

The ethological analysis of imitation

ÁDÁM MIKLÓSI

Department of Ethology, Eötvös University, Budapest, Hungary

(Received 29 April 1998; revised 14 April 1999; accepted 14 April 1999)

ABSTRACT

Theorists and experimental researchers have long debated whether animals are able to imitate. A variety of definitions of imitation have been proposed to describe this complex form of social learning. Experimental research on imitation has often been hampered by either a too loose ‘anthropomorphic’ approach or by too narrow ‘behaviourist’ definitions. At present neither associative nor cognitive theories are able to offer an exhaustive explanation of imitation in animals. An ethological approach to imitation offers a different perspective. By integrating questions on function, mechanism, development and evolution one can identify possible directions for future research. At present, however, we are still far from developing a comprehensive theory of imitation.

A functional approach to imitation shows that, despite some evidence for imitative learning in food processing in apes, such learning has not been shown to be involved in the social transmission of either tool-use skills or communicative signals. Recently developed procedures offer possible ways of clarifying the role of imitation in tool use and visual communication. The role of imitation in explorative play in apes is also investigated and the available data suggest that copying during play might represent a behavioural homologue of human imitation.

It is proposed that the ability to copy the behaviour of a companion is under a strong genetic influence in many social species. Many important factors have not been examined experimentally, e.g. the effect of the demonstrator, the influence of attention and memory and the ability to generalize. The potential importance of reinforcement raises the possibility that copying abilities serving divergent functions might be partly under the control of different mechanisms.

Key words: Imitation, copying, social learning, explorative play.

CONTENTS

I. Introduction	348
II. Definitions and categories of imitation	348
III. Behavioural analysis of copying: description, novelty and complexity.....	349
(1) Measuring and describing behaviour	349
(2) Novelty.....	350
(3) Levels of complexity.....	350
IV. Function	352
(1) The role of copying in feeding	352
(a) Food processing	353
(b) Manipulation of tools	354
(2) Communication.....	355
(3) ‘Non-functional’ imitation.....	356
(4) Conclusions	357
V. Mechanism	357
(1) Associative learning and/or cognitive performance?	357
(2) The role of reward.....	358
(3) The effect of the demonstrator.....	359
(4) Attention and memory.....	360
(5) Categorization and generalization	361

(6) Motor and neural aspects	361
(7) Genetic predisposition	362
(8) The social process of imitation	362
VI. Development	363
(1) Relationship between age and copying	363
(2) Imitation and play	364
VII. Evolution	366
VIII. Conclusions	367
(1) The ethological concept in the study of imitation	367
(2) Critical issues for future investigations	368
IX. Summary	370
X. Acknowledgements	370
XI. References	371

I. INTRODUCTION

‘On the playground a man has painted a wooden pole in white colour. After the work is done he goes away leaving behind a pot of white paint and a beautiful brush. I observe the only chimpanzee who is present, hiding my face behind my hands, as if I were not paying attention to him... very soon... he takes the brush, puts it into the pot of colour and paints a big stone which happens to be in the place, beautifully white’ (Köhler, 1926, pp. 156–157).

The above description would be interpreted by contemporary investigators of imitation in many different ways, and many would not treat this as a case of imitation at all. During the last 5–10 years there has been an ongoing debate about whether animals can be credited with the ability to copy their companions’ behaviour, and whether this ability can be compared to the superior capacity for imitation in humans. Whilst psychologists have always been interested in the study of imitative behaviour both in humans and animals, recently, philosophers and ethologists have also shown renewed interest in this phenomenon.

Despite countless anecdotes of imitative behaviour, many laboratory experiments either fail to demonstrate imitation or produce results that have been strongly criticized by others (e.g. Heyes, 1993, 1995; Byrne & Tomasello, 1995; Byrne & Russon, 1998).

Ethology, as an approach to the study of animal behaviour, has the advantage of utilizing various subdisciplines of biology, for example ecology, evolutionary biology and neurobiology. The integrative role of ethology in the study of animal behaviour was summarized in a fundamental paper by Tinbergen (1963) who urged ethologists to seek explanations of the function, mechanism, development and evolution of any behaviour under

investigation, and stimulated them to pursue an integrated approach when dealing with complex behavioural phenomena. One possible reason for the present confusion in imitation research may be due to the lack of such an integrated approach, in spite of numerous recent attempts to review imitation behaviour in animals (e.g. Mitchell, 1987; Galef, 1988; Whiten & Ham, 1992; Heyes, 1993; Byrne & Russon, 1998). The aim of the present review is to summarize the current state of imitation research from an ethological perspective (see also Bekoff, 1995; Jamieson & Bekoff, 1992).

In this review, because of the current controversy over whether or not a given species can imitate, when describing the results of particular experiments I will use the more neutral expression word ‘copy’. However, I will use the term imitation in a general sense where I discuss present theories that were intended to explain this type of social learning. In the ethological literature, there is little reference to the only species which all researchers do credit with the ability for ‘true’ imitation: *Homo sapiens*. I think we should not exclude any species from a comparative study. In the case of humans, I will retain the use of ‘imitation’ if appropriate.

II. DEFINITIONS AND CATEGORIES OF IMITATION

In the study of imitation, as in studies of other psycho-biological phenomena such as language, intelligence, deceit etc., acceptable definitions are difficult to find. Only the most important definitions are considered below.

Thorpe (1956) defines ‘true’ imitation as copying a novel behaviour for which there is no instinctive tendency or for which other parsimonious explanations (Morgan, 1894) can be ruled out. Whiten & Ham (1992, p. 250) argue that the observer should

copy 'some aspect(s) of the intrinsic form of an act'. Heyes (1993, 1994) states that imitation is taking place whenever 'individuals acquire, as a result of observing a conspecific's behaviour, X, the capacity to execute a behaviour that is topographically similar to X' (Heyes, 1994, p. 1000). These and similar definitions are descriptive on a purely behavioural level and incorporate neither the enabling conditions for imitation to occur or the function and mechanism of this form of social learning.

The cognitive approach to behaviour aims to categorize imitational phenomena by the supposed 'computational requirement' on the part of the observer. Whiten & Byrne (1991) argued that because the observer views the action from a different spatial perspective it needs the capacity to re-represent the action from its own point of view. This re-representation is necessary for the duplication of the observed act (Whiten & Ham, 1992). In short, the observer takes the perspective of the demonstrator. As these authors argue that such abilities are restricted to apes and humans only, they conclude that imitation in this sense should only be possible in these primates. Call & Tomasello (1995) insist that for 'true' imitation to occur the observer needs both to recognize the goal of the demonstrator and to realize that reaching this goal is only possible by copying the act(s) of the other animal.

Copying which does not involve recognition of a goal has been termed 'mimicking' (Tomasello, Kruger & Ratner, 1993a) or 'response facilitation' by Byrne & Russon (1998). In mimicking, the observer copies the action precisely but does not understand the goal of the model. If observation enhances the relative frequency of an act that is already in the repertoire of the animal, it is referred to as response facilitation. The main disadvantage of such 'cognitively inspired' definitions is that they restrict the number of potential species that can show imitative behaviour and by doing this, they fail to give an evolutionary account for the homologies of these phenomena.

In a recent account, Byrne (1995) and Byrne & Russon (1998) offered a different approach to imitation by discriminating two forms of imitation: 'action-level' and 'program-level' imitation. In the case of the former, the observer copies details of a simple action: the motor patterns of the observer and the model match closely. In program-level imitation, it is not the motor patterns but the structural organization of the task that is copied and the details of motor patterns are learned by trial and error (see also Russon, in press). Without doubt, this

definition also demands a high level of 'computation' on the part of the observer.

III. BEHAVIOURAL ANALYSIS OF COPYING: DESCRIPTION, NOVELTY AND COMPLEXITY

(1) Measuring and describing behaviour

One advantage of the ethological approach is that it is always concerned with the proper description of the behaviour. The continuous flow of behaviour is divided into carefully defined discrete events and studies investigate the presence (frequency, duration, etc.) of these well-defined units or elements in the sequence of behaviour (e.g. Slater, 1973; Drummond, 1981). Behavioural units can be conceptualized by stressing their hierarchical structure. These levels range from the movements of individual muscles to the movements of the animal's body in space. In practice, ethologists choose a particular level of analysis that is judged to be the most appropriate for answering their questions.

The analysis of imitation includes the problem of comparing the behaviour of two individuals: the model and observer. Since the presence of imitation has to be judged by the degree of resemblance to the model, methods based on a proper description of the behaviour are necessary. However, most published investigations lack such detailed descriptions, and in many cases the behaviour of both the demonstrator and the observer is judged arbitrarily by human observers.

In a recent study by Custance, Whiten & Bard (1995), for example, chimpanzees (*Pan troglodytes*) were trained to copy arbitrary gestural actions performed by a familiar experimenter in front of their cage. After training with a finite number of gestures, the chimpanzees were presented with new ones that they had not been shown during the training phase. The decisive question with regard to imitation was whether the observers would copy these novel actions. The results showed that the two chimpanzees copied 13 and 17 actions out of the 48 novel actions presented to them. In one of these novel actions, the human demonstrator touched her nose with her index finger. This was always carried out by placing the tip of the right index finger on the end of the nose (Custance *et al.*, 1995, p. 844). The apes, however, used either the thumb or middle finger in copying nose touching. It seems that the manifestation of imitation in this case depends on our level of behavioural description. One could

conclude that chimpanzees copied ‘nose touching’; however, they did not reproduce the actual lower-level description of the demonstrated behaviour (‘nose touching with right index finger’). (No distinction between right or left hand was made.)

For theoreticians the question is whether this provides evidence of ‘imitation’ or not? Recent references to this particular experiment give us an opportunity to compare the evaluations of different investigators. Whiten & Custance (1996) and Tomasello & Call (1997) regard these results as clear evidence of imitation. However, Heyes (1998), whilst acknowledging that this observation might be interpreted as imitation, also notes that earlier general social reinforcements by humans might have had facilitative effects on the production of gestures. This does not rule out the imitative interpretation. Byrne & Russon (1998) see the chimpanzees’ reproductions as instances of action-level imitations. However, it should be noted that many of the copied gestures violate the assumption of action-level imitation that the observed and reproduced motor patterns should show close matching.

(2) Novelty

Many theorists of imitation seem to agree that ‘novelty’ is an important aspect of copying (e.g. Thorpe, 1963; Visalberghi & Fragaszy, 1990; Byrne, 1995; Byrne & Tomasello, 1995; Zentall, 1996), whereas Heyes (1995) disputes the presence of novelty as a vital condition for imitation to occur. A novel motor act (i.e. never made before by the observer) would increase the researchers’ ability to identify occurrences of imitation, and more importantly the actual learning aspect of imitation would be more obvious (the incorporation of a new motor pattern).

Were the chimpanzees learning something new whilst touching their nose in the above example? As we have seen, the behavioural level of copying was ‘nose touching’ (and not nose touching with the right index finger as shown). However, there are no data presented regarding how ‘novel’ this act was to the observing chimpanzees. The novelty of the act in the chimpanzees behavioural repertoire should have been assessed by comparing the frequency of this behaviour in the presence of an inactive human with its frequency in the presence of a demonstrating human. Chimpanzees might perform nose touching by modifying earlier motor actions of face touching (for similar argument see also Whiten, 1998*b*). A

proper description of the range of behaviours including face touching in chimpanzees is clearly necessary.

The foregoing analysis suggests that only a detailed behavioural description can establish what was actually learnt by the observer. For example, it may turn out that nose touching was not a new act for the chimpanzee, and promoters of the ‘novelty criterion’ may classify this instance as a case of response facilitation (Byrne & Russon, 1998) or mimicking (Tomasello *et al.*, 1993*a*).

There is no agreement among researchers as to how novelty might be defined. Whiten & Custance (1996) and Whiten (1998*b*) noted that novelty is a relative concept, and identified a list of aspects (e.g. shape, extent, orientation) that might be sources of novelty. Any form of novelty can, however, be detected only by a detailed description of the actions of both the models and observers.

(3) Levels of complexity

As many authors have recognized, in theory one can discriminate four possibilities regarding the complexity of copying behaviour (see also Meltzoff, 1988*a*; Whiten & Custance, 1996).

(1) The observer is copying a motor act that is already in its repertoire, and, as a result of copying, the frequency of the particular behavioural act increases. The observer has not learnt anything about the motor pattern; Byrne & Russon (1998) apply the term ‘response facilitation’ to such cases. Galef (1988) argues that response facilitation is a necessary but not sufficient condition for ‘true’ imitation to occur.

In many studies claiming to demonstrate ‘imitation’ at this simple level, the lack of a description of the actual motor aspects of the behaviour make it difficult to judge whether observers really modified their motor pattern as a result of observation. For example, as recognized by Whiten & Ham (1992) animals can use different body parts to displace a manipulandum in an operant task. Therefore, reports of increased numbers of level pushes or joystick displacements etc. do not reveal whether motor learning took place. In some cases, a detailed analysis might offer a different perspective on copying. Compare, for example, two recent accounts both claiming to present a case for ‘imitation’. Akins & Zentall (1996) report that Japanese quail (*Coturnix japonica*) copy pecking or stepping on a treadle depending on the behaviour of

the demonstrator. Both acts are already present in the behavioural repertoire of the species as shown by the behaviour of the non-observer (control) birds. Bugnyar & Huber (1997) showed that marmosets (*Callithrix jacchus*) pulled a door (behind which food was hidden) more frequently if they had been exposed to an experienced model. Pulling is also a general behavioural strategy in marmosets, since control animals also pull. Bugnyar & Huber (1997) realized, however, that it is very important to observe and compare the behaviour of both the model and the observer. A detailed analysis of the motor aspects of pulling showed that as a result of the observation two out of five marmosets modified their pulling behaviour by using a different arm or keeping the door open for a longer duration. It might be the case that in quails pecking is a relatively invariant behaviour; however, stepping could be performed in different ways or the operant task could be designed to require a more specific motor act on the part of both the model and observer.

It should be noted that in the case of minor changes in motor behaviour observed in a small number of animals the chance effect of individual variability cannot be ruled out entirely. Within-subject comparisons could make the case even stronger if one includes baseline observations of, for example, pulling activities in the marmosets, before exposure to the model. This would support the conclusion that any change in the behaviour of the individuals is indeed the result of observation.

(2) An observer might copy a novel motor act. The inherent problems associated with this level of complexity were noted above. For example, there is some argument (e.g. Heyes, 1993, 1995; Byrne & Tomasello, 1995) about whether a change in the orientation to a stimulus can be regarded as a 'new' component in copying. It seems that in this case animals learn, instead, about the spatial relationship between their behaviour and the environment. If a given motor act is already in the repertoire of the animal then it is likely that it has been performed in various orientations to objects in the environment. A new orientation presents only a minor change. Moreover many investigators do not indicate what they regard as the novel component or aspect of the act to be learned. One might also note that the 'novelty' aspect in a motor task also requires more training on the part of the demonstrator, which in turn makes it less likely that an observer would have the capacity to acquire similar information only by observation.

In some species, it is possible to increase the chance of novelty by using 'arbitrary' acts for which it is certain that the animal has never performed before. For example, chimpanzees observed a human demonstrating the opening of a box ('artificial fruit') that contained a food reward (Whiten *et al.*, 1996). One of the actions used to open the box involved spinning a pin (however, the pin could be removed without performing this movement). This spinning movement was unlikely to have been performed previously by any particular chimpanzee. Nevertheless one out of six chimpanzees copied spinning (combining the results of Whiten *et al.*, 1996 and Whiten 1998*b*). This relative reluctance to copy suggests that some arbitrary acts novel to the observer might also be more difficult to copy. However, it should be noted that most species are incapable of performing radically new motor act(s).

(3) At another level animals might be able to copy sequences of acts with the novelty of the imitation represented in the temporal structure of the motor acts (Visalberghi & Fragaszy, 1990; Byrne, 1995; Whiten, 1998*b*). The combination of actions would partly circumvent the problem of novelty as discussed above since the probability of copied acts occurring in sequence can be easily calculated and compared to their performance by chance. However, this 'innovation' is not a complete solution: by changing the conditions for imitation we must recognize that we are now dealing with a different level of learning. Observers are not learning new motor acts but new ways of combining them, therefore a higher level of motor behaviour organization is being investigated.

By using the two-action procedure (e.g. Dawson & Foss, 1965) demonstrators can perform a combination of motor acts that are already in the behavioural repertoire of the observer. For example, to one group of observers (e.g. quails) the model could display two actions one after the other (e.g. pecking followed by stepping) to achieve a reward in an operant box, while another group of observers is exposed to the reverse series of actions performed by another demonstrator. This procedure would show whether the observers can learn series of acts, or the structure of a complex action. A recent report on social learning in ravens (*Corvus corax*) suggests that these birds might have learnt the required sequential organization of species-specific behavioural acts to obtain access to food in a 'puzzle-box' (Fritz & Kortschal, 1999).

Using a similar procedure, Whiten (1998*b*) showed that chimpanzees could learn by observing

action sequences. Chimpanzees observed the opening of a food-box by different action sequences. After three observation trials, each followed by intermittent sessions where subjects were allowed to open the box themselves, the chimpanzees were able to copy the particular sequence of actions to which they were exposed. Two reservations should be made, first, the presence of sequence copying was based mainly on judgements of similarity by human observers and it is difficult to see how this method of decoding behaviour could be used in situations intrinsically less familiar to human coders (see also Whiten *et al.*, 1996). Second, the presence of objects (bolts, handle, pin) that have been manipulated by the demonstrator might have facilitated and/or guided the sequential reproduction by reducing the ‘memory-load’ in this task. Nevertheless, two out of four subjects succeeded in opening the box during their first trial and all animals showed an improvement of matching in subsequent trials.

(4) The behaviour of the demonstrator might consist of a series of novel actions. However, as indicated above, in a number of species the possibility of performing truly ‘novel’ actions is limited. Processing food or using tools is usually regarded as a series of actions that in some cases might be unfamiliar to the observer and need to be ordered in the correct sequential order to achieve the appropriate result. Although one might design a sequence of relatively arbitrary actions for food processing to be copied (see e.g. Whiten *et al.*, 1996), it is difficult to see how the novelty of similar motor actions can be evaluated under natural conditions.

It seems to be a safe hypothesis that the ‘cognitive load’ of imitation increases with the complexity of the motor act(s) to be imitated. In the latter case discussed above the observer would not only have to learn a new motor act by observation but also, at the same time, observe the sequential organization of these new acts. Evidence for such an ability is lacking in animals but 18-month-old children can imitate relatively new sequential actions on toys (Abravanel & Gingold, 1985).

Theoretically, one way of dealing with the problem of complexity is the introduction of programme-level imitation that relaxes the demand on the observer to produce both a perfect copy of the act and the sequence (Byrne, 1995; Byrne & Russon, 1998). Imitation is said to occur if observers copy the hierarchical structure of the task. However, as pointed out by Whiten (1998*a*) the hierarchy of behavioural actions is as relative a concept as novelty and it does not offer a better criterion.

In summary, it seems to be necessary to provide both a detailed description of the behaviour to be copied and that of the copy. Moreover, we need a fair assessment of the likelihood that the observer could have already seen or performed the behavioural act(s) in question. Finally, researchers should indicate the level of similarity between the actions of models and observers.

IV. FUNCTION

To date not many studies have addressed directly the question of the function of imitation. Moreover, Heyes (1993) has argued that it might be too early to perform such an investigation. Ethological approaches to behaviour have shown, however, that the neglect of a functional view can lead to serious misconceptions, as occurred similarly in debates on learning some years ago. Recently, Lefebvre (1995) proposed that we should consider the interspecific variation in social learning and cognition that might represent adaptive specialization in species living in different ecological niches (see also Russon *et al.*, 1997).

The functional approach to imitation should shed light on the question of whether copying the behaviour of a conspecific enhances the survival of the observer under natural conditions. Many investigators agree, however, that the answer to this ‘why’ question (why do some animals copy the behaviour of others?) will often be difficult to obtain. A proper analysis of function needs to be based on a task description, and investigators have to know what the behavioural problems are that the animal must solve (Johnston, 1981). Unfortunately, laboratory investigations of imitation usually precede our ecological knowledge of the natural demands that animal species face in the wild. The neglect of ecological considerations has led to many poorly designed laboratory studies, which often simply attempted to demonstrate the absence or presence of imitation.

In the following section, I will try to summarize both the observational and experimental evidence available to infer the possible functions of imitation. Most laboratory investigations have not been concerned with functional aspects of imitation but some such studies are included here to contrast them with more ethologically inspired studies on function.

(1) The role of copying in feeding

The huge variability in the form of feeding-related motor patterns within and between species has

provided many opportunities for studying imitation both under natural and laboratory conditions: indeed, most demonstrations of animal copying are closely connected with feeding.

In some cases, the animal is not able to eat the food in its natural form and has to perform some specific actions to obtain the edible parts. For example, gorillas (*Gorilla gorilla*) use special handling techniques to remove the stings of some plants (Byrne, 1995), and squirrels have to crack nutshells to gain access to the kernel. Similarly, the milk bottle opening behaviour of birds (Fisher & Hinde, 1949) can be regarded as food processing. In the laboratory various food-processing devices have been used. Animals have to manipulate bars or handles to gain access to food, sometimes the physical location of the reward is distant from the place of action (e.g. Heyes, 1993; Call & Tomasello, 1995). Recently, Whiten *et al.* (1996) introduced the artificial fruit (a transparent plastic box that can be opened by manipulating the catches restraining a hinged lid).

(a) Food processing

As argued above most experiments or observations are based on the assumption that copying the behaviour of a conspecific is advantageous in cases of food processing. More precisely, observers gain a net advantage by saving time and energy if they observe and subsequently copy the behaviour of an experienced companion instead of discovering the necessary action by themselves. The first published observations in the ethological literature described a number of cases where individuals seemed to copy special food-related activities of conspecifics (e.g. Fisher & Hinde, 1949; Goodall, 1973; Galef, 1985; Kawai, 1965).

Recently, Byrne (1995) argued that in the mountain gorilla (*Gorilla g. beringei*) the handling techniques of plant feeding can be described in terms of programme-level imitation. He suggested that the young gorilla learns about the structure of the food-processing task by observing its mother: that is, it anticipates the order of actions that must follow each other in sequence. The large individual differences at lower levels of actions (hand use, hand configuration, movement pattern etc.; Byrne & Byrne, 1993) could be the result of trial-and-error learning. Although the food processing in these gorillas has often been described as a case of imitation (see also Byrne & Russon, 1998) the lack of any experimental evidence of a socially mediated process has led other

authorities to regard this observation as a case of individual learning (see Tomasello & Call, 1997). By the means of an 'artificial fruit' task (see above) Whiten *et al.* (1996) demonstrated that observer chimpanzees spontaneously copied elements of one component of the task (see also Whiten, 1998*b*, for extension of this technique).

A series of observations described the cultural transmission of pine cone opening in the black rat (*Rattus rattus*) in pine forests near Jerusalem (Terkel, 1995). These animals developed a sophisticated technique to gain access to the nutritious pine seed by skillfully stripping off the scales in a circular or spiral direction. Carefully controlled laboratory experiments showed that neither adult rats (Aisner & Terkel, 1992) nor pups can learn this kind of food processing by observation alone, but pups learnt this handling technique if they were raised together with their mother. Moreover adults sometimes learn this behaviour if provided with a series of partially stripped pine cones (Terkel, 1995). These observations clearly supported the social transmission hypothesis of food processing but there was no indication of copying by observation.

Interestingly, a series of laboratory studies found that observers of the closely related laboratory rat (*Rattus norvegicus*) were able to copy the behaviour of the demonstrator by pushing a vertical joystick in the same direction as the demonstrator (Heyes & Dawson, 1990; Heyes, Jaldow & Dawson, 1993). For example, after watching 50 rewarded leftward pushes by the demonstrator, observers pushed the joystick more times leftward than rightward. Recent investigations of this procedure, however, revealed that odour cues left by the demonstrator on the joystick played a major role in promoting demonstrator-consistent behaviour (Gardner, 1997), leaving doubt as to the actual role copying has in these experiments.

In many other studies, the motor patterns of food handling were also 'equated' with actions on a manipulandum in a Skinner box. The classic observations of Dawson & Foss (1965) demonstrated that naive budgerigars (*Melopsittacus undulatus*) showed a tendency to copy particular behaviours of the model. These results were partially confirmed by Galef, Manzig & Field (1986) and more recently by Akins & Zentall (1996) who showed that Japanese quail (for similar results on pigeons, *Columbia livia*, see Zentall, Sutton & Sherburne, 1996) would increase the frequency of either stepping or pecking depending on the demonstrator's behaviour. The common objection to these and similar experiments

is that the copied act was very likely already part of the observer's behavioural repertoire, making these observations examples of 'response facilitation' (Byrne & Russon, 1998) or 'mimicking' (Call & Tomasello, 1995).

In contrast to the bird species mentioned above, orangutans (*Pongo pygmaeus*) did not copy actions on a manipulandum (Call & Tomasello, 1995). The authors argued that orangutans did not copy because they could not understand the relationship between the manipulation and the food. However, this does not explain copying in quails and pigeons, and as a result Heyes (1993) argued that an understanding of physical relationships is not necessary for copying to occur. Furthermore, Bugnyar & Huber (1997) found that marmosets reliably copied pulling actions performed by the demonstrator.

In contrast to the discrepancies between studies on non-human animals, investigators agree that human children (two and three years old) could imitate all tasks presented to apes (Call & Tomasello, 1995; Whiten *et al.*, 1996).

(b) Manipulation of tools

Interest in the use of tools by animals stems from human tool use. Some animals use simple tools under natural conditions; it seemed possible that imitation is important in the acquisition of tool use. However many apparently complex tool-using activities develop without social influence. In laboratory experiments of this type, the demonstrator is taught to use a simple tool for getting food. After a few observations of the demonstrator's actions, the observer is assessed for its use of the tool.

Chimpanzees perhaps make the most frequent and diverse use of tools in the wild (Goodall, 1973; Tomasello, 1990). Chimpanzees living in one region of West Africa use a pair of stones (a hammer and an anvil) to open oil-palm nuts (e.g. Sugiyama & Koman, 1979; Boesch & Boesch, 1983). The nut-cracking process is thought to be one of the most difficult learned tasks performed by any animal in the wild. Chimpanzees place a nut on a suitable stone or sometimes a root (the 'anvil') and hit it with a carefully chosen stone or piece of wood ('the hammer'). Chimpanzees not only transport hammers; some wooden hammers are made by the chimpanzees (Boesch & Boesch, 1990). One possibility is that the chimpanzees understand the logical structure of the task (Byrne, 1994) and the behaviour sequence (taking the stone into the hand, putting the

nut on the anvil, hitting... etc.) and the details of the acts are acquired by trial-and-error learning. This could be described as an instance of 'programme-level imitation' (a possibility not mentioned by Byrne & Russon, 1998). A second possibility is that observer chimpanzees might learn the simple acts by copying and acquire the sequence by trial-and-error learning ('action-level imitation'; Byrne & Russon, 1998). Third, the particular sequence of acts could be acquired by observation ('sequence imitation'; Whiten, 1998*b*).

In contrast, recent reports demonstrate that chimpanzees perform nut cracking reliably only after 4–5 years of learning which does not suggest a fast social learning by copying (Boesch, 1993). In a detailed study on the development of nut cracking, Inoue-Nakamura & Matsuzawa (1997) concluded that 'the chimpanzees did not copy the motor patterns or the way to relate nuts with stones' and suggested that 'this learning process might be called (goal) emulation'. This seems to be a fair conclusion given the data presented, however, the natural conditions of study, the lack of data on the demonstrator's behaviour and the broad categorization of actions do not exclude the possibility that at some level copying of motor pattern could have been at work. Boesch *et al.* (1994) and Boesch (1996) also argued that the presence of arbitrary culturally transmitted 'social conventions' among chimpanzee populations (e.g. leaf-clipping, killing of ectoparasites) and less well adapted cultural behaviour patterns (e.g. Gombe chimpanzees use a more efficient technique for dipping ants than their conspecific companions living in the Tai region) suggests a complex process of social transmission that also involves some forms of copying.

One suggestive example of the social transmission of tool use comes from a laboratory study where Nagell, Olguin & Tomasello (1993) found that although chimpanzees eventually came to realize the relationship between the use of a tool and the 'reward' they paid less attention to actually copying the details of the tool-using motor pattern of the demonstrator. This suggests that the behaviour of the demonstrator only drew the attention of the observer to the tool and to the physical relationship between the tool and the food. The actions of the observers were based on trial-and-error learning as they tried to emulate the goal of the demonstrator. Summarizing the tool use of chimpanzees under natural conditions and their performance in experiments, Tomasello (1990) concludes that imitation does not play an important part in the social

transmission of tool use, mainly because imitation can only take place if (1) the observer comes to understand the functioning of the tool or the relationship between the action and the goal of the demonstrator, and (2) understands that by copying the actions of the demonstrator the same goal can be achieved (Call & Tomasello, 1995).

However, in animals tool use does not necessarily mean that there is an understanding of the functioning of the tools. In a series of interesting experiments, Visalberghi (1993) showed that capuchin monkeys (*Cebus apella*) achieve success by trial-and-error learning and not by understanding (e.g. contact between a stick and reward is necessary for pushing the reward out of the tube). It also remains questionable what the chimpanzees 'understood' about the latches in the experiment with the artificial fruit (Whiten *et al.*, 1996).

One should distinguish carefully between two different levels of understanding. The understanding of physical interactions between two objects to produce a desired result (e.g. hitting a nut with a stone results in edible food etc.) should be separated from the understanding of why an animal performs an action (i.e. to get food). Call & Tomasello (1995) argue that apes lack the understanding of this latter, 'intentional' component which presumably hinders their ability to copy. However, the wide variety of behaviours copied by rehabilitated orangutans observing humans is relevant to this question of whether observers understand the actual goal of the demonstrator. For example, orangutans were observed to perform behaviours that closely resembled weeding activities of the staff in the rehabilitation centre (Russon & Galdikas, 1993). Weeding involved 'chopping the weeds off at the root with a hoe and then pushing the cut weeds into a neat row behind him along the centre of the path for later removal' (Russon & Galdikas, 1993, p. 154). We can assume that while the orangutans understood the physical relation between the hoe and the roots, they did not understand the aim of the task itself. Nevertheless, their individual motor patterns, as well as some action sequences revealed that their activities were the consequence of copying the process of weeding (Russon & Galdikas, 1993, 1995; Russon, 1996, 1999).

Tomasello *et al.* (1993b) found that 'enculturated' chimpanzees (chimpanzees reared with intensive human contact) could be trained to copy simple object-related actions of a human demonstrator. Most human infants out-perform the apes under similar experimental circumstances, and young

children were found to show high accuracy of copying (Nagell *et al.*, 1993). Nine to twelve months old human infants were also found to copy simple arbitrary tool-related acts (Meltzoff, 1988c), and 14-month-old infants could generalize across different objects to repeat the observed action (Barnat, Klein & Meltzoff, 1996). It seems that in humans copying plays an important role in learning about how to use tools. It remains a question, however, what these children understood about the functions of these objects/tools, and the relation between the object/tool and action (Whiten & Custance, 1996).

(2) Communication

Many researchers assert that imitation can play an important role in the social transmission of communicative signals. In the auditory domain, this phenomenon is already well established although it has been suggested that auditory-vocal imitation should be separated from the visual-motor imitation on computational grounds (for further details see Moore, 1992; Whiten & Ham, 1992). It has been demonstrated that in humans imitation plays a crucial part in language learning (e.g. Speidel & Nelson, 1989). Infants and children not only learn phonemes and words but also attain new grammatical structures by imitation (Rodgon & Kurdek, 1977).

Interestingly, in 'language teaching' experiments (e.g. Gardner, Gardner & van Cantford, 1989), the chimpanzee Washoe was not able to learn the gestural signs for words and verbs by copying; instead, her gestures had to be moulded by putting her arms, hands and fingers in the required positions. In contrast, Fouts, Hirsch & Fouts (1982) claimed that Washoe's infant learned gestural signs by copying the gestures of his mother. However, later it was reported that Washoe also used the moulding technique to teach the signals (Fouts, Fouts & van Cantford, 1989), therefore the significance of these observations with regard to copying remains uncertain.

There are two distinguishing features of imitation in communication compared to that in food processing and tool use. First, in the context of communication the role of direct reinforcement for copying is less obvious, and in most cases it would be of a social nature. Second, at the end of the learning process the copy must match exactly that presented by the model, otherwise the signal cannot be perceived reliably by other members of the group,

and furthermore, could not be transmitted across generations.

Tomasello *et al.* (1985) describing the development of communication gestures in captive chimpanzees found only little evidence for learning gestures by copying. For example, chimpanzees in that particular group used an 'arm-raise' gesture for soliciting play. It is suggested that this gesture developed from the modification of the hitting movement of the solicitor to attract the attention of the other. This developmental process in which interacting animals create or invent new communicative signals by modifying preexisting behaviour patterns, was first referred to as conventionalization (Tomasello *et al.*, 1985) but later re-named as ontogenetic ritualization (Tomasello & Call, 1997). In a subsequent study on the same group of chimpanzees Tomasello, Gust & Frost (1989) found that some signals (e.g. throwing woodchips to elicit play) might have dispersed among the infants by learning through copying, i.e. the behaviour of the inventor had been copied by the others. Given these semi-natural observations, the copying of play-soliciting gestures in chimpanzees deserves further experimental study.

The renewed interest in pointing behaviour in apes (e.g. Leavens, Hopkins & Bard, 1996) has also raised the question how these animals learn this gestural signal. Pointing is said not to occur in the wild (Goodall, 1986; Menzel, 1973) whilst it was observed among nut-cracking chimpanzees (Inoue-Nakamura & Matsuzawa, 1997). Recent observations suggest that 'enculturated' chimpanzees use a human-like referential pointing gesture (Leavens *et al.*, 1996; Krause & Fouts, 1997) and there is a report that chimpanzees (Washoe and Louise) also used this gesture for spontaneous communication between themselves (Fouts *et al.*, 1982). At present there is no evidence regarding whether pointing can be learned by copying human behaviour or whether it becomes conventionalized (Tomasello *et al.*, 1985) by modification of other similar gestures (e.g. reaching).

Uzgiris (1981) offered a further function of imitation in humans. She argued that in addition to learning language, imitation in human infants serves to express a kind of mutuality between the model and the observer. In this case, imitation by itself is communication. Meltzoff & Moore (1994) also suggest that human infants use imitation for communication with adults. Observations show that imitative behaviour both in mothers and infants plays an important role in early social interactions

(Moran *et al.*, 1987). Meltzoff (1990) showed that 14-month-old infants are able to recognize when they are being imitated and show more affective behaviours (e.g. attending, smiling) when this happens. Eckerman (1993) also suggests that in 2–3-year-old children imitation has a communicative function by facilitating joint attention and the maintenance of coordinated actions. Later, this function of mutual imitation will be replaced by verbal communication.

Imitative aspects of communication might also play a role in emotional synchronization among group members. Hatfield, Cacioppo & Rapson (1993) introduced the concept of emotional contagion to explain the tendency of humans automatically to mimic and synchronize expressions and vocalizations with those of another persons' and, consequently, to converge emotionally: for example, children showed facial sadness while watching a sad film on videotape (Eisenberg, McCreath & Ahn, 1988).

Since animal behaviour is always dependent in some way on inner motivational state, copying of the behaviour of another might result in similar motivational states of the group members. Such copying might be important in animals if group members have to harmonize their internal state before engaging in joint action (e.g. group hunting). This function of copying could play an important role in infants that lack language. One might speculate that a similar process could have operated during the pre-linguistic stage of human evolution (Donald, 1991).

(3) 'Non-functional' imitation

Whiten & Ham (1992) listed many anecdotal examples of relatively complex and sequenced actions that included interactions with tools. A common feature was that these observations came mainly from the field or were descriptions of activities in home-raised animals. Bruner (1972) suggested that copying the behaviours of a demonstrator helps the observer to attain appropriate movement combinations when dealing with objects. The essence of this argument can easily be understood if one considers that primates can produce a large range of motor patterns (they have a large degree of freedom of movement) and thus even a slight learning about the motor design of an act can markedly reduce the number of inaccurate attempts. In Bruner's (1972) view, copying is not a means to learn a specialized task but provides information on how to use the

arms, hands and legs to perform simple or more complex motor acts. This view takes us to the interesting, but debated, field of play behaviour. Play is often referred to as having the function of practising (Fagen, 1981) or executing actions that are only just beyond the abilities of the individual (Grastyán, 1985). Most anecdotal reports of copying can also be viewed as examples of play. The precise use of lipstick by the chimpanzee Viki (Hayes & Hayes, 1952), the description of 'serious play' by Köhler (1927, see introductory anecdote), the recent data on human-like activities in orangutans (Russon & Galdikas, 1993, 1995; Byrne & Russon, 1998) and a dolphin (*Tursiops aduncus*) copying a seal's swimming behaviour (Tayler & Saayman, 1973) are probably instances of animals playing. The issue of play and imitation will be discussed further below in relation to ontogeny.

(4) Conclusions

Neglecting functional considerations on how imitation could enhance the survival of an individual in the wild has led to diverse laboratory experimentation. Investigators attempted to find a good 'model' species for imitation without considering the possible function of imitation in that species. Direct experimental evidence from the field is also lacking. However, it should be noted that the many alternative explanations of imitation make such investigations very difficult although not impossible. It is likely that natural observations or field experiments on their own will never provide satisfactory evidence for imitation but at least they are able to suggest testable hypotheses for laboratory research.

In summary, the evidence to date shows that some animals may copy the behaviour of their companions in the context of food processing. This is supported by recent laboratory observations suggesting that under special circumstances chimpanzees engage in copying some aspects of the demonstrator's behaviour; however, natural observations have not validated a role for copying in the wild. There is no experimental evidence for the same tendency in tool use and communication.

The following points arise from the present state of imitation research: (1) laboratory investigations should be based upon a detailed description of the natural behaviour of the species (task description). (2) Modification of the original learning circumstances might interfere with the detection of imitation in the laboratory. For example, to a rat copying the pushing of a joystick may not be

equivalent to copying the removal of scales from a pine cone, even though in both cases they 'are working for their food' (see below). (3) In humans, some possible functions of imitation have been studied in detail (Yando, Seitz & Zigler, 1978; Uzgiris, 1981; Gopnik & Meltzoff, 1994) which should be taken into account when considering animal imitation.

V. MECHANISM

Most investigators in this field of social learning concentrate on demonstrating the presence of some kind of imitation within a species. Less time has been devoted to examining the actual mechanisms that control this process (see also Whiten, 1998*b*). Future research should attempt to identify the important variables that affect imitation. Although specific experimental studies on most of these issues are still lacking, there are some data available with which to present a preliminary analysis.

(1) Associative learning and/or cognitive performance?

The investigation of social learning in the framework of associative learning has a long history (e.g. Miller & Dollard, 1941; Gewirtz & Stinge, 1968). Recently Heyes (1994) provided a general account of social learning phenomena, and argued that these mirror the rules of associative learning elaborated in asocial learning theory. Copying, in this sense, is said to be a special form of response-stimulus (R-S) learning where by watching the demonstrator the observer learns the relationship between the motor pattern performed by the model and the appearance of the reward, so that the observer will reproduce the observed act later in time to gain access to the reward. The special feature of imitation is that it is not the learner but the demonstrator that is performing the response (Heyes, 1994). This account assumes that copying can only take place if the demonstrated act is rewarded. Rats seem to follow the basic rules of associative learning (Heyes & Dawson, 1990). For example, Heyes *et al.* (1993) trained rats to push a joystick to obtain a reward. Later, these animals were exposed to demonstrators that pushed the joystick in the same direction but did not receive a food reward. The non-rewarded extinction trials of observers revealed that these rats showed fewer responses (i.e. showed faster extinction) in the previously rewarded direction than rats in the control groups. This indicates that the learning

performance of the rats was probably under the control of reinforcement (but see also Gardner, 1997).

The problem of this approach is that it offers an overly broad basis for explaining imitation. In contrast to Heyes (1994), many investigators seem to believe that processes of social learning are to some extent different to those of other learning (e.g. Russon, 1997). Furthermore, since associative learning is thought to play an important role in most cases of learning, this argument does not explain the specificity of imitation. Since a variety of animal species are able to learn instrumental conditioning tasks why then is copying limited only to a small number of species?

Explaining imitation in a cognitive framework alone has the disadvantage of telling us little about the actual mechanisms in question. Orangutans showed a low level of performance when faced with similar problems as rats (i.e. manipulating a handle for a food reward, see above), which led Call & Tomasello (1995) to conclude that copying is not possible without understanding the goal of the action, and that non-human primates (and other animal species as well) lack this ability. However, in some cases we find evidence of copying when (1) there is not much to understand (e.g. imitation of gestures; see Custance *et al.*, 1995), or (2) understanding is not necessary (e.g. imitation of turning movements of a pin; Whiten *et al.*, 1996; Whiten, 1998*b*).

Some argue that copying in apes requires observers to re-represent the demonstrated behaviour (Whiten & Ham, 1992; Whiten, 1999*a, b*). The complexity of this re-representation depends on the actual complexity of the action to be imitated (novelty, delay etc.). As a result, the representation of the 'motor plan' in the demonstrator and the observer shares similar characteristics. To this extent, one could say that the observer has 'read the mind' of the demonstrator (Whiten, 1999*a*). At present, it is difficult to decide the importance of this given the different cognitive interpretations of complex copying of actions in apes. The programme-level imitation approach (Byrne, 1995; Byrne & Russon, 1998) asserts that the structural organization of the act is represented, and the observer learns to replicate the sequential regularity, co-ordination of the elements and subroutines, whilst low-level subgoals might be achieved by individual trial-and-error learning. Whiten (1999*a*), however, favours the view that the copied actions as well as their sequence should be represented (see also

Whiten & Custance, 1996). The distinction between these two approaches also relates to the question of how previous experience and 'insight' into a given task affect copying. In complex object- or tool-related actions, the observer has to decide when specified subgoals have been achieved. This approach can be exemplified by the re-analysis of the experiments of Tomasello *et al.* (1987) and Nagell *et al.* (1993) in Byrne & Russon (1998). In these experiments, observer chimpanzees could witness a trained conspecific who was using a rake-like tool to pull food into the cage. Observers were found more likely to succeed in getting food than non-observers; however, the use of the rake differed substantially from that of the demonstrator. The original authors argued that the observer did not imitate but tried to 'emulate' the observed behaviour. By emulation it is meant that the observer learns 'something about the changes of the world that are possible' (Tomasello & Call, 1997). In Byrne and Russon's (1998) account, the observer learnt to use the 'rake as a tool' (see also Whiten & Ham, 1992). However, the frequency of raking in non-observing control animals suggests that the chimpanzees had ideas on what a rake can be used for (see Fig. 4 in Nagell *et al.*, 1993), and therefore there was little room for learning about the actual motor structure of raking (Whiten & Ham, 1992; but see also Russon, 1999).

At present neither the associative nor the cognitive model in itself offers an acceptable general model for imitation. Closer observation of the actual process of imitation learning may provide information on the precise aspect a theory of imitation should explain.

(2) The role of reward

Rewards can influence the behaviour of the observer in at least three different ways: (1) in many cases it is necessary for the demonstrator to obtain a reward for copying to occur; (2) the presence of a reward during demonstration may distract the observer; (3) a reward obtained by the observer during exposure to the demonstrator's actions may reinforce a different behaviour from that performed by the demonstrator: i.e. scrounging might be learned.

(1) One feature of many learning tasks to be copied is that demonstration is accompanied by reward (food): observers see the demonstrator rewarded for successful performance. Chimpanzees were able to copy arbitrary actions if they had been trained to do so ('do as I do!'-method; Hayes & Hayes, 1952; Custance *et al.*, 1995). Although the results should be treated with caution (see above)

there was a strong component of copying. However, Custance *et al.* (1995) remarks that the withdrawal of food reward greatly inhibited the display of copied actions.

Pigeons (*Columba livia*) learned by observation to open a box containing food that was covered by paper (Palameta & Lefebvre, 1985). However, the most important aspect of this experiment was that copying only occurred if the demonstrator found food in the box. For similar observations in Japanese quails see also Akins & Zentall (1996). Similarly, Heyes *et al.* (1993) observation that rats withhold an already acquired action (joystick pressing), if they are exposed to unrewarded attempts of the demonstrator, shows that observed absence of reward leads to extinction.

Observers face even more serious difficulties if they have to copy sequential actions (e.g. in the artificial-fruit processing task; Whiten *et al.*, 1996). To be successful the observer must attend to the action sequence from the beginning since the observation of only the final act does not guarantee the reward (see also Fritz & Kortschal, 1999). This process is the opposite of the conventional operant conditioning procedure where a sequence of acts is trained in backward fashion, contradicting the predictions of the associative theory.

(2) Recently, Whiten (1998*b*) noted that the presence of the visible reward in the 'artificial food' box also interfered with the performance of the observers. Similarly, in the tool-using task of Tomasello *et al.* (1987) the chimpanzees were probably distracted by seeing the food directly and they paid much less attention to the demonstrated tool-using behaviour (raking, see above for a description of this experiment). Their behaviour, described as emulation, might also be viewed as a struggle to get the food as soon as possible! In a study by Boysen & Berntson (1995), 'counting' chimpanzees (who were able to comprehend numbers, see also Boysen & Berntson, 1989) were presented in turn with two different amounts of candy. If they chose the smaller amount then this was given to a companion and the chooser received the larger amount of candy. Neither chimpanzee could learn this task (they always chose the larger amount and as a consequence the smaller number of candies was gained); their performance increased if the candies were replaced with arabic numerals. Here again, the immediacy of the presence of the reward strongly interfered with the cognitive mechanisms needed for successful performance of the task.

(3) It is often assumed that scrounging has an inhibiting effect on social learning. For example, Giraldeau & Lefebvre (1987) demonstrated that scrounging inhibits transmission of social behaviour in pigeons. Under natural circumstances in many cases observers are able to snatch food from producers (as in the case of the nut-cracking chimpanzees where infants could easily gain pieces of food by taking them from others instead of struggling with the cracking itself). In the associative account, these conditions should not favour efficient social learning (see also Heyes, 1993). One might suppose that even if we assume that animals such as gorillas or chimpanzees learn by some kind of imitation in the wild, the observed lengthy learning period (2–4 years) is needed for the observer to become 'detached' from the direct influence of the reward. However, this might not be always the case since observer ravens (*Corvus corax*) learned to open a food box by observation despite having many opportunities to scrounge (Fritz & Kortschal, 1999).

In many cases, it is therefore highly probable that as a result of both distraction and scrounging observers will change their strategy to trial-and-error learning leaving little room for copying details of the demonstrated action. These conditions seem to imply that observers will show individually distinct motor patterns that differ from those of the model.

Tomasello, Savage-Rumbaugh & Kruger (1993*b*) found that enculturated chimpanzees could copy arbitrary actions on tools where no obvious reward was present. They concluded that this success can be explained by the fact that chimpanzees reared in human social environments are more likely to receive social reward for imitative actions. These arguments also have a long history in human psychology, and, for example, Gewirtz (1969) argued for an operant conditioning account of imitation based on social reinforcement. Interestingly, a parrot (*Psittacus erithacus*) was found to copy and reproduce in isolation a number of arbitrary human motor actions, and at present it is not clear what a form of social reinforcement, if any, was at work (Moore, 1992).

(3) The effect of the demonstrator

Most experiments on imitation have focused on the behaviour of the observers and the role of the demonstrators has often been neglected. This approach shows the strong influence of the traditional associative learning theory which assumes that the sight of the reinforced demonstrator provides the

situation necessary for copying to occur. Two major points require further consideration: (1) the physical separation of observers and demonstrators; (2) the social relationship between observers and demonstrators.

(1) Most if not all experiments have been arranged in such a way that the demonstrator is physically separated from the observer (only experiments on humans are exceptions). This experimental design allows the experimenter to control the learning process and reduce the effect of stimulus enhancement (for related arguments see also Galef, 1988; Whiten & Ham, 1992). Apparently, demonstrators were separated from observers throughout the duration of the experiments with rats of Heyes *et al.* (1993), and the same was probably true for the quails studied by Akins & Zentall (1996). However, this situation is unusual in nature! In group-living animals, members are not only in continuous visual contact but they are also in physical contact. A food item found by one member of a group might attract others and the discoverer will make efforts to try to escape with the food or to conceal its discovery. In a laboratory experiment, rats were taught to dive for food underwater. Naive members of the group tried to seize the food from the divers instead of learning to dive (Galef, 1985). Dominant chimpanzees do not allow juveniles to use their hammer (Inoue-Nakamura & Matsuzawa, 1997). Chalmeau & Gallo (1993) confronted a group of chimpanzees with an operant task where the manipulation of a handle resulted in food reward. Some members of the group learned how to operate the handle and gained the food reward. However, the dominant animal who obtained most of the food items never produced an operant response! These and other examples show that it does not always pay to copy the behaviour of group mates if there are other ways to obtain the food. The tendency of group members to get food directly from others (it might be viewed as a form of scrounging, see above) has a strong inhibitory effect on any copying to be realized. If we want to show the real effect of imitation in groups of animals we have to find ways of observing this phenomenon in interacting members of the group. Behavioural ecologists would never agree that animals confined to adjacent cages provide a good model of a social group.

(2) From many reports of laboratory experiments it is not clear whether the observers and demonstrators had any previous contact with each other, whether they came from the same or a different social group, how they were related etc. Observations

on home-reared chimpanzees and other animals seem to contradict the simple assumption that the relationship between model and observer can be neglected. Recently, Russon & Galdikas (1995) argued that not all demonstrators are similarly effective in eliciting copying from observers, and that the familiarity between observers and demonstrators has an enhancing effect. Closer contact between demonstrators and observers makes observation not only easier but the observer is also more familiar with the general motor patterns of the model and this can help him to recognize significant changes in the model's behaviour. This process could be especially important if observer animals copy the behaviour of humans, as in the case of the studies by Tomasello *et al.* (1993*b*) or Cusance *et al.* (1995) where chimpanzees had to reproduce human gestures and actions.

(4) Attention and memory

The enabling effect of attention and memory has not been addressed by students of imitation in animals. This lack of interest relates perhaps to the earlier general view (based on experience with humans) that observers should be able to reproduce an action after a short exposure to the model's action. However, it is clear that imitation is rarely a case of 'one-trial' learning. There is a relatively high 'computational' demand on the part of the observer during the demonstration. First, it has to watch the conspecific for a sufficient duration to perceive the act to be copied. The amount of the attention necessary depends partially on the relative novelty of the act. Behaviours that are already in the observer's repertoire might be recognized in shorter time than novel ones. The attention span of a given species might constrain the amount of information that it can learn at once.

Second, the observer has to have a relatively large short-term memory capacity for storing the observed behaviour. This is even more important when the observer has to store sequences of motor acts. In this case, it is not enough to remember the last act before the appearance of the 'reward'. Observers have to recall antecedent actions as well, and they cannot know beforehand when the relevant actions begin. This leads to the prediction that more complex demonstrations need more presentations; it is not surprising that chimpanzees exposed to a sequence of actions by Whiten (1998*b*) did not copy the sequence at the first instance. Similarly, it can be argued that 'emulative' actions in chimpanzees (e.g. Tomasello

et al., 1987) occur as a result of insufficient exposure to the model's behaviour; observers simply do not remember the particular details of the task at hand.

Both limited attentional and memory capacity can be counterbalanced by increasing the number of performances by the demonstrator. However, this creates two further problems. First, it is difficult to ensure that the demonstrator always performs the act which is to be copied in a similar manner. This variability presents a new difficulty for the observer since it has to recognize similarity among demonstrated actions. Secondly, extended periods of demonstrations are likely to give the observer the opportunity to act out the behaviour himself, and various other learning processes (e.g. trial-and-error learning) start to operate.

Some have argued that 'true' imitation can only be inferred if individuals are able to perform the copy in the absence of the demonstrator and after a considerable time has elapsed since the last presentation ('deferred imitation') (Piaget, 1962). For imitation to fulfil its social utility function observers should be able to imitate long after the demonstration (Meltzoff, 1988*c*). This view implies that imitation can only be acknowledged if the observer is able to enact the copy from memory. A few experiments have aimed at investigating the effect of delay on imitation. For example, Tomasello *et al.* (1993*b*) found that enculturated chimpanzees could reproduce the copy after 24 h, and Meltzoff (1988*b, c*) showed that 9-month-old human infants duplicate acts after 24 h, but 14-month-olds can perform a copy of motor acts after a delay of 1 week.

(5) Categorization and generalization

The generalization of learnt information is an important ability since under natural conditions animals face a relatively variable environment. With regard to imitation we should seek to determine the extent to which animals might use information learnt by copying in a different context from that observed. Observers have to display two different kinds of abilities with regard to copying. They have to be able to recognize and categorize the actions of the demonstrator. For example, when modelling nut cracking chimpanzees might use different tools, at different places, and the executed motor patterns might differ because of the particular characteristics of the hammer or nut at hand. When performing a previously observed act, however, the former observer has to show an ability to generalize because the conditions during the re-enactment will probably

differ from those present during observation. It is not always a good strategy to copy the fine details of the motor patterns displayed by the demonstrator (see also Russon, 1999). There are no relevant data from animals but 14-month-old human infants are able to generalize imitative behaviour to different contexts or objects (Barnat *et al.*, 1996).

(6) Motor and neural aspects

Recently, investigators argued that at the neural level imitation is a 'demanding variety of visual-tactile cross-modal performance' (Heyes, 1993), or is based on kinesthetic-visual matching (Mitchell, 1994). To account for early infant imitation Meltzoff & Moore (1994) introduced the active intermodal mapping hypothesis that proposes that the movements of infants provide proprioceptive information that is compared to the visual target.

The significance of cross-modal association in animals is a seriously under-researched field. In a relatively recent and exhaustive review, Ettlinger & Wilson (1990) came to the conclusions that (1) cross-modal performance (CMP) does not depend on special neural processes, and different senses can directly access each other from their sensory-specific systems; (2) CMP is a specialization of within-modal performance, and that new brain structures are required to support it. Monkeys, apes and humans share similar abilities to perform CMP tasks, and under appropriate circumstances all show relatively high levels of performance. Rats also demonstrated reliable learning in cross-modal (visual-audio) transfer tests (e.g. Church & Meck, 1983). The most important and yet unanswered question is, how the sensory codes of the two modalities achieve isomorphism (see Ettlinger & Wilson, 1990). Since there are many unknown aspects of CMP, at present this model offers only limited help in understanding the neural mechanism of imitation.

With regard to copying there is another neural mechanism that could play an important role in the reproduction of the observed behaviour. Perrett *et al.* (1992) found neurons in the temporal cortex of macaque species that are view selective in their response to hand movement. They also observed that there is a population of neurons in the superior temporal sulcus that seems to be selectively responsive to the body positions of an observed person. It is argued that one function of these cells is to determine to what the attention of the observer individual is directed. However, the neural representation of this visual information might be

accessible for other neural systems. In the premotor area of pigtail macaque (*Macaca nemestrina*), Pellegrino *et al.* (1992) described neurons that were responsive to both the grasping act of the monkey itself and the similar movements of an observed person or conspecific. This provides a clear example of how visually perceived, topographically different movements are mapped onto the same neuron. Such neurons allow a difference of hand posture to be detected, and play then a key role in coping. Given the possibility that there are other neurons with similar representational ability, one might think of possible structures that might play an important role in executing observed actions. For example, if other species-specific behaviours are mapped similarly in the brain then this would explain why in some species the production of an action after observation can be brought under control of reinforcement. This mechanism could also help in the rapid recognition of the basic actions of others allowing more attention to be devoted to learning about the specific features of the motor act.

It can be assumed that similar neural structures exist in other species that do not copy actions of conspecifics, and although some devoted neural structures might indeed be necessary for a species to copy the behaviour of other conspecifics their mere presence does not guarantee the emergence of imitative abilities (see also Miklósi, 1999).

(7) Genetic predisposition

The question of interest is why the observation of a conspecific's action should release a similar response in the observer. Most asocial learning processes are driven by some form of stimulus-reinforcement contingencies that affect the individual 'learner' directly. A feature of copying is that observers do not seem to need such a direct input or, even when rewarded for an alternative behaviour (see for example Whiten, 1998*b*), they prefer to perform the demonstrated action. Therefore, in contrast to the general learning approach, one might assume that some species are genetically predisposed to copy the behaviour of conspecifics in a similar manner to some bird species that are predisposed to learn about their companions soon after hatching (imprinting). Since, in many cases, the first reproductions of the demonstrator's actions might not achieve the desired results, a genetic predisposition could play an important role in maintaining the copying activities in the observer.

This view has not received particular attention in

spite of the fact that humans seem to operate in this manner. Even one-day-old infants show evidence of copying the facial gestures of others (e.g. Meltzoff & Moore, 1977; see also Myowa, 1996, for facial imitation in a chimpanzee), and a number of studies suggest that infants are very good at copying acts of others, and that they copy functional and arbitrary actions even in the absence of an extrinsic reward (Meltzoff, 1988*d*). There is also documentary evidence from abandoned children who grew up together with animals (e.g. dogs) showing that these infants copied a number of behavioural acts (eating by licking, 'walking on four feet' etc.) from their companions (Gesell, 1942). A recent unfortunate case in Hungary provides such an example. A child abandoned for most of the time by its parents spent most of his time with their dog. After being rescued it was found that at first he licked soup from plates, used sounds similar to those of the dog and preferred to walk on all fours (reported on Hungarian television: Night News at 10 o'clock, 8.10.1995). It should be also pointed out with reference to the social-conditioning hypothesis, that these children received little if any 'social reward' for their imitative behaviour. It is also known that the lack of appropriate models seriously retards the development of social as well as cognitive skills in humans (Lane, 1976). In contrast to humans, cross-fostering experiments to a limited extent are possible in animals, but apart from some anecdotal reports it is not known whether the cross-fostered young of any species are able to copy species-typical motor patterns of the foster parent which are not naturally present in the behavioural repertoire of the offspring.

Recently, Meltzoff (1996) argued that humans are the only species where there is no need for any enculturation or other reinforcement for imitation to develop. In his view, humans are genetically predisposed to imitate others, and this predisposition allows us to become an imitative generalist (*Homo imitans*: Meltzoff, 1988*d*).

(8) The social process of imitation

In most cases, the role of the demonstrator is mainly a passive one. Both under natural conditions and in laboratory experiments demonstrators do what they are supposed to do and pay little attention to whether others are watching or not. In this sense, imitation is based on eavesdropping, the observers' success in copying depends on their ability to observe. Reporting on nut-cracking behaviour of chimpanzees, Inoue-Nakamura & Matsuzawa

(1997) noted that there was neither social reinforcement nor any feedback from the mother to the nut-cracking attempts of the infants, and many hundreds of hours of observation of nut cracking revealed only two instances of active teaching in this species (Boesch, 1991).

It is only in humans where from being a uni-directional process, imitation becomes truly interactive. In humans, the model has the ability to recognize the fact that he or she is being copied (Meltzoff, 1990). This means that the demonstrator can also influence the effectiveness of the copying act by performing the act slowly or repeatedly etc. Since infants as young as 14 months old are able to recognize if they are being copied, in humans the ability to imitate and the recognition of being imitated seems to develop in parallel.

VI. DEVELOPMENT

(1) Relationship between age and copying

One of the most surprising facts about research on imitation in animals is the partial ignorance of the developmental aspects of this phenomenon. In most laboratory experiments, an adult animal observes an adult conspecific and for many investigators this seems to represent the best condition for studying imitation. It is often assumed that most tasks of copying require considerable computational abilities on the part of the observer. These abilities develop with age therefore older/adult animals are more likely to be able to copy the behaviour observed. However, it could be argued that older animals are likely to be more resistant to changing their behaviour as a result of observation, and younger animals might benefit more from copying since this could give them an opportunity to enhance their motor repertoire. Field observations of social learning have revealed that young animals are more likely to incorporate new actions into their behavioural repertoire as, for example in the case of potato washing in the Japanese monkey (*Macaca fuscata*) (Kawai, 1965) or pine cone opening in black rats (Terkel, 1995). Similarly, in chimpanzees both complex forms of food processing and tool-use behaviour emerge by the end of infancy or during the juvenile ages (Inoue-Nakamura & Matsuzawa, 1997; Goodall, 1986).

The close contact between young offspring and the mother (or other group member), and the common long-term interest might create ideal con-

ditions for social learning in a number of species, including the copying of behavioural acts. Furthermore, infants usually have a protected status in their early development, adults tolerate their presence and closeness, and are less aggressive towards them. For example, infant chimpanzees were observed to get easier access to tools of the adults than juveniles (Inoue-Nakamura & Matsuzawa, 1997). This suggests that in theory infants have better opportunities to observe the behaviour of adults.

In contrast to the associative learning theory of imitation, the cognitive account of imitation asserts that the observer has to reach a certain level of cognitive processing to perform an imitative act. For example, Custance *et al.* (1995) argued that they used chimpanzees older than 4 years of age because 'they were old enough to be cognitively capable' of copying the demonstrated gesture. Whiten *et al.* (1996) found that 4–5-year-old chimpanzees copied a component of a demonstrated action whilst in a recent study older, 10–26-years-old (and more 'enculturated') chimpanzees were able to copy the sequence of the observed action. However, one study (with one subject) indicates that five-week-old chimpanzees might be able to copy facial gestures of humans which is comparable to abilities of human babies (Myowa, 1996).

The general belief that under special circumstances older animals might copy more complex actions than younger ones is mirrored in the description of copying activities of rehabilitant orangutans in the field (Russon & Galdikas, 1995). However, they also reported instances where younger orangutans duplicated actions even if they 'did not achieve the results modeled'. Moreover, younger infants ($n = 4$) were observed to copy 102 simple acts of their mother's behaviour. In another study (Hayes & Hayes, 1952), the chimpanzee, Viki, aged two years was observed to copy acts, e.g. she was observed putting on lipstick in a similar manner to humans (Hayes & Hayes, 1952, p. 451). It is highly possible that apes younger than four years old might be able to copy simple or less complex actions. It might also be the case that young apes are more selective and sensitive to both their relationship with the demonstrator (e.g. they only copy the behaviour of the mother etc.) and the particular social situation.

More data are available on the development of imitative abilities in humans. Object-related imitation emerges as early as nine months after birth when the representational abilities of the infants are believed to be limited (Meltzoff, 1988*a*). Older

infants and children show more complex forms of imitation. In a developmental study, Abravanel & Gingold (1985) showed that 18-month-olds were able to imitate serial and sequential coordinations in contrast to 12-month-old children (see also Parker & Milbrath, 1995). Many studies seem to demonstrate that children are not very selective in their imitative response. In appropriate experimental (play) situations, most children imitated behaviour that was demonstrated by strangers. This decreased selectivity might be an important difference between ape and human imitation.

In a series of experiments, Eckerman & Didow (1989) and Eckerman & Stein (1990) observed the emergence of spontaneous imitation in play during development. At the age of 2–3 years the role of imitation in play becomes dominant, and they argued that imitation is a means to induce co-ordinated actions before the full-fledged use of language (see Eckerman, 1993 for a review). Furthermore, imitation is thought to have a facilitatory effect on the development of language skills for organizing joint actions. However, later in development (at the end of the third year) the frequency of imitation decreases, probably in parallel with the consolidation of language ability in children. Informal observation in humans also show that spontaneous imitation remains at low level after childhood but that humans retain their ability to imitate throughout their life.

(2) Imitation and play

Given the functional aspects discussed above in mind most studies have focused on the goal-oriented aspects of copying and seemingly ‘non-functional’ imitative actions remained a mystery. In the literature on imitation, however, there is a line of argument that suggests a possible close relationship between play and imitation in some species. In contrast to imitation, most students of behaviour agree (at least in the case of birds and mammals) when they observe animals playing. Both phenomena, however, suffer from the lack of an acknowledged definition and functional explanation (Bekoff, 1976; Fagen, 1981; Martin & Caro, 1985).

It is, however, worthwhile listing some features of play that might help to understand why in some cases imitation can be a part of playing. On a structural level in play behavioural acts can be similar but not identical to those performed by the adult, their sequence can vary, and behaviour acts

with different functional roles can be combined (Bekoff & Byers, 1981; Fagen, 1981). There is also no consummatory phase in play activity (Fagen, 1981).

It is perhaps not accidental that many experiments on ape or human imitation have been performed in a play context. Tomasello *et al.* (1993*b*) report that their experiment took place in a free play situation; Whiten *et al.* (1996) note that children seem to imitate the non-functional part of the model’s action, probably because they perceive the situation as play. In contrast, while orangutans had to work for food, children were presented with a game version of the same task, and Call & Tomasello (1995) found that the children but not the orangutans were able to copy the demonstrated actions. Given the copying abilities of rehabilitant orangutans (Russon & Galdikas, 1993), these species-specific differences can also be explained by the different experimental conditions under which humans and orangutans were tested.

Of the many possible functions proposed for play, its function in explorative learning and as a means of learning about the intentions of others will be considered. The similarity of both hypotheses is that the animal has to perform certain acts in order to learn either about the physical environment (‘knowing through action’; Werner, 1948) or about oneself and other companions by interacting with them (Parker & Milbrath, 1995; Bekoff & Allen, 1998). It is assumed that young animals and human infants learn about objects by acting on them in the context of object-play. For example, Schiller (1952) found that if chimpanzees had the opportunity to play with sticks then later they were able to use a stick in a more efficient way as a tool for pulling in food. In exploratory play, 9–16-month-old infants transferred knowledge gained through prior experience with one toy to interaction with another toy (Baldwin, Markman & Melartin, 1993). It is also interesting to note that although Tomasello *et al.* (1987) used a broad definition of tool play in their experiments, subjects that showed more play with the tool appeared to be more successful in getting a reward, moreover there was a tendency towards an inverse relationship between play behaviour and success, since tool-related play appeared to decrease as subjects became more skilled in obtaining the food.

In humans, it is clear that children can imitate actions demonstrated on a toy, and that they are able to transfer this information to a similar object (Meltzoff, 1988*c*; Barnat *et al.*, 1996). Similarly, observing chimpanzees’ copying abilities in the

context of play, Tomasello *et al.* (1993*b*) also found that the apes copied simple actions demonstrated with objects.

Bekoff & Allen (1998) proposed that interactions between conspecifics during play might promote learning about the intentions of others. They suppose that, for example, in the social play of dogs participants come about to know that the partner wants to play by knowing what they feel when they elicit play in the other. Meltzoff & Moore (1994, p. 83) argue that 'imitation is to understanding people as physical manipulation is to understand things'. The context of play provides an advantageous opportunity for this type of imitation to take place.

The concept of exploratory play for copying activities in some species has the following important features (Miklósi, 1998). (1) The context of play affords a special 'state of mind' for imitative behaviours to emerge. Animals are playing if they are 'relaxed' and free from any immediate needs (e.g. hunger) or threats (Martin & Caro, 1985). This is highlighted by the observation that the presence of any extrinsic reward (e.g. food) inhibits play (animals usually stop playing when given the opportunity to eat) and the subjects will try persistently to get the food (see also Schiller, 1952). In a series of experiments, Harlow, Harlow & Meyer (1950) and Harlow (1951) clearly showed how manipulative play in rhesus monkeys (*Macaca mulatta*) can be inhibited by the introduction of food. Monkeys were presented with complex mechanical puzzles that they learnt to solve after several attempts. Subsequently, monkeys ($n = 3$) made only four errors during the tests where there was no food present but the same animals made, on average, 15 errors if the puzzle contained hidden raisins.

(2) Liberation from reinforcement contingencies widens opportunities for copying to occur. Under these conditions observers may try to copy actions that they did not observe in full or do not fully understand. This can result in incomplete reproductions of the demonstrated motor pattern and/or the sequence of the actions. Yando *et al.* (1978, p. 163) suggest that 'children probably imitate most when they are confronted with a problem that is just beyond the cutting edge of their abilities'. Independent evidence of language imitation also suggests that children prefer to imitate linguistic items that they only partly understand (e.g. Clark, 1977).

(3) In play, the result of the action actually copied is of limited importance, e.g. whether any

'reward' can be gained or whether any new action has been learnt. In play, observers have the opportunity to execute perceived motor acts in different forms or combinations, and observe their effect on the environment and themselves. One could assume that during play copying animals do not strive to produce an exact copy of the demonstrated action (and/or sequence). During play, the general mental experience gained through copying is what is important and not the effect of a particular copy on subsequent behaviour.

For example, consider the studies of Russon & Galdikas (1993, 1995) who described behavioural acts of rehabilitant orangutans that showed strong resemblances to actions performed by human caretakers. Orangutans copied various human activities such as making fire, sharpening an axe blade, hammering nails into wood, sawing etc. (see also Russon, 1999). More than 65% of the acts copied were also described as non-functional, and their description closely resembles the picture that was presented by Köhler (1926; and see also introductory quotation). Probably the simplest explanation for the occurrence of most of these behaviours is that the orangutans or chimpanzees were playing and that in the course of the play they incorporated several actions or combinations of actions that they had observed in humans. From the original description (Russon & Galdikas, 1993) it is also clear that, for example, orangutans trying to reproduce fire-making behaviour of the carers were facing a difficult task, because humans apparently used different acts and their combinations for making fire. Since orangutans do not know about the physics of fire making it is difficult to judge whether the discrepancy between their fire making attempts and those of the humans was the result of limited capacity for copying because of the variability in the demonstrated behaviour, or the lack of the ability to reproduce long sequences of behaviour actions (for other interpretations see also Byrne & Russon, 1998; Whiten, 1999*b*). If we accept that these apes were playing then one can also explain the difficulties of Russon & Galdikas (1995) in their effort to replicate these observations. For example, one orangutan was observed hammering nails etc. for a short period of time. On a second occasion one of the authors failed to elicit this behaviour by presenting the same tools again. One possible reason for this is that the orangutan lost its interest in these objects after extensive use and experience of them. This phenomenon can also be observed in human children when the solution of a problem in the play context

decreases the attractiveness of a toy or game later. The repeated presentation of a toy does not guarantee that play will follow, and perhaps it is more difficult to elicit play in orangutans. Considering the explorative function of copying during play, it is not difficult to see why many attempts have failed to find evidence for 'true' imitation in the laboratory.

In play, however, the important thing is the play itself. It can be said that in such circumstances the animals duplicate actions 'for the mere sake of imitating' (G. J. Romanes, cited in Whiten & Ham, 1992). Regarding the 'knowing through action' hypothesis one might suppose that orangutans were interested in either what 'it feels like' to make fire or hammer a nail (intentional function of play) and/or to learn about the affordances of the object they came into contact with (for related interpretations see also Russon & Galdikas, 1995). Having gained this experience the particular task/object/situation/action loses its initiative power.

VII. EVOLUTION

There are three important evolutionary issues that should be answered separately in future studies. First, the origin of the superior imitative abilities of humans should be explained. The copying activities of enculturated chimpanzees and other apes living in close contact with humans might reveal that human-like imitation evolved early in primate evolution (Tomasello *et al.*, 1993*b*; Russon & Galdikas, 1993, 1995; Whiten, 1998*b*). Whiten & Ham (1992) present a working hypothesis that assumes that copying activities of apes result in qualitatively different representations compared to those of other mammalian or avian species. Whiten & Byrne (1988, 1997) have argued that since these apes show some forms of 'mindreading' abilities, imitation is a behaviour strategy used to build 'metarepresentations' of others' actions (see also Whiten, 1998*b*).

With regard to the evolutionary origins of social abilities the argument of exaptation may be relevant. Gould & Vbra (1982) suggested that certain abilities may appear earlier in evolution, well before they present any adaptive advantage for the species. For example, they argue that the feathers of birds can be viewed as an exaptation for flight. Based on paleontological evidence, feathers appeared earlier than the enhanced flying ability in birds. This means that although feathers did not evolve for flight, later

in evolution they became a useful means for enhancing the flight abilities of birds. In similar fashion it might be argued that some socio-cognitive abilities, such as some forms of imitation, evolved before they could have contributed fully to the social life of the species. Therefore, imitation in primates might be a form of both object-related and social exploration that only in humans became integrated into the process of cultural transmission along with the ability to teach. Interestingly, the same argument can be put forward with regard to play (see also Martin & Caro, 1985). Play behaviour might originally have evolved for a very different reason to the role that it plays now in the social life of primates. For example, as a result of new selection pressures the cognitive capacities of some species may have altered, and some forms of social learning, including imitation, became incorporated into play behaviour that in turn changed also the function of play.

The present analysis has shown that there are also fundamental differences between copying in apes and humans (level of complexity, difference in age, selectivity of the model etc.). We should not forget that in humans the ability to imitate and the recognition of being imitated are both present, and that these processes seem to complement each other. If there was perfect imitation, then there would be no need for teaching. The recently established strong functional connection between imitation and teaching in humans underlines the possibility of genetic changes in these behaviour systems during the course of evolution (Tomasello *et al.*, 1993*a*).

However, it should be kept in mind that to some extent imitative actions of apes and humans show many similarities if they are displayed during play, and it is worth considering that the homology of primate imitation can be studied best by the comparative observation of imitative play in these species.

The second main question should focus on the convergent and homologue aspects of imitation, i.e. how the imitative activities of divergent species could be related to each other in evolutionary terms. Moore (1992) concludes that avian imitation is not homologous with copying in mammals. Both differences in the copying process itself and the lack of copying behaviours in living reptiles (descendants of the common ancestors of birds and mammals) suggest that copying in birds and mammals evolved independently. Until now only a few bird species (quails, pigeons, ravens(?), parrots) have shown any evidence of copying at different levels of complexity,

presenting too narrow a picture for further contemplation of the evolution of imitative behaviours within the order of birds.

Since some recent evidence suggests that dolphins might also show evidence of copying (Tayler & Saayman, 1973; Bauer & Johnston, 1994), there is a possibility that visuo-motor imitative abilities evolved at least twice independently within the mammalian order. In a recent summary, Tomasello & Call (1997) found no evidence of copying in monkeys, and maintain that only enculturated apes (animals raised in human environments) and humans display abilities for copy. Challenging this view, other investigators (e.g. Whiten *et al.*, 1996; Byrne & Russon, 1998) have argued that imitative abilities manifested earlier in primate evolution since they are present in all ape species. Tomasello & Call (1996) also note that the effect of enculturation is not clear and should be addressed experimentally. However, it would be strange if imitative abilities of apes could only emerge in a human environment without having played a role earlier in evolution of the Pongidae. It might be that the exaptive feature of imitation restricts this ability to manifest only in particular conditions, and until now most laboratory investigations have failed to create the appropriate experimental circumstances. The neglect of functional issues of imitation may also have led to the confused situation we are facing today. For example, the ability to copy should not be separated from the evolution of social behaviour in various species. This ability should be seen as form of interaction between group members even when the demonstrator appears to be passive in most cases.

Third, the question of the role of copying activities in cultural behaviour should be addressed. By clarifying the problems mentioned in the foregoing discussion, the function of imitation in cultural transmission can also be assessed. It is almost certain that imitation plays some part in cultural transmission (but see Heyes, 1993 for an argument to the contrary). Recently, Boesch (1996) argued that imitation, together with other forms of social learning, might form the basis of culture by a process of canalization. Given the complexity and sensitivity of copying activities it is highly probable that just by observation of animals in the wild the role of imitation in cultural transmission can never be determined.

VIII. CONCLUSIONS

(1) The ethological concept in the study of imitation

In a review of the available literature, copying activities of animals (including humans) were categorized based on four possible functions of imitation, and eight important aspects relating to the mechanisms involved were also discussed in some detail. It is recommended that to develop a fruitful research programme for the future, issues of function, mechanism and development should be handled in an integrated fashion.

It is still an open question whether the different functions of imitation (food processing, tool use, communication, exploration, skill learning) are based on the same or similar mechanisms across different species but our present understanding of the bewildering array of imitative behaviours supports the possibility that different functions of copying to some extent invoke different behavioural mechanisms. As for other features of behaviour, which have a strong genetic component, copying ability might also be under selection pressures which might favour or oppose its presence. The seemingly independent emergence of imitative behaviours in taxonomically unrelated animal groups might also point to the involvement of divergent mechanisms.

There is both experimental and observational evidence that the copying of a companion's behaviour plays a part in the learning process of food processing. In this case, a role of the external reinforcement gained by the demonstrator is also inevitable, since this assures that observers learn behaviour acts that are successful. A predisposition for this type of social learning also might be necessary. Many species-specific feeding behaviours might be coded genetically in a form of neural representation, and the demonstrator's actions induce similar or the same actions in the observer. The strong dependence on reinforcement also offers the possibility of investigating associative aspects of copying, and the role of trial-and-error learning in the learning of food processing. Under natural conditions animals learn food-processing techniques when young and in many species older animals are more resistant to learning from others by observation; the development of these abilities is an important issue. Offspring with a less developed nervous system might be more willing to copy slavishly than older animals, but they might be also more sensitive to their relationship to the model.

Tool use presents, in most cases, an inherently more complex task since animals need not only to realize the relationship between parts among their body and some external goal but they also need to take into account a threefold relationship of their body, the goal and the tool. The many unsuccessful attempts required to learn such a task will limit the role of reinforcement, making the role of genetic predisposition in maintaining copying activity very important. Tool-using species usually exhibit strong preferences for objects matching those that become their tools later. This preference for particular objects in itself only enables trial-and-error learning and does not explain copying by observation. Copying of the companion's behaviour in tool-use situations with the possibility of reward has not been supported experimentally until now. However, in certain circumstances, e.g. during play, animals have been observed to copy difficult object related actions. The copying of tool-use behaviour requires enhanced attention and memory, furthermore observers should have the ability to generalize from the observed action to the action performed by themselves. Similarly to food processing, in tool use, young observers may be better at copying demonstrated actions even if they do not 'understand' what they are doing.

In contrast to humans, where imitation has an important role in the transmission of communicative signals between generations, in animals such a role for visuo-motor copying is still debated. Although the acquisition of a motor pattern serving as a communicative signal might not present a great difficulty for the observer, the particular circumstances of these types of learning make all the difference. The observer not only needs to extract the actual signal to be learnt from the continuous flow of behaviours but it should also aim to perfect the signal to perfection (in most cases) without any positive influence by the demonstrator and with limited use of trial-and-error learning. Without any predisposition to reproduce the behaviour of a companion this kind of copying could never arise. In other cases, the communicative signal might involve a new motor pattern that again decreases the chances of easy reproduction. The ambiguous influence of reinforcement makes this situation difficult to analyse with methods originally developed for the analysis of classical associative learning.

Copying has also been implicated in playing a general enhancing role in skill learning. The proximate cause for this function is difficult to prove experimentally but circumstantial evidence suggests

that some animals copy many more behavioural actions than they actually incorporate into their everyday behaviour. Although very little is known about the nature of this kind of copying, which occurs mostly in animals that are strongly associated with humans, it can be assumed that it has an exploratory function. This form of copying seems to relate to play activities and depends on the novelty of the observed behaviour. This might also explain the rarity of such observations in nature where frequency of novel behaviours to be copied is probably much lower. The relationship between play and imitation has not been investigated but might present a good opportunity to compare the similarities and dissimilarities between human and ape copying. The lack of reinforcement, and the insignificance of both 'understanding' and accuracy in a play context might offer the best situation for the nature of the genetic predisposition behind copying to be revealed.

(2) Critical issues for future investigations

From the foregoing discussion it should be clear to the reader that attempting to find a simple and informative definition of imitation is a waste of time. The phenomenon is too complex to describe with a short sentence. Based on the previous suggestions of Byrne & Russon (1998) and Whiten (1998*a*) the following levels can be proposed: (1) copying increases the frequency of an already acquired motor pattern or changes its orientation in space ('response facilitation'); (2) copying modifies the motor pattern of an already acquired action ('action-level imitation'); (3) copying changes the sequential relationships between actions ('sequence imitation').

These levels represent increasing complexity of the supposed neural representation of the actions but are not exclusive, for example an animal might modify a motor pattern and at the same time re-order the sequences of its actions. The ability to assign any copied motor behaviour to one of these categories will depend crucially on the detailed description and comparison of the motor patterns. In other words, the detection of any copying activity rests crucially on the investigators' ability and willingness to compare the behaviour of the demonstrator and the observer. In future studies on imitation, investigators should aim to present evidence for distinguishing between the levels of copying. For example, observers might reproduce motor acts belonging to the same behavioural category (e.g. pulling) while not

copying lower-level motor details of the same action (e.g. pulling with both hands at the same time).

We have to take seriously the warning of ethologists that any hypotheses on aspects of animal behaviour should originate from field observations (e.g. Lehner, 1996). Interspecific differences observed under natural conditions might lead to hypotheses about the role of imitation in social transmission (Lefebvre, 1995). However, the number of detailed descriptions of the motor acts used in food processing and tool use in the wild is still limited. The assessment of the individual variability of these motor actions within a group together with the social relationships among individuals might indicate whether any form of social learning could be involved. For example, is the skilfulness or clumsiness of the mother reflected in her offspring's behaviour, or are youngsters that spend more time in the vicinity of their feeding or tool-using mother better at executing such kinds of behaviour? One might compare similar behaviour patterns of populations of the same species and make predictions as to how these can be maintained over generations (e.g. Boesch, 1996). In some special cases, researchers could even perform field experiments. For example, in the colony for rehabilitation of orangutans one might deliberately introduce new human activities (e.g. 'playing golf') that these animals have not witnessed before. By controlling the number, timing etc. of these demonstrations researchers could follow precisely the process of copying.

In the laboratory, three points have to be taken seriously (see also Bugnyar & Huber, 1997). (1) For any task presented to the animals, the variation in the motor actions should be quantified by exposing control observers to the context of the task in the absence of a demonstrator ('non-exposed controls'; Heyes *et al.*, 1993; see also Boesch, 1996). This type of observation is not only important in providing a control for the presence and actions of the demonstrator but also offers the possibility of determining the level of analysis of the motor pattern. It should be noted that this procedure does not in itself control for the effects of social facilitation. For example, an observer could watch a human experimenter hiding food behind a door before being given the opportunity to retrieve the food itself. The behaviour of the observers should allow the researcher to estimate the 'power' of trial-and-error learning in the given species, and also the type of motor pattern that might emerge during the solution of the task in the naive animal. If all subjects show a low variation in their low-level motor pattern during the acquisition

of the task, then there might be little to learn as a result of the observation of a conspecific. In contrast, high variation in the motor pattern might indicate that the observation of a skilled conspecific would enhance the success of the observer.

(2) The training of the demonstrators is also important. The behaviour of the demonstrators should reflect the level of analysis. An exact description of the motor behaviour of the demonstrators at the end of the training and during their role as demonstrator is essential.

(3) After exposure to the demonstrators, the behaviour of observer animals should be described in a similar manner. The reason for this can be understood easily when attempting to explain the results of a study. For example, if it is shown that naive animals displayed gross motor activities (e.g. 'pulling', 'pecking') during trial-and-error learning, and in the observers the frequency of the relevant action increases after observation, then the copying witnessed can be described as 'response facilitation'. However, if one shows that the particular motor pattern is virtually absent in naive animals but is frequent after observation, then it is more likely that animals have modified the motor details of their action and the results can be interpreted as 'action-level' imitation. Thus, by changing the level of analysis one might be better able to determine the particular features that they have learnt as a result of the exposure.

In my view, future laboratory experiments should concentrate on the following four aspects of copying. (1) For any species and task under investigation it should be clear whether copying is under the control of reinforcement. It is likely that copying behaviour with divergent reinforcement or without reinforcement are related to its divergent functions in the social life of the species. It can be proposed that species with a strong genetic predisposition to copying will copy motor behaviour of conspecifics in the absence of reward. In some species, this might also be a function of age, i.e. younger animals may be more likely to copy. The tendency to copy without reinforcement can be examined by allowing a subject to learn by trial and error to solve a task, and then exposing it to an alternative method of task solving presented by a demonstrator. Observers that are eager to copy will attempt to incorporate the demonstrator's behaviour into their own behavioural repertoire.

(2) The effect of separation of the demonstrator from the observer, and of its relationship to the observer (unfamiliar, familiar or close relative etc.)

should be given more attention. Experiments could establish whether copying is more likely to occur in unseparated animals or whether it is inhibited by the presence and interaction of other group members (see also Russon, 1996; Lefebvre & Helder, 1997). For example, observers could be exposed to two different demonstrators (one at a time) performing different behaviours. One could ask whether observers show a preference for copying the behaviour of one or the other demonstrator depending on their familiarity, relatedness, age etc.

(3) Only a limited number of studies have aimed at examining the role of memory in animal copying. At present we do not know how the number of demonstrations and the delay between observation and reproduction affects copying. It might be the case that for more complex motor behaviours even chimpanzees need an 'incubation period' before successful reproduction of the observed action (see Moore, 1992; Whiten, 1998*b*).

(4) It is unlikely that the conditions of demonstrations will conform to those present during reproduction by the observer. Therefore, one should suppose some ability to generalize on the part of the observer. Studies are seriously lacking where the context for demonstration and reproduction is systematically varied.

The effect of the age of the observer should also be taken into account by conducting developmental studies on copying activities. It needs to be examined whether there is a relationship between the ability to understand and copy or whether the genetically driven copying activities of younger animals counter-balance their lack of understanding. The relationship between play behaviour and imitation needs to be reexamined. It seems that in some species animals are more likely to reproduce observed motor patterns if they are playing.

Species clearly differ to a large degree in their species-specific motor movements and in the extent to which these behaviours can be modified. This means that there are genetically determined constraints on an animal regarding the representation of its and others actions. At this stage it is difficult to assess whether in relative terms, by copying others, marmosets or chimpanzees perform the more difficult computational processes given that these species also differ in their computational demands for the 'everyday' execution of behaviour. It might be that for a marmoset it is as difficult to copy the behaviour of a conspecific as for a chimpanzee. However, it is another question whether information gained by imitation will be

accessible to other functional parts of the brain, and whether re-representations of imitations can be 'used' in mindreading. Until these issues are clarified to some degree, it is difficult to ascertain what types of representations play a role in imitation.

IX. SUMMARY

In this review, I have attempted to demonstrate that detailed ethological analysis of imitation is not only possible but also necessary. The history of ethological research on animal behaviour has proved that the search for general mechanisms can be misguided. Recent evidence suggests that imitation might be involved in the transmission of food-processing skills but at present there is little, if any, widely accepted evidence for its role in the learning of tool use or visuo-motor communicative signals. Using the results of observational studies the role of imitation in play was also considered. In some species, imitation of other's behaviour can be a part of explorative play, however, more experimental evidence is needed.

Imitation is a complex form of learning and can be separated only with difficulty from other forms of social learning. Therefore, it is important that future studies recognize the significance of describing both the behaviour of the observer and the demonstrator in detail at different levels of motor action. By investigating the mechanisms of imitation it was shown that there might be an important distinction as to whether species imitate only in the presence of extrinsic 'reinforcement' or not which could be connected with a genetic predisposition to imitation that also has been neglected in studies to date. Imitative behaviour serving different functions across species might be based on different mechanisms. Only an integrated approach to function and mechanism will eventually lead to the understanding of imitation.

Imitation in apes is often regarded as homologous with similar capacities of humans. However, the interactive nature of imitation (between demonstrator and observer) in humans has not been found in other animals, and this ability greatly enhances the importance of imitation in humans compared to other forms of social learning.

X. ACKNOWLEDGEMENTS

This paper was written while the author enjoyed the hospitality of the Centre of Neuroscience at the University of Sussex and was supported by a fellowship of the Royal

Society. I also would like to thank Colin Allen, Marc Bekoff, Gordon Burghardt, Vilmos Csányi, George Kemenes and Carolyn Ristau for commenting on an earlier version of this manuscript and correcting with enthusiasm my 'frail' English. I would especially thank Andrew Whiten for his exhaustive comments and criticism that helped me to a great degree in clarifying my own thoughts about issues on imitation. Richard Andrew gave valuable advice on how to express my thoughts in a precise way. My work on social learning is also supported by a grant of the Hungarian OTKA foundation.

XI. REFERENCES

- ABRAVANEL, E. & GINGOLD, H. (1985). Learning via observation during the second year of life. *Developmental Psychology* **21**, 614–623.
- AINER, R. & TERKEL, J. (1992). Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. *Animal Behaviour* **44**, 327–336.
- AKINS, C. K. & ZENTALL, T. R. (1996). Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *Journal of Comparative Psychology* **110**, 316–320.
- BALDWIN, D. A., MARKMAN, E. M. & MELARTIN, R. L. (1993). Infants' ability to draw inferences about non-obvious object properties – evidence from exploratory play. *Child Development* **64**, 711–728.
- BARNAT, S. B., KLEIN, P. J. & MELTZOFF, A. N. (1996). Deferred imitation across changes in context and object: Memory and generalization in 14-month-old infants. *Infant Behavior Development* **19**, 241–251.
- BAUER, G. B. & JOHNSTON, C. M. (1994). Trained motor imitation by bottle-nosed dolphins (*Tursiops truncatus*). *Perceptual and Motor Skills* **79**, 1307–1315.
- BEKOFF, M. (1976). Animal play, problems and perspectives. In *Perspectives in Ethology*, vol. 2 (ed. P. P. G. Bateson and P. H. Klopfer), pp. 165–188. Plenum Press, New York.
- BEKOFF, M. (1995). Cognitive ethology and the explanation of nonhuman animal behaviour. In *Comparative Approaches to Cognitive Science* (ed. H. L. Roitblat and J.-A. Meyer), pp. 119–150. MIT Press, Cambridge, Massachusetts.
- BEKOFF, M. & ALLEN, C. (1998). Intentional communication and social play: how and why animals negotiate and agree to play. In *Animal Play* (ed. M. Bekoff and J. A. Byers), pp. 97–114. Cambridge University Press, Cambridge.
- BEKOFF, M. & BYERS, J. A. (1981). A critical reanalysis of the ontogeny of mammalian social and locomotor play. An ethological hornet's nest. In *Behavioural Development, The Bielefeld Interdisciplinary Project* (ed. K. Immelman, G. W. Barlow, L. Petrinovich and M. Main), pp. 296–337. Cambridge University Press, New York.
- BOESCH, C. (1991). Teaching in wild chimpanzees. *Animal Behaviour* **41**, 530–532.
- BOESCH, C. (1993). Transmission of tool-use in wild chimpanzees. In *Tools, Language, and Cognition in Human Evolution* (ed. K. R. Gibson and T. Ingold), pp. 171–183. Cambridge University Press, New York.
- BOESCH, C. (1996). The emergence of cultures among wild chimpanzees. In *Evolution of Social Behaviour Patterns in Primates and Man* (ed. W. G. Runciman, J. Maynard-Smith and R. I. M. Dunbar), pp. 251–268. The British Academy.
- BOESCH, C. & BOESCH, H. (1983). Optimization of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* **83**, 265–286.
- BOESCH, C. & BOESCH, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica* **54**, 86–99.
- BOESCH, C., MARCHESI, P., MARCHESI, N., FRUTH, B. & JOULIAN, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution* **26**, 325–338.
- BOYSEN, S. T. & BERNTSON, G. G. (1989). Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavioral Processes* **21**, 82–86.
- BOYSEN, S. T. & BERNTSON, G. G. (1995). Numerical competence in a chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology* **103**, 23–31.
- BRUNER, J. S. (1972). Nature and uses of immaturity. *American Psychologist* **27**, 687–708.
- BUGNYAR, T. & HUBER, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour* **54**, 817–831.
- BYRNE, R. W. (1994). The evolution of intelligence. In *Behavior and Evolution* (ed. P. J. B. Slater and T. R. Halliday), pp. 223–264. Cambridge University Press, Cambridge.
- BYRNE, R. W. (1995). *The Thinking Ape. The Evolution of Intelligence*. Oxford University Press, Oxford.
- BYRNE, R. W. & BYRNE, J. M. E. (1993). Variability and standardization in the complex leaf-gathering tasks of mountain gorillas (*Gorilla g. beringei*). *American Journal of Primatology* **31**, 241–261.
- BYRNE, R. W. & RUSSON, A. E. (1998). Learning by imitation: A hierarchical approach. *The Behavioural and Brain Sciences* **21**, 667–721.
- BYRNE, R. W. & TOMASELLO, M. (1995). Do rats ape? *Animal Behaviour* **50**, 1417–1420.
- CALL, J. & TOMASELLO, M. (1995). Use of social information in the problem solving of orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology* **109**, 308–320.
- CHALMEAU, R. & GALLO, A. (1993). Social constraints determine what is learned in the chimpanzee. *Behavioural Processes* **28**, 173–180.
- CHURCH, R. M. & MECK, W. H. (1983). Acquisition and cross-modal transfer of classification rules for temporal intervals. In *Quantitative Analyses of Behaviour*, vol. 4 (ed. M. L. Commons, R. J. Herrenstein and A. R. Wagner), pp. 75–97. Ballinger, Cambridge.
- CLARK, R. (1977). What's the use of imitation? *Journal of Child Language* **4**, 341–358.
- CUSTANCE, D. M., WHITEN, A. & BARD, K. A. (1995). Can young chimpanzee (*Pan troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour* **132**, 837–857.
- DAWSON, B. V. & FOSS, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour* **13**, 470–474.
- DONALD, M. (1991). *Origins of the Modern Mind*. Harvard University Press, Cambridge, Massachusetts.
- DRUMMOND, H. (1981). The nature and description of behaviour pattern. In *Perspectives in Ethology*, vol. 3 (ed. P. P. G. Bateson and P. H. Klopfer), pp. 1–30. Plenum Press, New York.
- ECKERMAN, C. O. (1993). Imitation and toddlers' achievement of co-ordinated action with others. In *New Perspectives in Early Communication and Development* (ed. J. Nadel and L. Camaioni), pp. 116–138. Routledge, London.

- ECKERMAN, C. O. & DIDOW, S. M. (1989). Toddlers social coordinations: changing responses to another's invitation to play. *Developmental Psychology* **25**, 440–453.
- ECKERMAN, C. O. & STEIN, M. R. (1990). How imitation begets imitation and toddlers' generation of games. *Developmental Psychology* **26**, 370–378.
- EISENBERG, N., MCCREATH, H. & AHN, R. (1988). Viscarious emotional responsiveness and prosocial behaviour. *Personality and Social Psychological Bulletin* **14**, 298–311.
- ETTLINGER, G. & WILSON, W. A. (1990). Cross-modal performance: behavioural processes, phylogenetic considerations and neural mechanisms. *Behavioral Brain Research* **40**, 169–192.
- FAGEN, R. (1981). *Animal Play Behaviour*. Oxford University Press, New York.
- FISHER, J. & HINDE, R. A. (1949). The opening of milk bottles by birds. *British Birds* **42**, 347–357.
- FOUTS, R. S., HIRSCH, A. D. & FOUTS, D. H. (1982). Cultural transmission of a human language in a chimpanzee mother–infant relationship. In *Child Nurture*, vol. 3. Studies of development in nonhuman species (ed. H. E. Fitzgerald, J. A. Mullins and P. Gage). Plenum Press, New York.
- FOUTS, R. S., FOUTS, D. H. & VAN CANTFORT, T. E. (1989). The infant Loulis learns signs from cross-fostered chimpanzees. In *Teaching Sign Language to Chimpanzees* (ed. R. A. Gardner, B. T. Gardner and T. E. Van Cantfort), pp. 280–292. State University of New York Press, New York.
- FRITZ, J. & KORTSCHAL, K. (1999). Social learning in common ravens (*Corvus corax*). *Animal Behaviour*. In Press.
- GALEF, B. G. (1985). Social learning in wild Norway rats. In *Issues in the Ecological Study of Learning* (ed. T. D. Johnston and A. T. Pietrewicz), pp. 143–166. Lawrence Erlbaum Associates, Hillsdale.
- GALEF, B. G. (1988). Imitation of animals: history, definition and interpretation of data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives* (ed. T. R. Zentall and B. G. Galef), pp. 207–223. Lawrence Erlbaum, Hillsdale.
- GALEF, B. G., MANZIG, L. A. & FIELD, R. M. (1986). Imitation in budgerigars: Dawson & Foss (1965) revisited. *Behavioral Processes* **13**, 191–202.
- GARDNER, R. A., GARDNER, B. T. & VAN CANTFORT, T. E. (1989). *Teaching Sign Language to Chimpanzees*. State University of New York Press, Albany.
- GARDNER, M. R. (1997). Imitation: The methodological adequacy of directional control tests. Unpublished doctoral thesis. University of London.
- GESELL, A. (1942). *Wolf Child and Human Child*. London: The Scientific Book Club.
- GEWIRTZ, J. L. (1969). Mechanisms of social learning: some roles of stimulation and behaviour in early human development. In *Handbook of Socialized Theory and Research* (ed. D. A. Goslin). Rand McNally, Chicago.
- GEWIRTZ, J. L. & STINGE, K. G. (1968). Learning of generalized imitation as the basis for identification. *Psychological Review* **75**, 374–397.
- GIRALDEAU, L. A. & LEFEBVRE, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour* **35**, 387–394.
- GOODALL, J. (1973). Cultural elements in a chimpanzee community. In: *Precultural Primate Behaviour* (ed. E. W. Menzel), pp. 144–181. Krager, Basel.
- GOODALL, J. (1986). *The Chimpanzees of Gombe: Patterns of Behaviour*. Harvard University Press, Cambridge, Mass.
- GOPNIK, A. & MELTZOFF, A. N. (1994). Minds, bodies, and persons: Young children's understanding of the self and others as reflected in imitation and theory of research. In *Self-Awareness in Animals and Humans. Developmental Perspectives* (ed. S. T. Parker, R. W. Mitchell and M. L. Boccia), pp. 166–186. Cambridge University Press, Cambridge.
- GOULD, S. J. & VBRA, E. S. (1982). Exaptation – a missing term in the science of form. *Paleobiology* **8**, 4–15.
- GRASYÁN, E. (1985). *The Neurobiology of Play*, pp. 1–66. Akademiai Kiadó, Budapest (in Hungarian).
- HATFIELD, E., CACIOPPO, J. T. & RAPSON, R. L. (1993). Emotional contagion. *Current Directions in Psychological Science* **2**, 96–99.
- HARLOW, H. F. (1951). Learning and satiation of response in intrinsically motivated complex puzzle performance by monkeys. *Journal of Comparative Psychological Physiology* **43**, 289–294.
- HARLOW, H. F., HARLOW, M. K. & MEYER, D. R. (1950). Learning motivated by manipulation drive. *Journal of Experimental Psychology* **40**, 228–234.
- HAYES, K. J. & HAYES, C. (1952). Imitation in a home-raised chimpanzee. *Journal of Comparative Physiology Psychology* **45**, 450–459.
- HEYES, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour* **46**, 999–1010.
- HEYES, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Review of the Cambridge Philosophical Society* **6**, 207–231.
- HEYES, C. M. (1995). Imitation and flattery: a reply to Byrne & Tomasello. *Animal Behaviour* **50**, 1421–1424.
- HEYES, C. M. (1998). Theory of mind in nonhuman primates. *The Behavioural and Brain Sciences* **21**, 101–154.
- HEYES, C. M. & DAWSON, G. R. (1990). A demonstration of observational learning using a bidirectional control. *Quarterly Journal of Experimental Psychology* **42b**, 59–71.
- HEYES, C. M., JALDOW, E. & DAWSON, G. R. (1993). Observational extinction: observation of non-reinforced responding reduces resistance to extinction in rats. *Animal Learning Behavior* **21**, 221–225.
- INOUE-NAKAMURA, N. & MATSUZAWA, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **111**, 159–173.
- JAMIESON, D. & BEKOFF, M. (1992). On aims and methods of cognitive ethology. *Philosophical Science Association* **2**, 110–124.
- JOHNSTON, T. D. (1981). Contrasting approaches to a theory of learning. *The Behavioural and Brain Sciences* **4**, 125–173.
- KAWAI, M. (1965). Newly-acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima Islet. *Primates* **6**, 1–30.
- KÖHLER, W. (1926). *The Mentality of Apes*. Routledge & Kegan Paul.
- KRAUSE, M. A. & FOUTS, R. S. (1997). Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology* **111**, 330–336.
- LANE, H. (1976). *The Wild Boy of Aveyron*. Harvard University Press, Cambridge, Mass.
- LEAVENS, D. A., HOPKINS, W. D. & BARD, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **110**, 346–353.
- LEFEBVRE, L. (1995). Ecological correlates of social learning problems and solutions for the comparative method. *Behavioral Processes* **35**, 163–171.
- LEFEBVRE, L. & HELDER, R. (1997). Scrounger numbers and

- the inhibition of social learning in pigeons. *Behavioral Processes* **40**, 201–207.
- LEHNER, P. N. (1996). *Handbook of Ethological Methods*. Cambridge University Press, Cambridge.
- MARTIN, P. & CARO, T. M. (1985). On the functions of play and its role in behavioural development. *Advances in the Study of Behaviour* **15**, 59–103.
- MELTZOFF, A. N. (1988a). Imitation, objects, tools and the rudiments of language in human ontogeny. *Human Evolution* **1–2**, 45–64.
- MELTZOFF, A. N. (1988b). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental Psychology* **24**, 470–476.
- MELTZOFF, A. N. (1988c). Infant imitation and memory: Nine-month-old in immediate and deferred tests. *Child Development* **59**, 217–225.
- MELTZOFF, A. N. (1988d). The human infant as homo imitans: In *Social Learning: Psychological and Biological Perspectives* (ed. T. R. Zentall and B. G. Galef), pp. 319–341. Lawrence Erlbaum, Hillsdale.
- MELTZOFF, A. N. (1990). Foundations of developing a concept of self: The role of imitation in relating self to other and the value of social mirroring and self practice in infancy. In *The Self in Transition: Infancy to Childhood* (ed. D. Cicchetti and M. Beeghly), pp. 139–164. University Chicago Press, Chicago.
- MELTZOFF, A. N. (1996). The human infant as imitative generalist: A 20-year progress report in infant imitation with implications for comparative psychology. In *Social Learning in Animals: The Roots of Culture* (ed. B. G. Galef and C. M. Heyes), pp. 347–370. Academic Press, New York.
- MELTZOFF, A. N. & MOORE, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science* **198**, 75–78.
- MELTZOFF, A. N. & MOORE, M. K. (1994). Imitation, memory, and the representation of persons. *Infant Behavior Development* **17**, 83–99.
- MENZEL, E. W. (1973). Leadership and communication in young chimpanzees. In *Precultural Primate Behaviour* (ed. E. W. Menzel), pp. 192–225. Karger, Basel.
- MIKLÓSI, Á. (1998). In the search for the functional homology of human imitation: Take play seriously! *The Behavioural and Brain Sciences* **21**, 699–700.
- MIKLÓSI, Á. (1999). From grasping to speech: imitation might provide a missing link. *Trends in Neurosciences* **22**, 151–152.
- MILLER, N. E. & DOLLAR, J. (1941). *Social Learning and Imitation*. Yale University Press, New Haven, Conn.
- MITCHELL, R. W. (1987). A comparative developmental approach to understanding imitation. In *Perspectives in Ethology*, vol. 7 (ed. P. P. G. Bateson and P. H. Klopfer), pp. 183–215. Plenum Press, New York.
- MITCHELL, R. W. (1994). Primate cognition: Simulation, self-knowledge, and knowledge of other minds. In *Hominid Culture in Primate Perspectives* (ed. D. Quiatt and J. Itani), pp. 177–232. University Press of Colorado, Nivet.
- MOORE, B. R. (1992). Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* **122**, 231–263.
- MORAN, G., KRUPKA, A., TUTTON, A. & SYMONS, D. (1987). Patterns of maternal and infant imitation during play. *Infant Behavior Development* **10**, 477–491.
- MORGAN, C. L. (1894). *Introduction to Comparative Psychology*. Scott, London.
- MYOWA, M. (1996). Imitation of facial gestures by an infant chimpanzee. *Primates* **37**, 207–213.
- NAGELL, K., OLGUIN, R. S. & TOMASELLO, M. (1993). Process of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology* **107**, 174–186.
- PALAMETA, B. & LEFEBVRE, L. (1985). The social transmission of a food-finding technique in pigeons: what is learned? *Animal Behaviour* **33**, 892–896.
- PARKER, S. T. & MILBRATH, C. (1995). Contributions of imitation and role-playing games to the construction of self in primates. In *Self-awareness in Animals and Humans. Developmental Perspectives* (ed. S. T. Parker, R. W. Mitchell and M. L. Boccia), pp. 166–186. Cambridge University Press, Cambridge.
- PELLEGRINO, DI G., FOGASSI, L. F., GALLESE, V. & RIZZOLATTI, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research* **91**, 176–180.
- PERRETT, D. I., HIETANEN, J. K., ORAM, M. W. & BENSON, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society London B* **335**, 23–30.
- PIAGET, J. (1962). *Play, Dreams and Imitation in Childhood*. W. W. Norton, New York.
- RODGON, M. M. & KURDEK, L. A. (1977). Vocal and gestural imitation in 8-, 14-, and 20-month-old children. *Journal of Genetic Psychology* **131**, 115–123.
- RUSSON, A. E. (1996). Imitation in everyday use: Matching and rehearsal of the spontaneous imitation of rehabilitant orangutans (*Pongo pygmaeus*). In *Reaching into Thought* (ed. A. Russon, K. Bard and S. T. Parker), pp. 152–176. Cambridge University Press, Cambridge.
- RUSSON, A. E. (1997). Exploiting the expertise of others. In *Machiavellian Intelligence II. Extensions and Evaluations* (ed. A. Whiten and R. W. Byrne), pp. 174–206. Cambridge University Press, Cambridge.
- RUSSON, A. E. (1999). Orangutans' imitation of tool use: a cognitive interpretation. In *The Mentalities of Gorillas and Orangutans in Comparative Perspectives* (ed. S. T. Parker, R. M. Mitchell and H. L. Miles), pp. 117–146. Cambridge: Cambridge University Press.
- RUSSON, A. E. & GALDIKAS, B. M. F. (1993). Imitation in free-ranging rehabilitant orangutans. *Journal of Comparative Psychology* **107**, 147–161.
- RUSSON, A. E. & GALDIKAS, B. M. F. (1995). Constrains on great apes' imitation: Model and action selectivity in rehabilitant orangutan (*Pongo pygmaeus*) imitation. *Journal of Comparative Psychology* **109**, 5–17.
- RUSSON, A. E., MITCHELL, R. W., LEFEBVRE, L. & ABRAVANEL, E. (1997). The comparative evolution of imitation. In *Piaget, Evolution & Development* (ed. J. Langer and M. Killen), pp. 103–143. Lawrence Erlbaum Associates: Hillsdale.
- SCHILLER, P. H. (1952). Innate constituents of complex responses in primates. *Psychological Review* **59**, 177–191.
- SLATER, P. J. B. (1973). Describing sequences of behaviour. In *Perspectives in Ethology*, vol. 3 (ed. P. P. G. Bateson and P. H. Klopfer), pp. 131–151. Plenum Press, New York.
- SPEIDEL, G. E. & NELSON, K. E. (1989). *The Many Faces of Imitation in Language Learning*. Springer Verlag, New York.
- SUGIYAMA, Y. & KOMAN, J. (1979). Tool-using and making behaviour in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524.
- TAYLER, C. K. & SAAYMAN, G. S. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*). *Behaviour* **44**, 286–298.

- TERKEL, J. (1995). Cultural transmission in the black rat: Pine cone feeding. In *Advances in the Study of Behaviour* (ed. P. J. B. Slater, J. S. Rosenblatt, C. Beer and M. Milinski), pp. 119–152. Academic Press, New York.
- TINBERGEN, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.
- THORPE, W. H. (1956). *Learning and Instinct in Animals*. Methuen, London.
- TOMASELLO, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In *'Language' and Intelligence in Monkeys and Apes* (ed. S. T. Parker and K. R. Gibson), pp. 247–273. Cambridge University Press, Cambridge.
- TOMASELLO, M. & CALL, J. (1997). *Primate Cognition*. Oxford University Press, Oxford.
- TOMASELLO, M., DAVIS-DASILVA, M., CAMAK, L. & BARD, K. (1987). Observational learning of tool use by young chimpanzees and enculturated chimpanzees. *Human Evolution* **2**, 175–183.
- TOMASELLO, M., GEORGE, B. L., KRUGER, A. C., FARRAR, M. J. & EVANS, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution* **14**, 175–186.
- TOMASELLO, M., GUST, D. & FROST, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzee. *Primates* **30**, 35–50.
- TOMASELLO, M., KRUGER, A. E. & RATNER, H. (1993a). Cultural learning. *The Behavioural and Brain Sciences* **16**, 495–552.
- TOMASELLO, M., SAVAGE-RUMBAUGH, S. & KRUGER, A. C. (1993b). Imitative learning of actions on objects by children, chimpanzees and excultured chimpanzees. *Child Development* **64**, 1688–1705.
- UZGIRIS, I. C. (1981). Two functions of imitation during infancy. *International Journal of Behavioral Development* **4**, 1–12.
- VISALBERGHI, E. (1993). Capuchin monkeys: A window into tool use in apes and humans: In *Tools, Language, and Cognition in Human Evolution* (ed. K. R. Gibson and T. Ingold), Cambridge University Press, Cambridge.
- VISALBERGHI, E. & FRAGASZY, D. (1990). Do monkeys ape? In *Language and Intelligence in Monkeys and Apes* (ed. S. T. Parker and K. R. Gibson), pp. 247–273. Cambridge University Press, Cambridge.
- WERNER, N. (1948). *Comparative Psychology of Mental Development*. International Universities Press, New York.
- WHITEN, A. (1998a). How imitator represent the imitated: the vital experiments. *The Behavioural and Brain Sciences* **21**, 707–708.
- WHITEN, A. (1998b). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **112**, 270–281.
- WHITEN, A. (1999a). Chimpanzee cognition and the question of mental re-representation. In *Metarepresentation* (ed. D. Sperber), Oxford University Press, Oxford. *In Press*.
- WHITEN, A. (1999b). Primate culture and social learning. *Cognitive Science*. *In Press*.
- WHITEN, A. & BYRNE, R. W. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Clarendon Press, Oxford.
- WHITEN, A. & BYRNE, R. W. (1991). The emergence of metarepresentation in human ontogeny and primate phylogeny. In *Natural Theories of Mind* (ed. A. Whiten), pp. 267–281. Blackwell, Oxford.
- WHITEN, A. & BYRNE, R. W. (1997). *Machiavellian Intelligence II. Extensions and Evaluations*. Cambridge University Press, Cambridge.
- WHITEN, A. & CUSTANCE, D. (1996). Studies of imitation in chimpanzees and children. In *In Social Learning in Animals: The Roots of Culture* (ed. B. G. Galef and C. M. Heyes), pp. 347–370. Academic Press, New York.
- WHITEN, A., CUSTANCE, D. M., GÓMEZ, J. C., TEIXIDOR, P. & BARD, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* **110**, 3–14.
- WHITEN, A. & HAM, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In *Advances in the Study of Behaviour* (ed. P. J. B. Slater, J. S. Rosenblatt, C. Beer and M. Milinski), pp. 239–283. Academic Press, New York.
- YANDO, R., SEITZ, V. & ZIGLER, E. (1978). *Imitation: A Developmental Perspective*. John Wiley & Sons, New York.
- ZENTALL, T. R. (1996). Analysis of imitative learning in animals. In *In Social Learning in Animals: The Roots of Culture* (ed. B. G. Galef & C. M. Heyes), pp. 347–370. Academic Press, New York.
- ZENTALL, T. R., SUTTON, J. E. & SHERBURNE, L. M. (1996). True imitative learning in pigeons. *Psychological Science* **7**, 343–346.