

Christine A. Caldwell · Andrew Whiten

Evolutionary perspectives on imitation: is a comparative psychology of social learning possible?

Received: 10 May 2002 / Revised: 12 August 2002 / Accepted: 22 August 2002 / Published online: 12 October 2002
© Springer-Verlag 2002

Abstract Studies of imitation in animals have become numerous in recent times, but do they contribute to a comparative psychology of social learning? We review this burgeoning field to identify the problems and prospects for such a goal. Difficulties of two main kinds are identified. First, researchers have tackled questions about social learning from at least three very different theoretical perspectives, the “phylogenetic”, “animal model”, and “adaptational”. We examine the conflicts between them and consider the scope for integration. A second difficulty arises in the methodological approaches used in the discipline. In relation to one of these – survey reviews of published studies – we tabulate and compare the contrasting conclusions of nine articles that together review 36 studies. The basis for authors’ disagreements, including the matters of perceptual opacity, novelty, sequential structure, and goal representation, are examined. In relation to the other key method, comparative experimentation, we identify 12 studies that have explicitly compared species’ imitative ability on similar tasks. We examine the principal problems of comparing like with like in these studies and consider solutions, the most powerful of which we propose to be the use of a systematic range of task designs, rather than any single “gold standard” task.

Keywords Imitation · Social learning · Comparative psychology · Animal cognition

“Do monkeys ape?” asked Visalberghi and Frigaszy (1990), to which Byrne and Tomasello (1995) added “Do rats ape?”, followed by Tomasello’s (1996) “Do apes ape?” Implicit in these questions is the assumption that some kind of comparison is indeed possible, that there is a singular and definite, albeit as yet undetermined, yes or no answer. However, the contrasting kinds of arguments presented by these different authors would suggest that the field of comparative social learning still lacks any universally accepted solutions. Since studies of social learning across different species have become increasingly common in recent years (e.g. Box and Gibson 1999; Galef 1988; Heyes and Galef 1996; Heyes and Ray 2000; Miklosi 1999; Nicol 1995; Russon 1997; Tomasello et al. 1993; Webster and Fiorito 2001; Whiten and Ham 1992; Zentall 2001), this review aims to outline both the potential theoretical value and the likely pitfalls that are entailed in a comparative approach.

Before we begin to review the area of comparative approaches to social learning, we should ask why researchers are, or perhaps might be, interested in taking such an approach. The body of literature on social learning in animals is now vast and still growing rapidly, and interest in the topic comes from a wide variety of theoretical perspectives. For instance, some researchers have been interested in issues of welfare (e.g. Cloutier et al. 2002; Munksgaard et al. 2001), or issues of rehabilitation (e.g. Beck 1997; Box 1991; Custance et al. 2002), and of course these are questions that are not only of scientific interest, but also extremely important from a practical point of view. However, this review will be concerned only with research that is explicitly comparative, rather than merely “comparative” in the sense that the subjects are non-human, which is the case in many of these applied studies, as well as others.

Social learning in this review refers to any situation in which the behaviour, or presence, or the products of the behaviour, of one individual influence the learning of another. Thus the term social learning itself implies nothing about underlying mechanisms, which remain to be identified. However, many authors have differentiated several

C.A. Caldwell (✉)
School of Psychology, Washington Singer Laboratories,
University of Exeter,
Exeter EX4 4QG, UK
e-mail: C.A.Caldwell@exeter.ac.uk,
Tel.: +44-1392-264694, Fax: +44-1392-264623

A. Whiten
Centre for Social Learning and Cognitive Evolution
and Scottish Primate Research Group, School of Psychology,
University of St Andrews,
St Andrews, Fife KY16 9JU, UK

possible forms of social learning, in terms of the mechanisms potentially involved (e.g. Galef 1988; Heyes 1994; Whiten and Ham 1992; Zentall 2001). To attempt here to cover all of the proliferating terms and definitions used in recent years would therefore be somewhat futile. We shall briefly describe three that have been commonly referred to in the literature. “Stimulus enhancement” (e.g. Galef 1988; Spence 1937; Whiten and Ham 1992) is said to have occurred when the presence of an individual draws an observer’s attention to a particular object or part of an object, thus enhancing the observer’s opportunity to learn about the object. In “emulation” (Tomasello et al. 1987; Whiten and Ham 1992) the learner gains information from observing a demonstration, but in achieving the same goal, may use a different method. It should be noted that many different subclasses of emulation are now being discerned, and its role in relation to other forms of social learning debated. Comprehensive coverage of these issues can be found in Custance et al. (1999) and Whiten et al. (2002). One of these proposed subclasses of emulation, object movement re-enactment, will be discussed later in this review.

Imitation, however, “learning to do an act by seeing it done” (Thorndike 1898, p. 50; Whiten and Ham 1992), is often said to be the most cognitively complex form of social learning (e.g. Byrne 1995; Galef 1988; Heyes 1993). As this review is concerned in particular with the cognitive processes underlying social learning (and methodological issues associated with investigating these), it is therefore imitation specifically that will form the main focus of this article from now on.

It should be noted at the outset that this review is by no means intended to represent an exhaustive catalogue of research on social learning (or even imitation) in animals. Rather, the examples given have been selected for their particular pertinence to the points that we wish to make as part of our examination of methodological approaches to the comparative study of social learning. We do not wish to give the impression that we have overlooked certain species or phyla, or that we consider the issues raised here to have only selective relevance. Indeed, we very much hope that the reverse is the case and that our argument will prove useful to a broad range of researchers.

Theoretical perspectives

So far in the literature, we discern three main theoretical motives for comparing the relative social learning skills of different species. The first of these we shall label the *phylogenetic perspective*, which involves the evolutionary tracing of a collection of socio-cognitive abilities, believed to be related. The second we call the *animal model perspective*, which is principally concerned with identifying a suitable animal model for the study of imitation as a general phenomenon. And finally there is the *adaptationist perspective*, whose main aim is to investigate the functional significance of social learning, such as the question of whether there is a relationship between social learning and living in social groups.

The phylogenetic perspective

Under this perspective, cognition is studied from a phylogenetic viewpoint, the basic premise being that similar cognitive abilities found in closely related species were likely inherited by each from a common ancestor whose mental capacities can thereby be reconstructed. Research therefore encompasses the identification of both ancestral commonalities and evolutionary differentiation. This approach is set out with great clarity by Byrne (1995), who concludes that, “with the aid of the comparative method, the evolutionary history of a trait – even a behaviour that leaves no trace to fossilise – can be inferred from its pattern of occurrence in surviving animals” (p. 6).

Researchers taking this perspective are typically interested in a whole suite of socio-cognitive skills, including theory of mind, self-awareness, and pretence, and may view imitation as a part of this combination of skills (e.g. Parker 1996; Suddendorf and Whiten 2001; Tomasello and Call 1994; Whiten and Byrne 1991). From this perspective, then, the most interesting aspects of social learning are the underlying cognitive abilities. This approach has therefore generally disregarded issues of function or social context and focussed almost exclusively on analysing cognitive mechanisms in the individual social learner.

It seems to be universally accepted that human beings are the most imitatively prolific species (e.g. Meltzoff 1988, 1996), and the phylogenetic approach has generally been characterised by an expectation that the other great apes will be most likely to share imitative abilities with humans, with other taxa following in accordance with their closeness of relationship with *Homo sapiens*. Although this view is not always made explicitly apparent, the viewpoint may be manifested either in terms of research focus (selection of great ape subjects for the investigation of animal imitation (e.g. Nagell et al. 1993; Tomasello et al. 1993; Whiten 1998; Whiten et al. 1996), or by a judgement (despite the relative scarcity of imitation research on many primate species) that human beings and great apes show advanced forms of imitation, not shared by monkeys (e.g. Byrne 1995; Parker 1996; Russon et al. 1998; Whiten and Byrne 1991; Whiten and Ham 1992).

The animal model perspective

Like the phylogenetic perspective, the animal model perspective is also concerned primarily with cognitive processes, and the two approaches thus share a common goal of identifying imitative ability in non-humans. In contrast to the phylogenetic perspective, where the interest lies in patterns of evolutionary change, the animal model perspective strives to identify similarities. The approach is motivated by the hypothesis that imitation may be a special case of associative learning, hence potentially available to many species.

Heyes (1994) places imitation within the framework of animal learning theory, as a case of response-reinforcer

learning, where “it is the demonstrator, not the learner, who makes the response that is learned” (p. 225). Heyes and Ray (2000) take this idea further, proposing a new theory of imitation, the associative sequence learning (ASL) theory. The ASL model suggests that “development of the imitation mechanism is highly experience-dependent” (Heyes 2001, p. 258). Therefore we should not necessarily expect imitative ability to have any phylogenetic specificity. And any individual, regardless of species, would be unable to imitate had the appropriate prior experience been unavailable to it.

Purely experiential theories of imitation are by no means radical, earlier incarnations having been proposed by Holt (1931) and Miller and Dollard (1941), amongst others. Another was recently proposed by Laland and Bateson (2001), who use a connectionist model under which imitative processes are generated purely on the basis of the experience of synchronous behaviours. As Laland and Bateson point out, what sets these models apart from the models typically proposed by those working from the phylogenetic perspective (e.g. Tomasello and Call 1997) is that they require no “‘black box’ that is assumed to pre-exist, and to be capable of complex cognition” (p. 197).

From this perspective, therefore, there are two main reasons why researchers have been interested in comparative data on imitation. Firstly, under the assumption that imitation is an experience-dependent process common to many animals, models of imitation could be tested using a single, well-chosen species. This animal model could then allow an understanding of imitation generally, in all animals, including humans. This rationale is made most explicit by Heyes and Ray (2000), who state, “the principal significance of imitation in animals lies in its potential to provide insight into the psychological mechanisms of imitation learning” (p. 242). Heyes and Ray (2000), therefore, go on to review the data on imitation in animals for the purpose of determining which species would provide the most appropriate model, based on prior demonstration of their imitative ability, and practical considerations regarding their suitability as a lab animal. In addition to this motivation, however, the models proposed by Heyes (2001) and Laland and Bateson (2001) also give rise to certain predictions about which animals would be likely to be proficient imitators: those that typically perform behaviours in synchrony, such as gregarious bird species, are proposed in both articles to be the likeliest candidates. Accordingly, both Heyes (2001) and Laland and Bateson (2001) have discussed data on imitation in several different species in terms of the predictions made by their models.

The adaptational perspective

The adaptational perspective is concerned with resolving the issue of whether social learning is a specialised adaptation associated with social living, or purely an aspect of more general learning processes. Thus far, the majority of recent research stemming from this perspective has been

produced by Lefebvre and colleagues (e.g. Lefebvre and Giraldeau 1996; Lefebvre et al. 1996; Reader and Lefebvre 2001). However, interest in the possibility of social learning as an adaptive specialisation dates back over 40 years, when it was first suggested by Klopfer (1959, 1961). More recently, adaptive specialisation explanations of a wide variety of cognitive and learning processes have become increasingly popular (e.g. Sherry and Schacter 1987; Shettleworth 1993, 1998), and these have been followed by a corresponding resurgence of interest in this approach to social learning (e.g. Lefebvre et al. 1996, 1997; Templeton et al. 1999). The basic prediction of an adaptive specialisation view of learning and cognition is that interspecific variation in learning and/or cognitive ability should correspond to species diversity in terms of ecology. This view of social learning therefore predicts that, as Klopfer (1959) originally suggested, the most proficient social learners will be those species that live in social groups and those that forage opportunistically.

This perspective is therefore concerned primarily with the function of social learning, as opposed to the mechanism, which is the focus of interest of the previous two perspectives. It follows, then, that a further difference between this approach and the others is that this one tends to emphasise social learning generally, rather than just the mechanism of imitation. However, several researchers have made the more specific suggestion that imitation may itself represent an adaptive specialisation (e.g. Lefebvre et al. 1997; Parker 1996; Russon et al. 1998). Like social learning generally, it is suggested that this skill will be more likely to be found in highly social species (those that live in groups, or those that engage in scramble competition when feeding). More specifically, however, it will only be those species that use complex, difficult-to-learn food searching and handling techniques that possess imitative skill, as opposed to just general social learning abilities. Since the present review is principally concerned with the issue of making meaningful comparisons of social learning mechanisms, the arguments presented will be most relevant to this more specific issue of imitation, in relation to the adaptational perspective, rather than social learning generally.

Overview

We have contrasted three different perspectives on the comparative study of social learning. This will not be a perfectly neat division and some workers may feel they cannot be so clearly pigeon-holed, or do not subscribe to the “typical” characteristics we describe, but we hope our typology will prove useful in recognising the diversity of perspectives that exist and need to be reconciled if an integrated comparative psychology of social learning is to be achieved.

Each of the models is firmly grounded in evolutionary theory, although they emphasise to differing extents the forces of continuity of descent versus specialisation of adaptation. The animal model perspective, viewing imita-

tion as an ability based on relatively general learning processes, obviously emphasises continuity of descent. The adaptational perspective, however, entertains the possibility that imitation and/or social learning are highly specialised adaptations. The phylogenetic perspective views imitation as a specialised adaptation only in the sense that it comes as part of a compound skill package that has proven particularly valuable in a subgroup of the primate order. In this regard, this perspective also acknowledges continuity of descent, as it is assumed that closely related species are likely to share imitative ability. The phylogenetic and adaptational perspective are therefore perhaps best contrasted in terms of Timberlake's (1993) classification of methods of comparing behaviour, the adaptational approach being primarily concerned with evolutionary convergence, and the phylogenetic approach focussing on homologies.

It is not the intent of this review to weigh up the relative merits of the differing perspectives, but rather to consider what kinds of comparative research may be needed to assess their merits, and perhaps better investigate this in future. We firmly believe that the issue of which of these perspectives brings us closest to the truth is still open to question, and more importantly, open to empirical question. It seems clear that the different perspectives are currently, to varying extents, somewhat incompatible with one another. For instance, writers within the phylogenetic perspective often seem to expect that imitation will be found in humans, and then, with ever-decreasing likelihood, in other great apes, old world monkeys, other monkeys, other primates, and so on (see Parker and Gibson 1979 for a review that suggests imitation, amongst other cognitive skills, might show this pattern of distribution). Clearly this is incompatible with the "animal model" view that we can pick any appropriate species and investigate imitation as a general phenomenon. According to the adaptational perspective, again we might not necessarily expect a primate bias, and yet, it would certainly not predict that imitation would be a general phenomenon. Each of the theories therefore generates slightly different predictions about which species would be likely to imitate. However, as yet, the comparative approach to imitation has not provided data that would allow us to assess reliably the relative merits of the different viewpoints.

One reason why research to date does not allow us to draw such conclusions is that work from each viewpoint has tended to reflect underlying assumptions, rather than explicitly testing them. In work from the phylogenetic perspective, discussion does occur over the phylogenetic appearance of imitation (e.g. Parker and Gibson 1979) but it is treated as a given that the data can be used to infer where, phylogenetically, imitation must have appeared as a skill. The animal model perspective has used comparative data to address the question of whether imitation could be a product of general learning processes (Heyes 2001; Laland and Bateson 2001), but the idea that a suitable animal model can be found (Heyes and Ray 2000) suggests that a positive answer has already been assumed. It seems that, just as work from the phylogenetic perspec-

tive has a tendency to assume that certain species are incapable of imitation, the opposite is true of the animal model perspective, whose researchers are prepared to assume that imitative ability is shared by many species (albeit that existing data may be considered an inadequate demonstration of such; e.g. Heyes 1993). Neither of these perspectives has as yet been used to generate novel predictions about how different species might perform that would differentiate between alternative perspectives. The adaptational perspective appears to have the best track-record in hypothesis testing, as work from this perspective has set out expressly to test whether social learning is a specialised adaptation. However this is not yet true for complex forms of social learning like imitation, with which this review is principally concerned. Lefebvre et al. (1997) claim to show support for an adaptive specialisation view of imitation. However, as only one species is tested, the data do not allow us to differentiate between alternative explanations. Comparisons of at least two species (for which opposite predictions would be made) are required.

Even when species have been compared with the intention of testing predictions, there may still be ambiguities of interpretation. For instance, researchers investigating adaptational hypotheses in terms of general social learning abilities have noted that social living biases could arise from experience, rather than specialised genetic disposition. Animals that live in groups obviously have more opportunities to learn that attending to group members can reap rewards, and these animals may show greater tendencies to learn socially as a result. Following this line of reasoning, Templeton et al. (1999) suggest that their results, supporting the adaptational hypothesis in corvid species, could be explained in terms of either adaptive specialisation or "simply the result of ontogeny" (p. 454). Carlier and Lefebvre (1996) point out that "differences in foraging ecology may lead to different learned responses to local reward contingencies as well as natural selection for different genotypes affecting learning. In some cases, the standard comparative prediction of ecologically correlated learning differences may therefore not distinguish between adaptive specialisation and general process theories" (p. 1197). In fact some work from this perspective has provided support for experiential models of social learning. Dolman et al. (1996) found that Zenaida doves from a gregarious population learned more effectively from conspecific tutors, whereas individuals taken from a territorial population exhibited a stronger learning effect when the tutor was a heterospecific. The doves were therefore learning from the species that they would have tended to encounter most often in past non-aggressive foraging situations. Dolman et al. (1996) conclude that the results "suggest that social learning pathways in Zenaida doves are flexible rather than species-specific" (an interpretation that is clearly eminently compatible with the experiential models).

It may emerge that there is more than a grain of truth in the assumptions and expectations associated with each one of the perspectives. Some authors have already presented viewpoints that endeavour to reconcile a phyloge-

netic and adaptational interpretation of imitation, for example. Russon et al. (1998) view imitation as a specialised adaptation occurring in social species that feed on embedded substrates, but they account for the particular imitative facility of great apes in terms of their requiring a highly complex suite of socio-cognitive abilities. "This review leaves an image of imitation as a heterogeneous rather than a homogeneous phenomenon; even mentally, and in only one of the three evolutionary lines that appear to have generated it, it appears to operate via complex sets of mechanisms that incorporate cognitive, motivational, social, and perceptual processes" (p. 133). A similar view is expressed by van Schaik et al. (1999) and by Parker (1996), who proposes that imitation, teaching, and mirror self-recognition evolved in the great apes due to the need for extractive foraging based on "intelligent tool use".

Methodological approaches

As we have seen, there are several reasons why researchers have been interested in a comparative psychology of social learning, and this has generated numerous publications that treat data on imitation from one of the comparative perspectives mentioned above. There have been two main types of methodological approach to this, these being (1) the comparative experiment, in which two or more species are subjected to approximately analogous procedures; and (2) the comparative analysis of results already accumulated in the literature. In the latter, data are evaluated on different species, which have been studied under often quite different conditions. A further, extremely prom-

ising comparative approach to social learning also merits note here. This is the method of systematically reviewing the *total number* of published reports of social learning. This approach is best exemplified by Reader and Laland's (2002) analysis of the relationship between brain size and social learning in primate species. However, this approach is geared towards evaluating a species' *propensity* towards social learning and can tell us very little about cognitive mechanisms. Lefebvre and Bouchard (2002) have used a similar methodology to investigate social learning in birds, and as they point out, much of the data comes from anecdotal reports from amateur observers. We shall therefore concentrate on the first two approaches in this review.

To date, only four research groups have published systematic comparative experiments applying similar tasks to different species. However, many researchers working from different perspectives have carried out comparative literature reviews concerned with the specific issue of imitation and we consider these first.

Accordingly, Table 1 collates details of reviews of imitation in animals, showing the populations that were judged by the authors to have shown evidence of imitation, and also those for which the authors judged the evidence to be either lacking or insufficient. Particular studies that the reviewers cited in support of their conclusions are listed and detailed in the table footnotes. It should be noted that the later reviews have of course been influenced by research that was not published when some of the earlier reviews were written.

Table 2 turns to the experimental literature and displays details of experiments in which more than one spe-

Table 1 Imitation literature reviews. Species listed are those that were explicitly stated in the text of the listed article^a as having displayed either positive evidence of imitative ability or a lack of/insufficient evidence of imitative ability

Article/chapter	Authors' judgement	
	Positive evidence of imitation	Lack of/insufficient evidence of imitation
Galef (1988)	Budgerigars ^{9, 12}	Pigeons ²⁸
Whiten and Ham (1992)	Chimpanzees ^{14, 18, 20} ; dolphins ³⁰	Monkeys ^{15, 16} ; orangutans ^{11, 34} ; gorillas ⁶ ; rats ²¹ ; budgerigars ^{9, 12} ; pigeons ²⁸
Heyes (1993)	Rats ^{21, 22} ; budgerigars ^{9, 12}	
Byrne (1995)	Parrots ²⁶ ; orangutans ²⁹ ; chimpanzees ¹⁹ ; gorillas ³ ; dolphins ³⁰	Rats ^{21, 22}
Byrne and Tomasello (1995)	Apes ^{19, 29}	Budgerigars ¹² ; rats ^{21, 22}
Tomasello and Call (1997)	Human children ²⁴ ; human raised apes ^{19, 31}	Rats ^{21, 22}
Shettleworth (1998)	Chimpanzees ³³	Rats ^{21, 22} ; orangutans ⁴ ; pigeons ³⁶ ; quail ¹ ; parrots ²⁶
Heyes and Ray (2000)	Pigeons ³⁶ ; quail ¹	Marmosets ² ; chimpanzees ^{27, 32, 33} ; capuchins ⁸ ; rats ^{13, 25} ; budgerigars ^{9, 12} ; starlings ⁵ ; carib grackles ²³
Zentall (2001)	Pigeons ³⁶ ; quail ¹ ; parrots ²⁶ ; chimpanzees ^{7, 19} ; dolphins ^{17, 35}	Capuchins ⁸ ; budgerigars ^{9, 12} ; rats ^{21, 22} ; starlings ⁵ ; marmosets ² ; ravens ¹⁰

^a Original references: ¹Akins and Zentall 1996; ²Bugnyar and Huber 1997; ³Byrne and Byrne 1993; ⁴Call and Tomasello 1994; ⁵Campbell et al. 1998; ⁶Carpenter 1973; ⁷Custance et al. 1995; ⁸Custance et al. 1999; ⁹Dawson and Foss 1965; ¹⁰Fritz and Kotrschal 1999; ¹¹Galdikas 1982; ¹²Galef et al. 1986; ¹³Gardner 1997; ¹⁴Gardner and Gardner 1969; ¹⁵Hall 1963; ¹⁶Ham 1990; ¹⁷H.E. Harley et al., unpublished manuscript (see also Herman 2002); ¹⁸Hayes and Hayes 1951; ¹⁹Hayes and Hayes 1952; ²⁰Hayes

and Hayes 1953; ²¹Heyes and Dawson 1990; ²²Heyes et al. 1992; ²³Lefebvre et al. 1997; ²⁴Meltzoff 1988; ²⁵Mitchell et al. 1998; ²⁶Moore 1992; ²⁷Myowa 1996; ²⁸Palameta and Lefebvre 1985; ²⁹Russon and Galdikas 1993; ³⁰Taylor and Saayman 1973; ³¹Tomasello et al. 1993; ³²Whiten 1998; ³³Whiten et al. 1996; ³⁴Wright 1972; ³⁵M.J. Xitco et al., unpublished manuscript (see also Herman 2002); ³⁶Zentall et al. 1996

Table 2 Comparative experimental studies of social learning

Research group	Article	Species compared	Task	Demonstration	Results and authors' conclusions
Tomasello	Nagell et al. 1993	<i>Pan troglodytes</i> , <i>Homo sapiens</i> (2 and 3 years old)	Tool use (raking in out of reach reward)	Adult human demonstration. Each subject sees one of two methods of raking in reward.	All groups were more successful following demonstration. Two-year-old children reproduced demonstrated method, but chimpanzees did not. <i>Authors' conclusion</i> : chimpanzees pay attention to task rather than the actions of a demonstrator.
	Tomasello et al. 1993	<i>P. troglodytes</i> , <i>P. paniscus</i> (two <i>Pan</i> species combined, rather than compared), <i>H. sapiens</i> (18 and 30 months old)	Manipulation of 16 novel objects	Adult human demonstration. Each subject sees two actions on each object and is asked (or has been given prior behavioural training) to "do what I do".	Children were judged to have matched the demonstrator's actions more closely than the non-human subjects did, apart from apes that had been raised by humans, which performed at the same level as the children. <i>Authors' conclusion</i> : a human-like socio-cultural environment is an essential component in the development of human-like imitative learning skills.
	Call and Tomasello 1994	<i>Pongo pygmaeus</i>	Replication of Nagell et al. 1993	Replication of Nagell et al. 1993	There was no effect of demonstration type on the actions performed by the subjects. <i>Authors' conclusion</i> : orangutans, like the chimpanzees, were paying attention to the task rather than to the actions of the demonstrator.
Whiten	Call and Tomasello 1995	<i>P. pygmaeus</i> , <i>H. sapiens</i> (3 and 4 years old)	Puzzle box containing reward	Adult human demonstration and conspecific demonstration. Each subject sees one of four different actions on the apparatus to obtain a reward.	Human children reproduced the actions of the demonstrator. Orangutans did not and, as a consequence, had a very low rate of success. <i>Authors' conclusion</i> : orangutans are not able to learn an instrumental task through observation.
	Whiten et al. 1996	<i>Pan troglodytes</i> , <i>H. sapiens</i> (2, 3, and 4 years old)	"Artificial fruit" (box containing food reward with single locking mechanism)	Adult human demonstration. Each subject sees one of two methods of unlocking apparatus to obtain reward.	Chimpanzees reproduced demonstrator's method on one component of the task but achieved demonstrated outcomes through their own techniques more than the children (all age groups). <i>Authors' conclusion</i> : results are evidence of imitation in the chimpanzee, although human children imitate with greater fidelity.
Whiten	Whiten 1998	<i>P. troglodytes</i>	"Artificial fruit" (box containing food reward with multiple locks)	Adult human demonstration. Each subject sees one of two methods of unlocking apparatus, and one of two sequential patterns of defence removal.	Chimpanzees reproduced both the sequential structure of the actions, and aspects of the techniques that made up the sequence. <i>Author's conclusion</i> : Results are evidence of imitation of a novel behavioural sequence in the chimpanzee.
	Custance et al. 1999	<i>Cebus apella</i>	Replication of Whiten et al. 1996	Replication of Whiten et al. 1996	Capuchins reproduced the demonstrator's method on one component of the task. <i>Authors' conclusion</i> : results are evidence of simple imitation, or possibly "object movement re-enactment" in the capuchin monkey.
Caldwell et al. 1999	Caldwell et al. 1999	<i>Callithrix jacchus</i>	Approximate replication of Whiten et al. 1996 ^a	Conspecific demonstration. Each subject saw one of two actions on the apparatus.	Marmosets did not reproduce the actions of the trained model. However, groups were compared according to how closely their behaviours matched those of their model, and corresponding differences were found. <i>Authors' conclusion</i> : results are suggestive of imitative ability in the marmoset. However, chimpanzees and capuchin monkeys imitate the task with a much greater degree of fidelity.
				Replication of Whiten 1998	Gorillas reproduced the demonstrator's technique on one component of the task but did not reproduce the sequential structure of the actions. <i>Authors' conclusion</i> : results show evidence for imitation in gorillas, on a par with that shown by chimpanzees, but, unlike chimpanzees, no evidence of imitation of the behavioural sequence.
Stoinski et al. 2001	Stoinski et al. 2001	<i>Gorilla gorilla gorilla</i>	Replication of Whiten 1998	Replication of Whiten 1998	Gorillas reproduced the demonstrator's technique on one component of the task but did not reproduce the sequential structure of the actions. <i>Authors' conclusion</i> : results show evidence for imitation in gorillas, on a par with that shown by chimpanzees, but, unlike chimpanzees, no evidence of imitation of the behavioural sequence.

Custance et al. 2001	<i>Pongo pygmaeus</i>	Replication of Whiten 1998	No significant overall matching tendency, but a correlation between age and degree of matching. <i>Authors' conclusion</i> : results show possible imitative ability in orangutans, limited to those aged 5 and over.
Bering and Bjorklund	<i>Pan troglodytes</i> , <i>Pongo pygmaeus</i>	Deferred imitation of seven actions on objects	Both species reproduced demonstrated actions, following a 10-min delay, on approximately half of the trials. <i>Authors' conclusion</i> : juvenile great apes raised in human-like conditions possess cognitive abilities that allow deferred imitation.
Bjorklund et al. 2000	<i>Pan troglodytes</i> , <i>Pongo pygmaeus</i>	Longitudinal study of deferred imitation (data from Bering et al. 2000, compared with performance on failed items and four new items 2 years later)	Chimpanzee subject showed an improvement in reproduction of demonstrated actions with age. Orangutan subject did not show a significant improvement. <i>Authors' conclusion</i> : juvenile chimpanzees, like human children, show Piagetian stages of sensorimotor development. Orangutan subjects may have already reached a "mature", although less competent than the chimpanzee, level of performance at initial testing.
Zentall	<i>Columbia livia</i>	Treadle-press task	A correlation was found between the responses seen and those produced by subjects. <i>Authors' conclusion</i> : results are evidence of true imitation in pigeons.
Zentall et al. 1996	<i>Coturnix japonica</i>	Replication of Zentall et al. 1996	A correlation was found between the responses seen and those produced by subjects. <i>Authors' conclusion</i> : results are evidence of true imitation in quail.

^a See section on behavioural propensities

cies has been tested using the same procedure. However, the table does not cover *all* of those examples in the literature of imitation studies involving more than one species (many of which predate those publications listed, e.g. Haggerty 1909; and see tables in Tomasello and Call 1997; and Whiten and Ham 1992). Examples included are those that are explicitly testing for species differences, rather than combining the data on more than one species to investigate, for example, imitation in non-human primates as a group.

The first research group to publish comparative experiments on imitation was that of Tomasello and colleagues. Their research has focussed on the great apes and children and has generally concerned the imitation of practical, goal-directed actions involving tool use. Table 2 shows brief details of each of these studies. Our own research group has also been engaged in comparative experimentation, and details of these publications, the majority of which have involved only one species are also presented in the table. However, our group has treated the data comparatively insofar as the same (or at least similar – a point returned to below) testing devices ("artificial fruits") were used in each, to test for imitation in a variety of primate species, including human children. These devices have also been used by other researchers studying keas (Huber et al. 2001) and adult human subjects (Horowitz 2001). Table 2 shows details of studies published by Bjorklund et al. (2000) and Bering et al. (2000). These studies have involved object manipulation and have compared the developmental stages of imitative ability in chimpanzees and orangutans. We have also included in the table research by Zentall and colleagues on pigeons and quail, as both studies (like our artificial fruit experiments) used the same apparatus design, involving treadle-press behaviours for a food reward.

Tables 1 and 2 point to one fairly obvious conclusion: despite all attempts to forge a coherent comparative psychology of imitation, it is far from being established. Even the briefest inspection of Table 1 shows that authors disagree on the correct interpretation of the data. We are therefore left with the question of how best to proceed in research on social learning so we can make comparisons that are valid and as unambiguous as possible, to converge on conclusions that can be generally agreed upon by the scientific community.

Comparative literature reviews

Despite the obvious disagreement between researchers as to which species have and have not been shown to imitate, six of the nine reviews referred to in Table 1 (Galef 1988; Heyes 1993; Heyes and Ray 2000; Shettleworth 1998; Whiten and Ham 1992; Zentall 2001) all select the same preferred method of testing for imitation [but see Byrne (2002) for a contrary view]. Each of these authors refers to the "two-action test" as the most powerful possible control for social learning effects other than imitation. The two-action test was initially employed by Thorndike

(1911/1970; cited in Shettleworth 1998), who wished to establish whether chicks could imitate a method of escaping from a box. He therefore designed the box such that there were two alternative ways in which this could be done. If observing chicks tended to use the method that they had seen, then it could be concluded that they had imitated. The method was then used by Dawson and Foss (1965) and was later identified by Galef (1988) as the standard for tests of imitative ability.

As well as having been used to study imitation in animals, two-action research designs have also been employed to investigate human neonatal imitation (e.g. Meltzoff and Moore 1977, 1983). This type of design is referred to as the “cross-target method” (Meltzoff 1996; Whiten 2002) within developmental psychology. The fact that this methodology appears to have been independently conceived within an entirely separate field of investigation only serves to further emphasise its power and practicality as a test for imitation.

However, despite some agreement that the two-action method offers the possibility of a gold standard within imitation research, authors are still in disagreement about the interpretation of such research designs. Essentially, the differences of opinion occur because researchers differ in their views of which aspects of social learning are cognitively significant, and therefore merit inclusion within their definition of imitation. The aim of the following sections is to detail which aspects of task designs researchers have considered to be crucial and to illustrate how this has influenced their interpretation of the literature.

Perceptual opacity

One aspect of response type that has been interpreted as cognitively complex by several authors is the level of *perceptual opacity* (Heyes and Ray 2000), or the degree to which the perception of oneself performing an action matches that afforded when observing the action demonstrated by another individual. Heyes (1993) gives the example of curtsying. “If I look down when I curtsy, I see something very different from what I see when I look across at somebody else curtsying” (Heyes 1993, p. 1006). Imitating a perceptually opaque action therefore involves translating visual input into motor output, the main feedback being in the form of kinesthetic information (e.g. Mitchell 1994). Heyes and Ray (2000) suggest that all actions belong somewhere along a continuum of perceptual opacity, with the most opaque actions being those that are actually invisible to the actor, such as head movements and facial gestures, and the most transparent being distal appendage movements, for which the performer has access to rich visual feedback.

Heyes (2001) identifies this issue as particularly significant in terms of the cognitive demands in imitation:

Many of the psychological requirements for imitation (e.g. detection and analysis of others’ movements, memory, motor control) are also prerequisites for other types of behaviour. The requirement that is unique to

imitation, and therefore the distinctive exploratory challenge for theories of imitation, is a mechanism that can translate visual information about the body movements of others into matching motor output. (p. 256)

Whiten and Ham (1992) also argue that imitation of perceptually opaque actions is cognitively complex, in that the action must be “re-represented in its original organizational form” (p. 271) by the imitator. On this basis, they also argue that vocal imitation is less cognitively demanding than movement imitation:

In song learning, the bird does not have to represent what is in effect the model’s representation of the act as it does in the case of visual imitation; instead, it need only adjust its own output until the sound of this matches what it originally heard (one level of representation). This may be an extra dimension in visual imitation that makes it more demanding than vocal imitation in its computational requirements. (p. 272)

Similarly, Heyes and Ray (2000) include vocalisations as examples of highly transparent actions on their continuum of perceptual opacity, and Zentall (2001) describes vocal imitation as “relatively easy” (p. 69).

Object movement re-enactment

Zentall (2001) takes the perceptual opacity argument slightly further, to argue that copying of highly transparent actions can be accounted for simply in terms of “stimulus matching”, where the observer need only make an association between two sensory stimuli to reproduce the behaviour, as exemplified by, “observing someone turning up the volume of a radio – when the knob turns to the right, the volume increases” (p. 69). This type of process (which can take perceptual transparency to its extreme, involving no need for matching of bodily movements but only the matching of the environmental effect of a behaviour), has been described by Custance et al. (1999) as “object movement re-enactment”. The observer learns about how an object or parts of an object move, and if the object’s movements are associated with a desirable outcome, the observer may be motivated to try to recreate it. On this basis, Heyes (1998; Heyes and Ray 2000) has suggested that data presented in Whiten et al.’s (1996) chimpanzee artificial fruit experiment do not qualify as imitation, because the observer may be copying only movements of parts of the fruit as it is dismantled. Tomasello (1996) makes a similar criticism, labelling this effect “emulation learning”, rather than object movement re-enactment.

However, some authors have argued that the imitation/object movement re-enactment distinction so implied is a misleading one. Whiten (2000) argues that imitation and certain emulative effects, like object movement re-enactment, should be viewed as a continuum rather than a dichotomy. Whiten and Custance (1996) suggested that, in tool use for example, copying could occur either at the level of limb movement, or at the level of tool movement.

The tool could be regarded as an extension of the limb, and its actions imitated in a similar way. Furthermore, researchers have argued that such social learning about objects may be cognitively complex in its own right (e.g. Byrne and Russon 1998; Tomasello 1998; Whiten and Ham 1992, although in these cases the learning referred to may go beyond what could strictly be defined as object movement re-enactment, involving some understanding of tool function and/or causality).

Novelty

Another feature that some researchers have identified as being crucial to the nature of imitation is the novelty of the response. Thorndike's original definition of imitation was "learning to do an act by seeing it done". On this basis, some (e.g. Byrne 1995; Byrne and Tomasello 1995) have argued that the imitated response must be a novel one, or it cannot be described as having been *learned* through imitation.

It is important to all researchers to distinguish imitation from social facilitation, in which nothing new is learned. Social facilitation (e.g. Galef 1988; Thorpe 1963; Whiten and Ham 1992; Zajonc 1965) is generally used to describe a contagious behaviour, in the sense that an individual's response acts as a releaser for the same response on the part of a conspecific. Examples of such responses include yawning in humans, or synchronous nervous flight in birds. However, Byrne (1994) extends the category of social facilitation, labelling it *response facilitation*, in which, "the probability of occurrence of an established behaviour pattern is temporarily increased in the individual's spontaneous repertoire after observation of the same behaviour pattern in a conspecific" (Byrne and Tomasello 1995, p. 1417). Thus, response facilitation would operate, via a priming process (Byrne 1995, 2002), on *any* response, as opposed to being limited to certain involuntary species-typical behaviours. On this basis Byrne (1995) and Byrne and Tomasello (1995) do not consider Heyes' (Heyes and Dawson 1990; Heyes et al. 1992) bidirectional control experiment with rats to be evidence of imitation, as the responses required were not novel. Byrne and Tomasello (1995) also reject Galef et al.'s (1986) budgerigar data for the same reason.

However, other researchers have argued that novelty may be a more problematic criterion than researchers such as Byrne and Tomasello have acknowledged (or, for that matter, demonstrated). It is very difficult to assess the full behavioural history of an individual to be sure that an action is truly novel, and even then, this may not satisfy some. Byrne (2002) criticises evidence of human neonatal imitation (Meltzoff and Moore 1977, 1983) as the actions involved are only novel in the "trivial sense that the infant has never performed them, but there is no doubt that the facial movements are in the child's latent repertoire" (p. 85).

Whiten and Cusance (1996) have argued that novelty cannot be reduced to an all-or-nothing matter, since an in-

dividual will probably have produced, at one time or another, all of the muscular movements of which it is physically capable. This makes novelty an issue of recombination of actions, or employing actions in novel contexts, where there will always be some degree of similarity to what the imitator has done before. Zentall (2001) agrees that an existing response directed at a novel object satisfies the novelty criterion and furthermore has advocated the use of an additional criterion: the baseline (no demonstration) probability of the behaviour must be very low. This is consistent with one of the most frequently quoted definitions of imitation: Thorpe's (1963) "reproduction of a novel *or otherwise improbable* act" (p. 122). Indeed, it appears that this latter criterion is now widely accepted within the field of social learning. A similar recommendation is made by Miklosi (1999). Furthermore, refereed articles have been published entitled "true imitation", based on the reproduction of responses that, although part of the existing repertoire, have been shown to be infrequent during control tests (e.g. Voelkl and Huber 2000; Zentall et al. 1996). Laland and Bateson (2001) have argued against the use of novelty as a criterion altogether, on the basis that if imitation exists as a phenomenon, it should be "perfectly possible to imitate an entirely familiar action in an entirely unfamiliar context" (p. 210).

Sequential structure

Several researchers consider the imitation of a sequence of actions to be cognitively significant, although each has a different reason for proposing this to be the case. Whiten (1998) suggests that imitation of a sequence of actions can be one way to satisfy the novelty criterion, as long as the sequence itself is novel, and the order of the elements is not constrained in any particular way such that the chosen sequence is in fact the most likely approach: "if the sub-component acts ... can be said to be 'in the repertoire', the performance of them so as to match the sequence observed cannot be said to be in the repertoire any more than [a] randomly assigned alternative sequence" (pp. 271–272).

Investigation into imitation of a sequence of actions will also be crucial to testing the ASL theory of imitation proposed by Heyes and Ray (2000). The ASL theory suggests that individuals develop, through experience, an "'imitation repertoire' – a set of action units that can be imitated when observed in novel sequences" (p. 240). Clearly, an ability to imitate sequences of actions must be demonstrated to test this theory. If no such ability can be identified, the theory would be challenged.

Byrne and Russon (1998) have argued that there are in fact two kinds of imitation that are cognitively very different from one another. The first they label *action level imitation*, in which "a novel action is added – as an unmodified whole – to an individual's motor repertoire" (p. 677). The second they call *program level imitation*, which involves the representation of the overall structure of an action sequence, including its ultimate and sub-

subsidiary goals, a process that they describe as “a high-level, constructive mechanism”. On this basis, Byrne (1995) has criticised much of the existing imitation literature for using tasks that are not sufficiently complex, and therefore just tapping into action level imitation, overlooking program level imitation.

As yet, the only empirical demonstration of the ability to imitate an arbitrary sequence, utilising the two-action method, has been Whiten’s (1998) experiment with chimpanzees (although see also Whiten et al. 2002). The subjects in Whiten’s study were shown one of two different methods of accessing a food reward, the component elements having been ordered differently in each. The chimpanzees tended to produce sequences of actions more like the ones they had seen demonstrated.

Demonstrator reinforcement

Miklosi (1999) has pointed out that whether a demonstrator receives reinforcement for a response may have implications for the cognitive processes involved in reproduction of that action. In Miklosi’s view, associative learning models of imitation [such as those proposed by Heyes (1994) and Heyes and Ray (2000), and described above in the section on the animal model perspective] would be challenged by an ability to imitate unrewarded actions. Indeed, Campbell et al. (1998) acknowledge that the issue of demonstrator reinforcement may be a potentially important one in terms of the cognitive processes underlying imitation. They suggest that their subjects (European starlings) may have learned either about a response or about a response–food relationship and suggest that “to distinguish between these two mechanisms it would be necessary to perform an experiment in which the relationship between the demonstrators’ responses and food reward was varied” (p. 157). Using such a method, Palameta and Lefebvre (1985) found that pigeons only performed a demonstrated behaviour if the tutor bird had been rewarded, and more recently, Akins and Zentall (1998) found that observation of demonstrator reinforcement was vital for quail to reproduce a response.

Whiten and Ham (1992) also point out that amongst the many anecdotal reports of imitation in animals, those that involve no apparent reward beyond “imitation for imitation’s sake” (p. 264) are typically the most convincing. These examples do not suffer from the criticism that the same behaviour could simply be acquired via a combination of stimulus enhancement and trial-and-error learning. The investigation of imitation of unrewarded actions need not depend entirely on anecdotal reports, however. Custance et al. (1995) found that chimpanzees would imitate arbitrary unrewarded actions, if trained to do so. Therefore the motivation for imitation can be provided within the experimental paradigm, without requiring that the action itself be intrinsically rewarding.

Goal representation

It could also be argued that, in fact, rational imitation might be quite dependent on identifying the purpose of a behaviour rather than blindly imitating, and according to some authors, the ability to infer and represent another individual’s goal or intention should be a defining component of imitation. Tomasello and Call (1997) draw a distinction between what they label *mimicking* and imitation. Mimicking “requires that the learner perceive and understand ... the bodily movements that another individual has performed”, whereas imitation entails that “the learner must also understand something of the ‘intentional’ relations ... (i.e. how the behaviour is designed to bring about the goal)” (p. 310). Using this criterion of imitation, Tomasello and Call (1997) conclude that there is no evidence for imitation in animals, with the possible exception of some great apes that have been raised in a human environment (see Tables 1, 2).

Experimentally distinguishing between the processes of imitation and mimicking, as defined by Tomasello and Call, however, is intrinsically extremely difficult. Simply arriving at the same goal certainly does not prove that the imitator understands the demonstrator’s intention. A good copy of another individual’s behaviour (whether mimicked or imitated) will tend to bring about the same goal.

Myowa and Matsuzawa (2000) attempted to examine imitation of intention using a variation on the two-action method in which the demonstrator was unsuccessful using one method, and then successful using a different one. Chimpanzees tended to use the method they had seen in the success phase. However, if the subjects perceived “success” (the opening of the manipulated object) as more reinforcing, then this example may simply represent an effect similar to that described by Akins and Zentall (1998), cited in the previous section.

It therefore remains unclear how to investigate this aspect of imitation under controlled experimental conditions. The distinction between mimicking and true imitation has resulted in what may be a distracting over-emphasis on goal-directed behaviours in the imitation literature. As noted in the previous section, reproduction of unrewarded responses may depend on processes distinct from those involved in reward-related copying, and therefore both merit investigation in their own right.

Deferred imitation

The ability to imitate actions some time after the original demonstration has also been viewed as a cognitively significant achievement. Deferred imitation has long been considered to be important in developmental psychology. The Piagetian (e.g. Piaget 1962) stage model asserts that deferred imitation requires “symbolic” representation, that is, the representation of actions in long-term memory stores. Meltzoff (e.g. Meltzoff 1988, 1995) has expressed a similar viewpoint.

Evidence from amnesic patients (e.g. McDonough et al. 1995) has shown that deferred imitation is impaired in

patients with frontal lobe damage that results in impaired declarative memory. These patients are impaired in their ability to consciously recall facts and details, such as an address, but have preserved implicit learning, which allows for the storing of skills, such as the ability to re-trace the route to a particular address. This suggests that deferred imitation and explicit learning may depend on related cognitive mechanisms.

A further reason why deferred imitation may be important to comparative research is that delayed copying may rule out simple social facilitation effects (or response facilitation, see the section on novelty). If the observer's response is not weakened by introducing a delay between demonstration and test, then it is much less likely that the effect is based on contagion, or similar excitatory processes.

It is interesting to note how few studies have set out expressly to test this aspect of imitation in animals. As can be seen in Table 2, Bering et al. (2000) and Bjorklund et al. (2000) tested deferred imitation in chimpanzees by delaying trials by just 10 min following demonstration (and see also Bjorklund et al. 2002). Most imitation research has used "delayed" trials, at least in the sense that trials follow demonstrations, rather than being concurrent. However, as yet the only explicit test of the effect of the length of delay on retention has been Dorrance and Zentall's (2001) experiment with Japanese quail. Using an immediate and a 30-min delay condition, these researchers found the same degree of behaviour matching regardless of the delay. It remains to be seen what length of delay will result in performance deterioration, in any species.

Comparative experiments

Clearly, there are problems associated with comparing performance on the different task designs spread through the animal literature. The different theoretical perspectives and research questions indicated above have resulted in species being tested using very different procedures, and this has often rendered comparison somewhat meaningless. One possible solution (and one that has already been employed in several studies, as evidenced by Table 2) is to compare species using task designs that have been intentionally selected to represent as close a match as possible. We would argue that this is a very worthwhile approach, but initial attempts have been far from perfect.

We should begin by noting that there are considerable difficulties associated with making *any* species comparisons of cognitive ability. Bitterman (1960, 1965b) in particular has discussed the problems associated with disentangling the combined effects of an individual's ability and the task's demands from the individual's performance on that task. Differences in performance could occur for a wide variety of reasons, including sensory, motor, or motivational constraints. For example, a task involving visual stimuli may present a considerably greater challenge to a more olfaction-dependent species such as the rat than

it would to a predominantly visual animal, such as a primate. Bitterman (1965a) referred to such effects as "contextual variables". Bitterman suggested that valid comparisons were nonetheless still possible, using a process of *control by systematic variation* (Bitterman 1960), involving gradual changes to the conditions (e.g. hunger levels) that might confound the detection of differences in the cognitive attribute of interest. However, MacPhail (1982, 1987) has taken this reasoning further, to argue that differences in performance can virtually *always* be accounted for in terms of contextual variables. If differences are still found using systematic variation it remains possible that if such manipulations were carried to even further extremes, the differences might be eliminated. On this basis, MacPhail finds no reason to reject the "null hypothesis" that there are no differences between species in intelligence. As some authors have pointed out (e.g. Goldman-Rakic and Preuss 1987; Kamil 1988), MacPhail's argument effectively prevents us from ever concluding that there might be species differences in cognition, since we can never fully rule out the possibility of "contextual variables".

In the field of social learning, we find that, in addition to the usual obstacles associated with comparing species' cognitive abilities, we are presented with a unique set of particular problems. The issues detailed in the following sections are the ones that we believe to be particularly challenging in social learning research.

Reward motivation

Firstly, variation in motivational levels may play a particularly significant role in social learning research. Virtually all research into social learning has so far involved some kind of rewarded behaviour, so differences between species in levels of motivation for particular reinforcers used in social learning experiments may well result in misleading differences in imitative performance. Dorrance and Zentall (2001), for example, have already found that showing an imitative effect in Japanese quail, *Coturnix japonica*, depended on the motivational state of the observer during the observation period. Quail were allowed to observe a trained model that received food reinforcement for producing either a pecking or a stepping response. Subjects that had been deprived of food prior to this observation tended to reproduce the particular method used by their demonstrator. However, those that had been fed prior to the demonstration showed no tendency to match the behaviour of the demonstrator. Motivational levels thus affected the tendency to imitate.

Social interaction

Social learning experiments have also necessitated placing animals in a social situation that brings with it a new set of complications. They can lead to instances in which, despite imitative competence, animals do not perform in ways that reveal their true ability. Recent data from our

own research, using the artificial fruit methodology, suggest that olive baboons' performance was detrimentally affected by particular social contexts. For example, subordinate individuals perform less proficiently in the presence of dominant individuals (C.A. Caldwell and A. Whiten, unpublished manuscript). The social effects we identified in baboons might confound comparisons with species with less steep hierarchies. In this respect our results are consistent with suggestions made by Coussi-Korbel and Fragaszy (1995), who suggested that socially learned traits would be more readily dispersed through populations with tolerant social structures.

There may also be different, but equally strong social effects involved in experiments using human subjects. Much of the research detailed in Table 2 has entailed comparisons of the performance of great apes with human children. In these experiments, involving demonstrations by an adult human, children may be more strongly subject to social conformity effects. These studies have found that apes are more likely to use their own, idiosyncratic methods of obtaining the task reward. However, this should not necessarily be taken as an indication that they are cognitively incapable of matching behaviours precisely. When great apes are trained to mimic novel behaviours on command (e.g. Call 2001; Custance et al. 1995) it is clear that they *can* reproduce demonstrated actions. Thus, social conformity effects may play a role in the apparent child-ape difference. Interestingly, the conclusion of one of the studies (Tomasello et al. 1993) is that only human-raised apes may be capable of imitation. For these individuals, the subject-demonstrator relationship is likely to be more similar to that of human children, compared with the other apes.

Behavioural propensities

Social learning research also requires overt actions on the part of the subject, another factor that contributes to the difficulties associated with making comparisons. One increasingly popular method of assessing underlying cognition within comparative psychology has been the expectancy violation procedure. This procedure, used increasingly to study cognition in human infancy, involves the recording of behavioural changes (such as looking times) as a measure of surprise when expectation is not fulfilled. "Because of the diversity of species that could be tested – all they need are eyes and an interest in visual displays – the expectancy-violation procedure provides a powerful technique for studying what animals know" (Hauser 2000, p. 61). This may well be the case for studies involving issues of cognitive representation alone, such as object permanence, concepts of number, or theory of mind. However, such approaches are of limited application for social learning research, where experiments will, by their nature, be constrained by the species' motor abilities and confounded by their behavioural differences.

Thus performance in social learning experiments is dependent on a whole set of other variables. Many of these

have been discussed by Lefebvre and colleagues (e.g. Carlier and Lefebvre 1996; Lefebvre 1995; Lefebvre and Giraldeau 1996). Traits such as neophobia, or habituation to human contact, can affect general performance in controlled experiments, and others, such as opportunism or omnivory, may be related to general learning abilities. Lefebvre suggests that species comparisons should therefore always involve a number of tasks that measure these, and that predictions about social learning should be tested on the residual deviation from regression of these potential confounds. Using this method, Lefebvre et al. (1996) found that pigeons (*Columbia livia*) were not only more rapid social learners than Zenaida doves (*Zenaida aurita*), but also solved individual learning tasks more rapidly. This led the authors to conclude that an apparent species difference in social learning could have been caused by some contextual variable, such as levels of habituation to humans.

Even when we intend to conduct comparative research using analogous procedures, true replication may be constrained by each species' level of behavioural flexibility. In its original conception (Whiten et al. 1996) an artificial fruit was designed such that it could potentially be employed for studying social learning mechanism in many species. A tool use task, for example, historically common in research in primate learning, is inappropriate for making comparisons between chimpanzees and other primates, as chimpanzees are typically much more expert tool users than other primates.

However, although the artificial fruit methodology has now been used on several other species, significant difficulties were discovered in replicating the design with marmosets (Caldwell et al. 1999). Marmosets lack manipulative skills possessed by many other primates tested, and as a consequence the task itself had to be simplified considerably before a marmoset demonstrator could be trained to open the apparatus. This more basic design was then used to study social learning. In comparison with chimpanzees, who have sometimes opened a fruit protected by four different defences in less than half a minute following demonstration, no marmosets succeeded in opening the artificial fruit after having observed a conspecific demonstration. Nevertheless, there was evidence that subjects matched aspects of the limited behaviours they had seen demonstrated. This raises the question of whether marmosets might have shown greater evidence of social learning if given a task that did not require as much dexterity, as suggested by the results of Bugnyar and Huber (1997) and Voelkl and Huber (2000). However, altering the task further means that analogous procedures are *not* being used. Due to the many potentially cognitively significant variables that this might affect (outlined above in the section on comparative literature reviews) we are wary of this approach.

In fact, behavioural constraints may effectively prevent us from testing in some species some of these cognitively significant aspects of imitation. For example, it is much easier to imagine an animal with considerable manipulative flexibility (a chimpanzee or a parrot, perhaps) per-

forming a response that we might be prepared to label “novel”, compared with those with more restricted behavioural repertoires (such as a marmoset or a pigeon). It is therefore unsurprising that some of the researchers working on these more limited species have tended to define novelty in different ways (see the section on novelty).

Conclusions

Is a comparative psychology of social learning possible? We believe that the answer is yes, although, like any area of comparative psychology, its conclusions are unlikely to go unchallenged. To date, comparative literature reviews have done little to clarify the picture and often have contributed to further confusion. We think that all of the variables outlined above in the section on comparative literature reviews are interesting in terms of cognitive process and merit investigation in their own right. Only extremely rarely is a literature review published that recognises this [e.g. see Miklosi (1999) for a broadminded and illuminating synthesis on the possible functions of the various brands of “imitation”]. Virtually all authors have tended to settle on single, preferred definitions of imitation, which may be quite different from each other, and this has led them to make different judgements about many of the same studies. Furthermore, the studies themselves are designed with often very different criteria for the kinds of social learning at stake. So when the species comparisons are made, like is rarely being compared with like.

Although we assume that eventually, the results of comparative experiments will be subsumed within the more global approach of an integrative review, we believe that attempts to do so in the past have been premature. Currently we need more comprehensive comparative experimentation.

How should we proceed with this? Despite the obstacles outlined above (see section on comparative experiments), we suggest that valid comparisons can still be achieved. Firstly, lessons can be learned from other fields of comparative cognition. In response to the impracticality of judging species differences by a process of systematic variation (see section on comparative experiments), Kamil (1988) went on to propose alternative approaches to the problem of contextual variables. He proposed that for each prediction, several experimental procedures should be designed, each testing the same ability, and that two or more species should be tested with all the procedures. If multiple predictions are fulfilled, it is unlikely that contextual variables are responsible. The example given by Kamil is of spatial memory in Clark’s nutcrackers. This food-caching bird has been shown to perform better than pigeons both on a radial maze task and in a spatial operant task (cited in Kamil 1988). Kamil (1988) also suggests that species differences could be predicted on the basis of some external criteria and tested using a number of sample species. If the theory accurately predicts the relative performance of several species, again contextual variables are unlikely to have produced this ef-

fect. Kamil cites the example of Rumbaugh and Pate’s (1984) index of encephalisation, which has been used to predict performance differences amongst seven primate species on a learning task.

In some cases, research in social learning is beginning to reach this level of rigor in terms of the comparisons made. For example, as we can see from Table 2, there are now several studies (Call and Tomasello 1995; Nagell et al. 1993; Whiten and Custance 1996) involving comparisons between chimpanzees and children, all of which converge on a conclusion that there are systematic differences in performance between these two groups. It appears that, whilst young children typically copy with a high degree of fidelity, chimpanzees often employ their own idiosyncratic techniques. These results can now be used to generate operational predictions about the circumstances under which each of these groups will tend to show high levels of fidelity (Whiten et al. 2002). Above all, it is important that we begin to make causal and predictive hypotheses about species differences, rather than correlational and postdictive ones. The different theories of the species distribution of imitation should be employed in terms of forming operational criteria against which to test predictions for a number of species.

As we outlined above, sometimes it is impossible to replicate fully a task with a different species. However, in situations where subjects’ capabilities necessitate modifying a task design, we suggest that attempts should be made as far as possible to retain aspects of the procedure that may be cognitively significant.

Since each of these cognitively significant variables are interesting in their own right, teasing them apart with a variety of different task designs may prove to be the most rewarding approach. This should provide a more complete understanding of social learning abilities and may also enlighten debate on the origins of imitation, as we may find that certain forms of “imitation”, and other forms of social learning, show very different patterns of species distribution.

Finally, we are encouraged by the number of researchers beginning to study social learning in a number of diverse species. To evaluate truly the nature of the phylogenetic distribution of imitation, researchers must be prepared to branch out from their familiar study species. The rats and pigeons studied by researchers from the animal model perspective will tell us little in isolation, and the same is true of the great apes favoured by those working from the phylogenetic perspective. Only through a truly integrative research program can we hope to challenge some of the assumptions of the traditional disciplines (whether those of comparative psychology, behaviourism, or ethology), and forge a coherent comparative psychology of social learning.

Acknowledgements Many thanks to Louis Lefebvre and Tom Zentall for providing constructive and encouraging feedback on a draft manuscript of this review. We are also grateful for the comments of three anonymous reviewers. C.C. was supported by a University of St Andrews doctoral scholarship. This work was carried out in compliance with current U.K. law.

References

- Akins CK, Zentall TR (1996) Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *J Comp Psychol* 110 (3):316–320
- Akins CK, Zentall TR (1998) Imitation in Japanese quail: the role of reinforcement of demonstrator responding. *Psychon Bull Rev* 5 (4): 694–697
- Beck B (1997) Reintroduction, zoos, conservation and animal welfare. In: Norton BG, Hutchins M, Stevens EF, Maple TL (eds) *Ethics on the ark*. Smithsonian Institution Press, Washington, D.C., pp 155–163
- Bering JM, Bjorklund DF, Ragan P (2000) Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Dev Psychobiol* 36:218–232
- Bitterman ME (1960) Toward a comparative psychology of learning. *Am Psychol* 15:704–712
- Bitterman ME (1965a) The evolution of intelligence. *Sci Am* 212: 92–100
- Bitterman ME (1965b) Phyletic differences in learning. *Am Psychol* 20:396–410
- Bjorklund DF, Bering JM, Ragan P (2000) A two-year longitudinal study of deferred imitation of object manipulation in a juvenile chimpanzee (*Pan troglodytes*) and orangutan (*Pongo pygmaeus*). *Dev Psychobiol* 37:229–237
- Bjorklund DF, Yunger JL, Bering JM, Ragan P (2002) The generalization of deferred imitation in enculturated chimpanzees. *Anim Cogn* 5:49–58
- Box H (1991) Training for life after release: simian primates as examples. In: Gipps JHW (ed) *Beyond captive breeding: reintroducing endangered mammals to the wild*. (Symposium of the Zoological Society of London) Clarendon Press, Oxford, pp 111–123
- Box HO, Gibson KR (1999) Mammalian social learning: comparative and ethological perspectives. (Symposia of the Zoological Society of London, 72) Cambridge University Press, Cambridge
- Bugnyar T, Huber L (1997) Push or pull: an experimental study on imitation in marmosets. *Anim Behav* 54:817–831
- Byrne RW (1994) The evolution of intelligence. In: Slater PJB, Halliday TR (eds) *Behaviour and evolution*. Cambridge University Press, Cambridge, pp 223–265
- Byrne RW (1995) The thinking ape: evolutionary origins of intelligence. Oxford University Press, New York
- Byrne RW (2002) Imitation of novel complex actions: what does the evidence from animals mean? *Adv Study Behav* 31:77–105
- Byrne RW, Byrne JME (1993) Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*) variability and standardisation. *Am J Primatol* 31:241–261
- Byrne RW, Russon AE (1998) Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21:667–721
- Byrne RW, Tomasello M (1995) Do rats ape? *Anim Behav* 50: 1417–1420
- Caldwell CA, Whiten A, Morris KD (1999) Observational learning in the marmoset monkey, *Callithrix jacchus*. In: Proceedings of the AISB '99 symposium on imitation in animals and artifacts. Society for the Study of Artificial Intelligence and Simulation of Behaviour, Edinburgh, pp 27–31
- Call J (2001) Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybern Syst* 32:97–119
- Call J, Tomasello M (1994) The social learning of tool use by orangutans (*Pongo pygmaeus*). *Hum Evol* 9 (4):297–313
- Call J, Tomasello M (1995) The use of social information in the problem-solving of orang-utans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *J Comp Psychol* 109:308–320
- Campbell FM, Heyes CM, Goldsmith A (1998) A demonstration of simultaneous stimulus learning and response learning by observation in the European starling using a two-object/two-action method. *Anim Behav* 58:151–158
- Carlier P, Lefebvre L (1996) Differences in individual learning between group-foraging and territorial Zenaida doves. *Behaviour* 133:1197–1207
- Carpenter CR (1973) An observational study of two captive mountain gorillas. *Hum Biol* 9:175–196
- Cloutier S, Newberry RC, Honda K, Alldredge JR (2002) Cannibalistic behaviour spread by social learning. *Anim Behav* 63: 1153–1162
- Coussi-Korbel S, Frigaszy DM (1995) On the relation between social dynamics and social learning. *Anim Behav* 50:1441–1453
- Custance DM, Whiten A, Bard KA (1995) Can young chimpanzees imitate arbitrary actions? Hayes and Hayes 1952 revisited. *Behaviour* 132 (11–12):835–859
- Custance DM, Whiten A, Fredman T (1999) Social learning of artificial fruit processing in enculturated capuchin monkeys. *J Comp Psychol* 113:13–23
- Custance DM, Whiten A, Sambrook T, Galdikas B (2001) Testing for social learning in the “artificial fruit” processing of wild-born orangutans (*Pongo pygmaeus*), Tanjung Puting, Indonesia. *Anim Cogn* 4:305–313
- Custance DM, Whiten A, Fredman T (2002) Social learning and primate reintroduction. *Int J Primatol* 23 (3):479–499
- Dawson BV, Foss BM (1965) Observational learning in budgerigars. *Anim Behav* 13:470–474
- Dolman CS, Templeton J, Lefebvre L (1996) Mode of foraging competition is related to tutor preference in *Zenaida aurita*. *J Comp Psychol* 110 (1):45–54
- Dorrance BR, Zentall TR (2001) Imitative learning in Japanese quail (*Coturnix japonica*) depends on the motivational state of the observer quail at the time of observation. *J Comp Psychol* 115 (1):62–67
- Fritz J, Kotschal K (1999) Social learning in common ravens, *Corvus corax*. *Anim Behav* 57:785–793
- Galdikas BMF (1982) Orang-utan tool use at Tanjung Puting Reserve, central Indonesian Borneo (Kalimantan Tengah). *J Hum Evol* 10:19–33
- Galef BG Jr (1988) Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In: Zentall TR, Galef BG Jr (eds) *Social learning: psychological and biological perspectives*. Erlbaum, Hillsdale, N.J., pp 3–28
- Galef BG Jr, Manzig LA, Field RM (1986) Imitation learning in budgerigars: Dawson and Foss 1965 revisited. *Behav Process* 13:191–202
- Gardner MR (1997) Imitation: the methodological inadequacy of bidirectional control tests. Unpublished doctoral thesis, University of London
- Gardner RA, Gardner BT (1969) Teaching sign language to a chimpanzee. *Science* 165:664–672
- Goldman-Rakic PS, Preuss TM (1987) Whither comparative psychology? *Behav Brain Sci* 10:666
- Haggerty ME (1909) Imitation in monkeys. *J Comp Neurol Psychol* 19:337–455
- Hall KRL (1963) Observational learning in monkeys and apes. *Br J Psychol* 54:201–226
- Ham R (1990) Do monkeys see monkeys do? Unpublished master's thesis, University of St Andrews
- Hauser MD (2000) *Wild minds: what animals really think*. Henry Holt, New York
- Hayes KJ, Hayes C (1951) The intellectual development of a home-raised chimpanzee. *Proc Am Philos Soc* 95:105–109
- Hayes KJ, Hayes C (1952) Imitation in a home-reared chimpanzee. *J Comp Physiol Psychol* 45:450–459
- Hayes KJ, Hayes C (1953) Picture perception in a home-raised chimpanzee. *J Comp Psychol* 46:470–474
- Herman LM (2002) Vocal, social and self-imitation by bottlenosed dolphins. In: Dautenhahn K, Nehaniv CL (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge, Mass., pp 63–108
- Heyes CM (1993) Imitation, culture and cognition. *Anim Behav* 46:999–1010
- Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69:207–231

- Heyes CM (1998) Theory of mind in nonhuman primates. *Behav Brain Sci* 21:101–148
- Heyes CM (2001) Causes and consequences of imitation. *Trends Cogn Sci* 5 (6):253–261
- Heyes CM, Dawson GR (1990) A demonstration of observational learning using bidirectional control. *Q J Exp Psychol B* 42: 59–71
- Heyes CM, Galef BG Jr (1996) Social learning in animals: the roots of culture. Academic Press, London
- Heyes CM, Ray ED (2000) What is the significance of imitation in animals? *Adv Study Behav* 29:215–245
- Heyes CM, Dawson BV, Nokes T (1992) Imitation in rats: initial responding and transfer evidence. *Q J Exp Psychol B* 45: 229–240
- Holt EB (1931) *Animal drive and the learning process*, vol 1. Williams & Norgate, New York
- Horowitz A (2001) Do humans ape? Or do apes human. Unpublished master's thesis, University of California, San Diego
- Huber L, Rechberger S, Taborsky M (2001) Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Anim Behav* 62:945–954
- Kamil AC (1988) A synthetic approach to the study of animal intelligence. In: Leger DW (ed) *Nebraska symposium on motivation*, vol 35. University of Nebraska Press, Lincoln, pp 257–308
- Klopfer PH (1959) Social interactions in discrimination learning with special reference to feeding behaviour in birds. *Behaviour* 14:282–299
- Klopfer PH (1961) Observational learning in birds: the establishment of behavioral modes. *Behaviour* 17:71–80
- Laland KN, Bateson P (2001) The mechanisms of imitation. *Cybern Syst* 32 (1–2):195–224
- Lefebvre L (1995) Ecological correlates of social learning: problems and solutions for the comparative method. *Behav Process* 35 (1–3):163–171
- Lefebvre L, Bouchard J (2002) Social learning about food in birds. In: Fragaszy DM, Perry S (eds) *The biology of traditions: models and evidence*. Cambridge University Press, Cambridge (in press)
- Lefebvre L, Giraldeau L-A (1996) Is social learning an adaptive specialization? In: Heyes CM, Galef BG Jr (eds) *Social learning in animals: the roots of culture*. Academic Press, London, pp 108–128
- Lefebvre L, Palameta B, Hatch KK (1996) Is group-living associated with social learning? A comparative test of a gregarious and a territorial columbid. *Behaviour* 133:241–261
- Lefebvre L, Templeton J, Brown K, Koelle M (1997) Carib grackles imitate conspecific and Zenaida dove tutors. *Behaviour* 134:1003–1017
- MacPhail EM (1982) *Brain and intelligence in vertebrates*. Clarendon Press, Oxford
- MacPhail EM (1987) The comparative psychology of intelligence. *Behav Brain Sci* 10:645–695
- McDonough L, Mandler JM, McKee RD, Squire LR (1995) The deferred imitation task as a nonverbal measure of declarative memory. *Proc Natl Acad Sci U S A* 92:7580–7584
- Meltzoff AN (1988) The human infant as *Homo imitans*. In: Zentall TR, Galef BG Jr (eds) *Social learning: psychological and biological perspectives*. Erlbaum, Hillsdale, N.J., pp 319–341
- Meltzoff AN (1995) What infant memory tells us about infantile amnesia. *J Exp Child Psychol* 59:497–515
- Meltzoff AN (1996) The human infant as imitative generalist: a 20-year progress report on infant imitation with implications for comparative psychology. In: Heyes CM, Galef BG Jr (eds) *Social learning in animals: the roots of culture*. Academic Press, New York, pp 347–370
- Meltzoff AN, Moore MK (1977) Imitation of facial and manual gestures by human neonates. *Science* 198:75–78
- Meltzoff AN, Moore MK (1983) Newborn infants imitate adult facial gestures. *Child Dev* 54:702–709
- Miklosi A (1999) The ethological analysis of imitation. *Biol Rev* 74:347–374
- Miller NE, Dollard J (1941) *Social learning and imitation*. Yale University Press, New Haven, Conn.
- Mitchell CJ, Heyes CM, Dawson GR, Gardner MR (1998) Limitations of a bidirectional control procedure for the investigation of imitation in rats: odor cues on the manipulandum. *Q J Exp Psychol B* 52:193–202
- Mitchell RW (1994) The evolution of primate cognition: simulation, self-knowledge and knowledge of other minds. In: Quiatt D, Itani J (eds) *Hominid culture in primate perspective*. University Press of Colorado, Boulder, pp 177–232
- Moore BR (1992) Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* 122 (3–4):231–263
- Munksgaard L, DePassille AM, Rushen J, Herskin MS, Kristensen AM (2001) Dairy cows' fear of people: social learning, milk yield and behaviour at milking. *Appl Anim Behav Sci* 73 (1): 81–82
- Myowa M (1996) Imitation of facial gestures by an infant chimpanzee. *Primates* 37:207–213
- Myowa M, Matsuzawa T (2000) Imitation of intentional manipulatory actions in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 114 (4):381–391
- Nagell K, Olguin K, Tomasello M (1993) Processes of social learning in tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J Comp Psychol* 107:174–186
- Nicol CJ (1995) The social transmission of information and behaviour. *Appl Anim Behav Sci* 44:79–98
- Palameta B, Lefebvre L (1985) The social transmission of a food finding technique in pigeons: what is learned? *Anim Behav* 33:892–896
- Parker ST (1996) Apprenticeship in tool-mediated extractive foraging: the origins of imitation, teaching, and self-awareness in great apes. In: Russon AE, Bard KA, Parker ST (eds) *Reaching into thought: the minds of the great apes*. Cambridge University Press, Cambridge, pp 348–370
- Parker ST, Gibson KR (1979) A developmental model for the evolution of language and intelligence in early hominids. *Behav Brain Sci* 2:367–408
- Piaget J (1962) *Play, dreams and imitation*. Norton, New York
- Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. *Proc Natl Acad Sci U S A* 99 (7):4436–4441
- Reader SM, Lefebvre L (2001) Social learning and sociality. *Behav Brain Sci* 24 (2):353–355
- Rumbaugh DM, Pate JL (1984) The evolution of cognition in primates: a comparative perspective. In: Roitblat HL, Bever TG, Terrace HS (eds) *Animal cognition*. Erlbaum, Hillsdale, N.J., pp 569–587
- Russon AE (1997) Exploiting the expertise of others. In: Whiten A, Byrne RW (eds) *Machiavellian intelligence II: evaluations and extensions*. Cambridge University Press, Cambridge, pp 172–206
- Russon AE, Galdikas BMF (1993) Imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). *J Comp Psychol* 107 (2): 147–161
- Russon AE, Mitchell RW, Lefebvre L, Abravanel E (1998) The comparative evolution of imitation. In: Langen J, Killen M (eds) *Piaget, evolution and development*. Erlbaum, Mahwah, N.J., pp 103–143
- Schaik CP van, Deaner RO, Merrill MY (1999) The conditions for tool use in primates: implications for the evolution of material culture. *J Hum Evol* 36 (6):719–741
- Sherry DF, Schacter DL (1987) The evolution of multiple memory systems. *Psychol Rev* 94:439–454
- Shettleworth SJ (1993) Where is the comparison in comparative cognition? Alternative research programs. *Psychol Sci* 4:179–184
- Shettleworth SJ (1998) *Cognition, evolution and behaviour*. Oxford University Press, New York
- Spence KW (1937) Experimental studies of learning and higher mental processes in infra-human primates. *Psychol Bull* 34: 806–850

- Stoinski TS, Wrate JL, Ure N, Whiten A (2001) Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *J Comp Psychol* 115 (3): 272–281
- Suddendorf T, Whiten A (2001) Mental evolution and development: evidence for secondary representation in children, great apes, and other animals. *Psychol Bull* 127 (5):629–650
- Taylor CK, Saayman GS (1973) Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour* 44:286–298
- Templeton JJ, Kamil AC, Balda R (1999) Sociality and social learning in two species of corvids: the pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). *J Comp Psychol* 113 (4):450–455
- Thorndike EL (1898) Animal intelligence: an experimental study of the associative process in animals. *Psychol Rev Monogr* 2(8)
- Thorndike EL (1970) Animal intelligence. Hafner, Darien, Conn. (Original work published 1911)
- Thorpe WH (1963) Learning and instinct in animals, 2nd edn. Methuen, London
- Timberlake W (1993) Animal behaviour: a continuing synthesis. *Annu Rev Psychol* 44:675–708
- Tomasello M (1996) Do apes ape? In: Heyes CM, Galef BG Jr (eds) Social learning in animals: the roots of culture. Academic Press, New York, pp 319–346
- Tomasello M (1998) Emulation learning and cultural learning. *Behav Brain Sci* 21:703–704
- Tomasello M, Call J (1994) Social cognition of monkeys and apes. *Yearb Phys Anthropol* 37:273–305
- Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York
- Tomasello M, Davis-Dasilva M, Camak L, Bard KA (1987) Observational learning of tool use by young chimpanzees. *Hum Evol* 2:175–183
- Tomasello M, Savage-Rumbaugh S, Kruger AC (1993) Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Dev* 64:1688–1705
- Visalberghi E, Fragaszy DM (1990) Do monkeys ape? In: Parker S, Gibson K (eds) "Language" and intelligence in monkeys and apes: comparative developmental perspectives. Cambridge University Press, Cambridge, pp 247–273
- Voelkl B, Huber L (2000) True imitation in marmosets. *Anim Behav* 60:195–202
- Webster S, Fiorito G (2001) Socially guided behaviour in non-insect invertebrates. *Anim Cogn* 4:69–79
- Whiten A (1998) Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 112 (3):270–281
- Whiten A (2000) Primate culture and social learning. *Cogn Sci* 24 (3):477–508
- Whiten A (2002) The imitator's representation of the imitated: ape and child. In: Meltzoff AN, Prinz W (eds) The imitative mind: development, evolution and brain bases. Cambridge University Press, Cambridge, pp 99–121
- Whiten A, Byrne RW (1991) The emergence of metarepresentation in human ontogeny and primate phylogeny. In: Whiten A (ed) Natural theories of mind: evolution, development and simulation of everyday mindreading. Basil Blackwell, Oxford, pp 267–281
- Whiten A, Custance DM (1996) Studies of imitation in chimpanzees and children. In: Heyes CM, Galef BG Jr (eds) Social learning in animals: the roots of culture. Academic Press, New York, pp 291–318
- Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Adv Study Behav* 21:239–283
- Whiten A, Custance DM, Gomez JC, Teixidor P, Bard KA (1996) Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110 (1):3–14
- Whiten A, Horner V, Marshall-Pescini SRJ (2002) Selective imitation in ape and child: a window on the construal of others' actions. In: Hurley S, Chater N (eds) Perspectives on imitation: from cognitive neuroscience to social science. MIT Press, Cambridge, Mass. (in press)
- Wright RVS (1972) Imitative learning of a flaked-tool technology – the case of an orang-utan. *Mankind* 8:296–306
- Zajonc RB (1965) Social facilitation: a solution is suggested for an old unresolved social psychological problem. *Science* 149: 269–274
- Zentall TR (2001) Imitation in animals: evidence, function, and mechanisms. *Cybern Syst* 32 (1–2):53–96
- Zentall TR, Sutton JE, Sherburne LM (1996) True imitative learning in pigeons. *Psychol Sci* 7 (6):343–346