at least seventy years, and yet there is no clearly identifiable period of popularity. Therefore (although this is not intended to be an exhaustive review of this area of research), the aim of this section is to introduce the reader to the predominant approaches within this field, as well as some of the more intriguing findings.

Overlapping Replacement Microcultures

Several studies with humans have employed the same methods which were used by Menzel et al. (1972), and other researchers (Galef & Allen, 1995; Laland & Williams, 1997; Laland & Williams, 1998), with animals. These studies have all created multiple overlapping “generations” of learners, by establishing small groups of subjects which are individually removed and replaced by new members.

Jacobs and Campbell (1961) used this approach to good effect, in order to determine whether participants’ tendencies to conform to majority opinion could result in long-lasting traditions within groups. Participants were asked to estimate the degree of movement of a point of light in a dark room (in fact the light did not move at all, but the perception of a small amount of movement is a persistent and reliable illusion). Groups (“microcultures” in their terminology) were founded by experimental confederates, instructed to respond with a significant overestimation of their true perception of the degree of movement. The responses of naïve participants who joined the group of confederates were swayed in the direction of the confederates’ answers, compared with a control group without confederates. However, what was more interesting was that the bias towards overestimation remained, even as the confederates were gradually replaced with naïve participants. Responses of experimental groups continued to be significantly higher than those of control groups for four generations after the final confederate had been removed.

It is worth noting though, that the overestimation bias showed a rapid decline over generations. A very strong bias was induced in early generations, stimulated by the responses of the confederates, but this effect dropped off sharply as soon as confederates began to be removed, and continued to do so until responses between

experimental and control groups were statistically indistinguishable (five or six generations after the final confederate was removed). Jacobs and Campbell (1961) in fact conclude that, “the outcome may well warn us against the assumption that a purely arbitrary cultural norm could be perpetuated indefinitely without other sources of support. Even if people weigh the opinions of their elders many times that of their own direct observations, the collective effect of their own observations probably soon erodes a *functionless* arbitrary belief” (p657, italics in original).

Weick and Gilfillan (1971) extended upon Jacobs and Campbell’s (1961) findings. They believed that arbitrary traditions could in fact be perpetuated within groups, as long as the traditions were not (in their terms) “unwarrantedly” arbitrary. In other words, they believed that particular behavioural alternatives could persist, as long as any differences between the alternatives was essentially inconsequential. They asked groups participants to play a game, the aim of which was to produce numbers which added up to a particular sum decided by the experimenter. Participants were not permitted to communicate, and therefore success on the game depended on having an agreed strategy. There were many possible strategies which could lead to success on the game, but founders of some groups were instructed in the use of one which was very easy, involving little mental arithmetic, whilst others were instructed in the use of one which was very difficult, requiring quite complicated calculations. After four generations, the difficult strategy was being used no more than it was by a control group who had received no instructions. However, the groups that had been instructed in the use of the easy strategy continued to use this method much more frequently than the control group did, right up until the end of the experiment (11 generations).

Similar methods have also been used by Insko and colleagues (Insko et al., 1980; Insko et al., 1983) and, more recently, by Baum et al. (2004). The value of this method for Insko et al. (1983), lay in its capacity for experimental manipulation. They were able to test competing hypotheses about the reasons for the emergence of leadership in human societies, by creating microcultures that operated under different governing rules. Thus, theoretical debates that were difficult to address on the basis of anthropological and archaeological data, could be tackled by re-creating hypothetical historical societies in miniaturised form under laboratory conditions. For Baum et al. (2004) the microculture method offered a window into the process of cultural evolution, illustrating how it can lead to adaptive strategies.

Serial Reproduction

The “Method of Serial Reproduction” was first used by Bartlett (1932) in his studies of human memory. What this approach has in common with the microculture research is that chains of multiple generations are involved, with participants learning from previous learners. However, it is quite different in a number of other important respects. Firstly, and perhaps most importantly, in this type of research, participants are explicitly instructed to copy, in that their aim is to reproduce information as accurately as they possibly can. In contrast, in microculture studies, participants are never instructed to copy other members, but rather such effects emerge spontaneously. During serial reproduction tasks, participants may also never meet one another, but rather, written material is passed on by an experimenter. Indeed, participants may never even be aware of their role as a member of a transmission chain. This contrasts strongly with the microculture approach in which social interaction and coordination tend to be all important.

The benefits of serial reproduction tasks lie in their ability to reveal people’s unconscious cognitive biases, as they allow researchers to investigate what sort of

information is omitted, or introduced, when participants are actively trying to reproduce material as accurately as possible. Bartlett (1932) used the method to show that stories passed on in this way were, over several generations, gradually influenced by participants' cultural backgrounds. Chains of Indian and English students were found to pass on somewhat different versions of the same story. The method has also been recently revived by Mesoudi and colleagues (Mesoudi & Whiten, 2004; Mesoudi et al., 2006), who have used it to illustrate people's biases towards hierarchical structure in event descriptions (Mesoudi & Whiten, 2004), and also their tendencies to preferentially reproduce social, as opposed to non-social, information (Mesoudi et al., 2006).

Other Approaches

A number of other experimental approaches have been taken which do not fit neatly into either of the two categories above. For example, Rose and Felton (1955) investigated how participants influenced each other's interpretations of Rorschach inkblot cards. Their design had similarities with the microculture method, but rather than using successive generations, individuals moved between three different groups, so the researchers could observe how ideas spread from group to group. Schotter and Sopher (2003), meanwhile, investigated how game strategies were influenced by word-of-mouth advice between non-overlapping generations of individual players.

A particularly interesting experiment by Garrod and Doherty (1994) used repeated dyadic interactions between a restricted pool of participants in order to show how linguistic conventions can be generated and maintained. In Garrod and Doherty's (1994) experiment, participants were asked to play a game which required a certain amount of communication and co-ordination between two players. Participants who played the game repeatedly with the same partner were compared with those that played the game repeatedly with multiple different partners, all of whom had also been playing the game with other members of the same group. In playing the game, participants needed to describe a maze to one another, and there were a number of possible alternative schemes which could be used to describe locations. Garrod and Doherty (1994) found that, initially, the isolated pairs showed a higher degree of convergence in terms of the descriptive schemes they adopted. However, further down the line, when more games had been played, the group began to show a higher level of convergence than the pairs. Garrod and Doherty (1994) argue that, once conventions were established, these were adhered to more strongly by the group than by the isolated pairs, as the isolated pairs could more readily update their schemes on the basis of previous interactions.

A final, recent, study merits mention. Salganik et al. (2006) took a very different approach to the experimental study of culture than any of the other studies cited here. They were interested in how information about other people's preferences affected consumer choice. They hypothesised that popularity can be self-perpetuating, in that the more a particular product is selected, the more likely it is to be selected by further individuals. In order to test this hypothesis, they created a virtual music market, in the form of a website where unknown songs could be downloaded. However, potential consumers were directed to one of a total of eight isolated cultural markets, all of which offered exactly the same products. Within each cultural market, information was available regarding which songs had been most frequently downloaded by others. These cultural markets were also compared with a non-cultural market, in which the information about others' downloads was not provided. What they found was that, although certain songs did well in all markets, and others poorly,

success was nonetheless relatively unpredictable. The eight isolated cultural markets each showed different patterns of popularity, and these were only weakly related to quality (as measured by success in the non-cultural market). The multiple simulated worlds of this experiment demonstrate brilliantly how divergent cultures can materialise spontaneously, and even self-perpetuate.

Taken together, these individual pieces of research allow us to draw some insightful conclusions about cultural transmission. For example, it is clear that arbitrary traditions can in fact be perpetuated, under a variety of circumstances. As Weick and Gilfillan (1971) showed, if alternatives are truly arbitrary, in the sense that any differences are fairly inconsequential, then arbitrary culturally transmitted variation can surely be maintained. Also, if there is some value in convention (as there is in communication, as one must make oneself understood to others), then initially arbitrary conventions are likely to stabilise and be maintained, as shown by Garrod and Doherty (Garrod & Doherty, 1994). Finally, if social learning is considerably less costly than individual learning (as it was in Salganik et al.'s, 2006, experiment, due to the fact that looking at the download information was much quicker than listening to each song individually) then likewise, cultural variation can readily emerge between groups.

Conclusion

Recent, high profile, research on culture in nonhumans (in particular nonhuman primates) has helped to highlight the value of similar research with humans. Although there is already existing research taking an experimental approach to the study of culture in humans, the examples are somewhat scattered throughout the literature. Furthermore, it is quite surprising that at no time have such approaches appeared to take off in terms of popularity (other than, just possibly, right now). It is perhaps ironic that there is no clearly identifiable tradition within the science of human traditions. However, the research within this area has much to offer, and it is clear that there are many promising avenues for future research in this area. The literature on culture in nonhuman primates is currently only beginning to address questions regarding how cultural behaviours might be maintained within groups, given the influence of individual learning. But the literature on social learning in humans is really starting to offer some answers. The recent excitement surrounding research on culture in nonhuman primates will, with any luck, serve to draw attention to some of these studies with humans, and encourage further work of this kind.

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