Imitative and Nonimitative Social Learning In a Two - Object / Two - Action Procedure

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"But rats..." I objected.

"Rats are highly intelligent creatures. If we want to find out anything new about the human body we experiment on rats. Rats indeed are ahead of us indisputably in one respect - they live underground. We only began to live underground during the last war. Rats have understood the danger of surface life for thousands of years. When the atom bomb falls the rats will survive. What a wonderful empty world it will be for them, though I hope they will be wise enough to stay below. I can imagine them evolving very quickly. I hope they don't repeat our mistake and invent the wheel."

(Travels With My Aunt, Graham Greene; p. 246-247)

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Abstract

It is widely believed that observation of a conspecific performing an action on an object for food can facilitate acquisition of the observed response via imitative, in addition to, nonimitative social learning. Imitative social learning consists of response learning by observation (Heyes, 1993; Heyes & Ray, in press). It allows animals to learn responses, actions, or patterns of behaviour; how to execute them and what are their consequences (observational learning or imitation). Nonimitative social learning, on the other hand, consists of stimulus learning by observation (Heyes, 1993; Heyes & Ray, in press). It is the means by which animals acquire information about stimuli, objects, or events in the environment; their presence or location (stimulus enhancement), dynamic properties (emulation learning), and/or value (observational conditioning).

The experiments reported in this thesis used a two-object/two-action procedure in an attempt to distinguish these two forms of learning (Ray, 1997). In Experiment 1, naive rats observed from one side of an operant chamber while demonstrators manipulated either a left or a right lever by lifting up or pressing down. When subsequently allowed access to the levers on test and rewarded for all responses, regardless of location and direction, observer rats showed a reliable tendency to manipulate the same lever in the same direction as their demonstrator. Unfortunately, these effects were not particularly robust. Numerous attempts to replicate Experiment 1 yielded either the location effect, the direction effect, or no effect of conspecific observation. Only in the reported experiment were both effects obtained simultaneously.

Despite this problem, these results are still consistent with the hypothesis that rats can acquire information about both a stimulus and a response through conspecific observation. However, follow-up studies failed to support this impression. Instead, they indicated that although

a number of different of social influences may act upon the rat's behaviour in a two-object/two-action procedure, response learning by observation may not be one of them.

In Experiments 4-7, whether rats were exposed to the delivery of food following each of their demonstrator's responses was manipulated in order to examine the role played by demonstrator reinforcement in lever choice. These experiments confirmed previous findings by showing that rats are exposed to levers as a result of observing them pressed (Heyes, Ray, Mitchell, & Nokes, 1999), and, in addition, revealed that reinforcement of demonstrators' responses increased the probability that rats would approach and contact the lever which their demonstrator operated. Once in the vicinity of the lever, rats encountered odour cues deposited by demonstrators during the course of instrumental responding. These cues were found to be sufficient to bias rats' responses in favour of their demonstrator's direction (Experiments 2 and 3).

A two-object/two-action procedure was also used in Experiment 8, where naive starlings observed demonstrators displacing either a red or a black plug from a hole in the lid of a plastic box by lifting up or pressing down. When presented with a sealed box on test, observer birds displaced the same plug in the same direction as their demonstrator. In contrast to rats, starlings showed strong effects of conspecific observation that could not be accounted for by demonstrator-deposited odour cues. Therefore, it is possible that this paradigm may be well-suited for the task of analysing both the psychological mechanisms of, and distinctive conditions favouring, imitative and nonimitative social learning.

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Chapter 1

Imitative and Nonimitative Social Learning In Animals

1. Introduction

Social learning refers to those instances in which the behaviour of a naive animal, the 'observer', is modified by observation of or interaction with another animal (typically a conspecific), the 'demonstrator', or its products (Heyes, 1994). Since formal research on the subject began a century ago (for a review see Galef, 1988), psychologists and biologists have investigated whether nonhuman animals (henceforward 'animals') are capable of some form of social learning, most notably imitation. However, attempts to demonstrate imitation in animals have been made difficult by the failure to define criteria by which it can be empirically distinguished from other forms of social learning.

In contrast, there are clear rules by which varieties of asocial learning (i.e. learning that does not involve social interaction) can be distinguished. According to animal learning theory, learning is a change in the animal that is caused by a specific experience at a certain time, t_1, and is detectable later, t_2, in the animal's behaviour (Rescorla, 1988). If, for example, animals are exposed to a single stimulus, then any change in the animal's behaviour would be classified as an example of habituation or sensitization depending on whether it constituted a decrease or an increase in responsiveness to that stimulus. Exposure to the relationship among stimuli (S-S) can also give rise to changes in responsiveness. However, in this instance the category of learning is classical conditioning. Finally, instrumental conditioning would be said to have occurred if, as the result of exposure to the relationship between a response and a reinforcer (R-S*), the animal's behaviour was modified.

Heyes (1994) has argued that similar rules can be used to define categories of social learning, which favours the hypothesis that the two sets of phenomena are mediated by common mechanisms. On the one hand, there is nonimitative social learning which consists of stimulus learning by observation (Heyes, 1993; Heyes & Ray, in press). It allows animals to learn about stimuli, objects, or events in the environment; their presence or location (stimulus enhancement), dynamic properties (emulation learning), and/or value (observational conditioning). On the other hand, there is imitative social learning which consists of response learning by observation (Heyes, 1993; Heyes & Ray, in press). It is the means by which animals acquire information about responses, actions, or patterns of behaviour; how to execute them and what are their consequences (observational learning or imitation).

The study of imitation in animals has been obstructed not only by the fact that it is difficult to isolate imitative from nonimitative social learning, but also from those processes that, although they do not constitute learning, may result in the behaviour of one animal resembling that of another. These processes have been assigned the generic name 'social enhancement' by Galef (1988), and can be placed in one of three different categories depending on whether the mere presence and/or behaviour of a conspecific:(i) acted as a releaser for the same behaviour in others (contagion), (ii) increased the rate at which other animals performed a target response (social facilitation), or (iii) attracted animals to an object or a site (local enhancement).

Over the course of the last 10 years, the two-action procedure has emerged as potentially the most powerful method for overcoming these problems. Animals in the two-action procedure are given the opportunity to observe conspecific demonstrators manipulating a single object in one of two different ways. During a subsequent test session in which the observers are given access to the object for the first time, a record is made of their responses. If animals engage in imitative social learning, or response learning by observation, then one would expect the observers to show a bias in favour of the demonstrator's action. Such an effect could not be due to social enhancement because, regardless of the topography of demonstrators' responses, the observers are exposed equally to the mere presence and/or behaviour of a conspecific. Nonimitative social learning, or stimulus learning by observation, is also an unlikely explanation because the observers differ only in their exposure to a stimulus array which is their demonstrator's behaviour.

Use of the two-action procedure is based on the assumption that in any given context it is possible to manipulate precisely the events to which animals are exposed in order to make strong inferences about which factors led to any change in the animal's behaviour (Zentall, 1996). It is likely that in most natural and experimental environments, providing animals with the opportunity to interact with demonstrators will result in both imitative and nonimitative social learning. By attempting to exclude all possibility of nonimitative social learning, two-action procedures may be creating situations far removed from the real world. Consequently, any paradigm which permits the simultaneous identification of behaviour which has been modified via response learning and stimulus learning by observation will be valuable. One potential example is the two-object/two-action procedure.

This chapter is divided into four parts. In Parts 1 and 2, categories of social enhancement and social learning are defined and distinguished. Part 3 is a survey of the most interesting and relevant studies of imitation in animals, which concludes with those employing the two-action procedure. Finally, Part 4 includes discussion of recent empirical work using a two-object/two-action procedure.

1.1 Social Enhancement

1.1.1 Contagion

Contagion refers to those instances in which "the performance of a more or less instinctive pattern of behaviour by one [animal] will tend to act as a releaser for the same behaviour in others" (Thorpe, 1963, p. 133). Examples of contagious behaviour include yawning in humans, chorusing in roosters, manoeuvring in flocks of birds and schools of fish, and the 'flying up' of partridge or quail (Galef, 1988).

The term contagious behaviour was first used to describe innate responses to releasing stimuli. However, it has since been applied in reference to acquired responses made in the presence of conditioned stimuli (e.g. Galef, 1988; Zentall, 1996). For example, birds that forage in flocks are likely to have considerable experience of pecking in the presence of other birds that are also pecking. Thus, the sight of another bird feeding might be expected to acquire, through a process of classical conditioning, the capacity to elicit pecking in the observer, or to serve as a conditioned stimulus (Clayton, 1978).

Innate and acquired contagious behaviour is usually avoided in experiments on social learning by studying novel or sufficiently improbable responses (Thorpe, 1963; Zentall, 1988).

1.1.2 Social facilitation

According to Zajonc (1965, 1969), social facilitation occurs when "the presence of others energizes all responses made salient by the stimulus situation confronting the individual at the moment. Among those, the dominant responses (i.e. those most likely to be emitted) are assumed to derive the greatest benefit from the presence of others" (1969, p. 10). If the dominant response is correct, performance will be improved by the presence of others. This may have been the case in a study by Bayer (1929), in which satiated hens resumed feeding when fed in the presence of a conspecific that had not eaten for 24 h. If, on the other hand, the dominant response is incorrect, performance will be impaired by the presence of others. For example, Gates & Allee (1933) found that groups of cockroaches trained to locate a dark shelter in a maze took longer to learn the task and made more errors than cockroaches trained in isolation.

Zajonc (1965) used the term social facilitation to describe the effects of passive spectators on a target individual's behaviour and coactors engaged in the same behaviour as the target individual. Both of which may have been demonstrated by Cadieu, Cadieu, & Lauga (1995). They found that juvenile canaries fed in the presence of their father ate more seed than juvenile canaries fed in isolation, and that this effect was particularly pronounced when the father had seed of his own available than when he had none. This suggests that while the mere presence of an adult bird increased the juveniles' rate of feeding, the general activity and/or consummatory behaviour of adult birds produced an additional increment in the juveniles' feeding rate.

However, these results do not provide unequivocal evidence of social facilitation as described by Zajonc (1965, 1969). First, juvenile canaries may have experienced considerable fear when isolated from their father. Consequently, the effect of the father's presence may not have been to increase feeding rate by raising arousal levels; it may have been to increase feeding rate by reducing isolation-induced fear (Clayton, 1978). Second, animals are not only less afraid when in the presence of others, they are also less vigilant. This suggests that juvenile canaries fed with their father may have eaten more seed than juvenile canaries fed alone, because they were able to devote more time to foraging. An interpretation which is strengthened by a study in which head-cocking and feeding rates were measured in individual woodpeckers that were foraging alone, with one or two other individuals, or in groups with three or more individuals (Sullivan, 1984). Sullivan found that head-cocking rate decreased with increasing group size, while feeding rate increased.

Thus, social facilitation refers to a heterogenous collection of phenomena that cannot be explained by a single underlying process. The mere presence and/or behaviour of a conspecific demonstrator may increase the rate at which an observer performs those responses most appropriate to the current stimulus situation in one of several different ways. The demonstrator may increase the observer's level of arousal, or reduce the observer's isolation-induced fear or the amount of time it devotes to vigilance.

1.1.3 Local enhancement

Local enhancement refers to "apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment" (Thorpe, 1963, p. 134). It has been used to account for the spread of a novel foraging behaviour, milk bottle opening, among populations of blue tits in England (Fisher & Hinde, 1949; Hinde & Fisher, 1951). If the spread of this behaviour occurred because the presence of feeding birds at milk bottles increased the attention paid to those milk bottles by naive birds, then this would be an example of local enhancement.

This interpretation is strengthened by an experiment in which naive black-capped chickadees observed conspecific demonstrators either opening and drinking from a tub of cream secured in the neck of a flask placed on a stand or sitting passively in the vicinity of a stand from which the flask and tub had been removed (Sherry & Galef, 1990). Sherry & Galef found that when birds observed tub-opening demonstrators they were no more likely to open tubs on test than when they observed demonstrators sitting passively in the vicinity of the stand. However, both groups were more likely to open tubs than birds that observed a stand but not a demonstrator during training. These findings suggest that the demonstrators drew the observers' attention to the stand and thereby facilitated acquisition of milk bottle opening.

The term local enhancement is usually reserved for those instances in which an animal's behaviour is modified by the opportunity to interact directly with one or more individuals. For example, individuals in groups forage more efficiently than isolates as measured by: (i) probability of finding food (great tit: Krebs, MacRoberts, & Cullen, 1972; dark-eyed junco: Baker, Belcher, Deutsch, Sherman, & Thompson, 1981; greenfinch: Ekman & Hake, 1988), (ii) mean food intake (downy woodpecker: Sullivan, 1984), (iii) rate of prey capture (cliff swallow: Brown, 1988; spider: Rypstra, 1989), (iv) food intake variability (cliff swallow: Brown, 1988; spider: Rypstra, 1989), and (v) time taken to find prey (osprey: Fleming, Smith, Seymour, & Bancroft, 1992). In each of these studies, the authors assumed that the advantages associated with group foraging resulted from local enhancement whereby animals were attracted to the site at which conspecifics were feeding. This assumption is supported by Knight & Knight (1983), who found that when arriving at an artificial food site bald eagles were more likely to land at patches attended by other eagles, crows, and/or ravens than at unattended patches. (See also Senar & Metcalfe, 1988 and Prior & Weatherhead, 1991 for a similar effect in siskins and turkey vultures).

However, demonstrators need not be present to influence another animal's behaviour, if as the result of their activity demonstrators bring about some change in the environment (Galef, 1988). In Israel, black rats feed on the seeds of Jerusalem pine cones which they open using a complex spiralling technique. Aisner & Terkel (1992) found that naive rats were unable to open pine cones even after three months of trial-and-error learning, whereas naive rats that were provided with cones from which a progressively decreasing number of rows of scales had been removed, either manually or by a conspecific, readily learned to open fully intact cones. Similarly, Sherry & Galef (1984) found that black-capped chickadees allowed to drink from milk bottles that had previously been opened by a conspecific, were more likely to open and drink from sealed milk bottles than chickadees that had never been given this opportunity.

According to Galef (1988), local enhancement may result from a tendency on the part of naive individuals to approach conspecifics or alterations conspecifics have made in the environment. For example, as the result of their tendency to swim with conspecifics, fish may exploit the food discovered by other individuals (juvenile walleye pollock: Ryer & Olla, 1992, 1995). They may also acquire a feeding route preference (guppies: Laland & Williams, 1997). Similarly, rats eat the same food other rats are eating as the result of their tendency to approach conspecifics (Galef, 1971; Galef & Clark, 1971, 1972) or residual cues that conspecifics have deposited (Galef & Beck, 1985), and begin feeding in their presence.

Thorpe (1963) used the term local enhancement to refer to those instances in which the presence of a demonstrator increases the amount of attention a naive animal pays to a particular object or to particular part of the environment. However, use of the term local enhancement in this manner is unnecessarily restrictive (Galef, 1988), because attentional processes cannot be measured directly and it is difficult to see how they could be inferred from behaviour (Heyes, 1994). Therefore, it may be more appropriate to regard local enhancement as resulting from increased exposure, rather than attention to, environmental stimuli.

Current use of the term local enhancement is consistent with the hypothesis that it facilitates learning about the stimulus to which demonstrators responded. However, if local enhancement is restricted to those periods in which two or more animals are interacting, or one animal is interacting with the products of another animal's behaviour, then it cannot conventionally be regarded as a form of learning. If, on the other hand, an animal continues to behave differentially towards stimuli when all traces of the demonstrator have gone, then local enhancement can be regarded as a form of learning, but it cannot be distinguished from stimulus enhancement (see Section 1.2.1.1). Thus, to retain local enhancement as a useful construct in research on social learning, it may be necessary to reserve the term for those instances in which an observer behaves differentially towards stimuli only in the presence of demonstrators or products of the demonstrators' activity (Heyes, 1994). Stimulus enhancement can then indicate cases in which an observer behaves differentially towards stimuli when all traces of the demonstrator have gone.

Local enhancement, as it is defined here, does not constitute a learning phenomenon. However, it may result from and/or result in learning. Both of these possibilities were identified in a study by Neuringer & Neuringer (1974) where pigeons were trained to follow and eat from an experimenter's hand. After training, the pigeons observed the hand approach and 'peck' a key whenever four overhead lights flashed. This action caused grain to appear in a hopper beneath the key at which the hand then pecked. These birds learned to peck the key for food, whereas birds that had been trained to follow the hand but had never seen the hand peck the key, or had seen the hand peck the key but had not previously been trained to follow it, did not. In this experiment, the hand exposed pigeons to the key and thereby facilitated learning about the key-food relationship, but only if the pigeons had been pretrained to follow the hand around the chamber.

1.1.4 Summary and conclusion

Social enhancement refers to those processes that, although they do not constitute learning, may lead to changes in another animal's behaviour. The mere presence or behaviour of a demonstrator may: (i) serve as a releaser for the same behaviour in others (contagion), (ii) increase the rate at which other animals perform those responses most appropriate to the current stimulus situation (social facilitation), and/or (iii) direct the animals' behaviour toward a particular object or site (local enhancement).

1.2 Social Learning

1.2.1 Nonimitative social learning

1.2.1.1 Stimulus enhancement

According to Spence (1937), stimulus enhancement is a "change in stimulus conditions, the enhancement of the particular limited aspect of the total stimulus situation to which the response is to be made" (p. 821). For example, Warden & Jackson (1935) placed pairs of monkeys in adjacent cages, each of which were equipped with one of several identical puzzle devices. One of the monkeys was restrained while the other monkey, which had previously been trained to solve the puzzle, demonstrated the solution a number of times. Observer monkeys were then released and given six 60 sec test sessions in which to solve the problem. On 46% of all such tests, the monkeys solved the puzzle immediately. If this was because the demonstrator's behaviour increased the probability that the observer would be exposed to stimuli of the same physical type as the demonstrator contacted, then this would be an example of stimulus enhancement.

To attribute a given instance of social learning to stimulus enhancement is to imply the operation of two learning processes. The first of which occurs during observation training when the demonstrator's behaviour renders attractive the stimuli with which it is interacting. The second process is instrumental learning and occurs in the presence or the absence of the demonstrator, when the observer gains access to stimuli of the same physical type as those to which the demonstrator was observed responding.

Stimulus enhancement differs from local enhancement in two respects. First, local enhancement refers to those instances in which animals behave differentially towards stimuli only in the presence of demonstrators or products of the demonstrators' activity. If animals behave differentially towards stimuli when all traces of the demonstrator have gone, stimulus enhancement can be said to have occurred. This may have been the case in a study by McQuoid & Galef (1992), in which naive Burmese red jungle fowl were allowed to observe conspecific demonstrators feeding from a bowl in one of four different locations. When subsequently allowed access to the bowls on test, observer fowl showed a reliable tendency to feed from the same location as their demonstrators. Local enhancement cannot account for this effect, because the demonstrators were not present when the observers were tested and testing was conducted 48h after the final demonstration trial, during which time any cues deposited by the demonstrators might be expected to have dissipated. Furthermore, the location of the four bowls was randomly interchanged between demonstration and testing such that any cues that were deposited by demonstrators and persisted during the 48h interval, would have been rendered irrelevant.

Second, local enhancement occurs when animals are attracted to the very same object (i.e. numerically identical) demonstrators contacted. Stimulus enhancement occurs when animals are attracted to objects with the same physical appearance (i.e. numerically distinct) as that demonstrators contacted. Petit & Thierry (1993) studied the use of stones by a group of captive Guinea baboons to dig holes in the floor of their enclosure. They suggested that following the discovery of stone use by a single individual, the behaviour spread to other group members by stimulus enhancement. However, for this interpretation to be supported it would be necessary to show that when first selecting a stone for use, baboons did not use the very same stone as the initiator of the behaviour, but selected one of a number of physically similar but numerically distinct stones.

Duplicate-cage procedures, in which demonstrators and observers contact numerically distinct stimuli have the potential to isolate stimulus enhancement from local enhancement. Laland & Plotkin (1990) allowed rats to observe, from one side of an enclosure, while a demonstrator dug up pieces of carrot buried beneath a layer of soil that covered the floor. These rats unearthed more pieces of carrot from their own side of the enclosure than rats that were exposed to the mere presence of a passive conspecific. This effect is unlikely to have been due to local enhancement, because rats were tested in a different area to that in which the demonstrators were observed. Thus, it may provide evidence of stimulus enhancement.

In studies where demonstrators and observers contact numerically identical stimuli, stimulus enhancement is confounded with local enhancement. Kohn (1976) allowed rats that had been trained to run down an alleyway into a goalbox and thereby avoid shock, to observe a demonstrator entering the goalbox via one of two different doors. Observer rats were then transferred into the alleyway and trained to enter either the same door as their demonstrator or the opposite door. Rats that were trained to enter the same door as their demonstrator took fewer trials to learn the discrimination than rats that were trained to enter the opposite door. These results are consistent with the hypothesis that response acquisition was influenced by the sight of the demonstrator contacting the door (stimulus enhancement). However, they fail to rule out the possibility that observer rats were attracted to the door on which demonstrators deposited odour cues (local enhancement). According to Kohn (1976), the apparatus was cleaned between observation and testing; although in the absence of information regarding the relative effectiveness of this procedure, local enhancement cannot be ruled out.

1.2.1.2 Emulation learning

Tomasello (1990) introduced the term emulation learning to refer to those instances in which a naive animal learns, as the result of observing the behaviour of another individual, about the affordances, or changes in state of, environmental stimuli. Tomasello, Davis-Dasilva, Comak, & Bard (1987) allowed juvenile chimpanzees to observe an adult female conspecific demonstrator using a metal T-bar to rake food into her cage. These chimpanzees subsequently learned to use the T-bar, whereas chimpanzees that had been allowed to observe the demonstrator in an unoccupied state throughout training trials did not. If this effect occurred because the chimpanzees learned by observation the affordances of the T-bar with respect to food, then this would be an example of emulation learning.

1.2.1.3 Observational conditioning

The term observational conditioning was coined by Cook, Mineka, Wolkenstein & Laitsch (1985), and is understood to be a form of classical conditioning in which a demonstrator's behaviour exposes an observer to the relationship between stimuli by acting as the source of the second stimulus. In the study by Cook *et al.* (1985), initially non-fearful rhesus monkeys observed a conspecific demonstrator behaving fearfully in the presence of real and toy snakes, and nonfearfully in the presence of neutral objects. When subsequently presented with the same stimuli on test, the observers became agitated in the presence of, and attempted to avoid, the snake stimuli. If this was because the observers learned a relationship between the demonstrator's fear display and the snake stimuli, then this would be an example of observational conditioning.

According to Heyes (1994), use of the term observational conditioning to describe situations in which a demonstrator's behaviour exposes an observer to the relationship between stimuli by acting as the source of the second stimulus, is inappropriately restrictive. There are numerous instances in the social learning literature where a demonstrator increases the likelihood that an observer will be exposed to an S-S relationship, but does not act as the source of the second stimulus. One example is provided by Palameta & Lefebvre (1985). They allowed pigeons to observe demonstrators piercing a hole in the paper lid covering a food bowl and eating from within. When provided with an intact food bowl on test, these pigeons solved the food-finding problem faster and with fewer pecks than pigeons that observed demonstrators either eating from a preexisting hole in the paper lid but not piercing it, or piercing a hole in the paper lid but not eating from it. This suggests that when pigeons observed pecking-and-eating demonstrators, they learned a relationship between the paper covered bowl and the availability of reward, and observational conditioning appears to be the most appropriate description of this effect.

In its original formulation, observational conditioning refers to acquisition of a pattern of behaviour which resembles that exhibited by a demonstrator. However, socially mediated exposure to an S-S relationship does not always yield matching behaviour. In a study by Mason & Reidinger (1982), red-winged blackbirds observed a conspecific demonstrator feeding out of one of two distinctively marked cups and then exhibit signs of illness. When subsequently presented with the same food cups on test, observer birds did not approach that out of which demonstrators had fed. Instead, they showed a strong tendency to avoid the demonstrator's food cup.

Furthermore, if observational conditioning and classical conditioning are mediated by common mechanisms, then one would expect observational conditioning to result in a wider range of phenomena than that described by Cook *et al.* (1985). Varieties of classical conditioning can be distinguished according to the nature of the relationship between stimuli (excitatory/inhibitory). The relationship between stimuli is excitatory if the first event predicts that the second event will occur, and inhibitory if the first event predicts that the second event will not occur. They can also be distinguished according to the value of the second stimulus for the animal, which may be either attractive (e.g. the delivery of food) or aversive (e.g. the delivery of shock). If this is correct, then one would expect that demonstrators would be able to expose observers to four different types of relationship between stimuli.

The effect of exposure to these four different types of relationship could be detected as a change in the capacity of the first stimulus to elicit a response. When the relationship between stimuli is excitatory and the second stimulus is attractive, then the first stimulus becomes more likely to elicit a response. This is called excitatory appetitive conditioning and may account for the study by Palameta & Lefebvre (1985). Excitatory aversive conditioning also refers to exposure to an excitatory relationship between stimuli, but in this case the second stimulus is aversive and there is a decline in the capacity of the first stimulus to elicit an active response. For example, Bunch & Zentall (1980) found that rats learned to avoid a candle flame after having observed a demonstrator making contact with the candle flame and getting burnt (see also Mason & Reidinger, 1982).

When the relationship between stimuli is inhibitory and the second stimulus is attractive, the first stimulus becomes less likely to elicit a response. This is called inhibitory appetitive conditioning and probably occurred in a study by Darby & Riopelle (1969), where rhesus monkeys observed demonstrators displacing one of two distinctive objects from above a hole in a tray. On half the trials the demonstrator's choice was rewarded with food, on the other half it was nonrewarded. When the demonstrator's choice was rewarded, the observers readily learned to select the object their demonstrator displaced. When the demonstrator's choice was nonrewarded, the observers selected the other object. This suggests that on nonrewarded trials the observers learned a negative relationship between the stimulus displaced by the demonstrator and food, and that on rewarded trials they learned a positive relationship between the same events.

Inhibitory aversive conditioning occurs when as a result of exposure to an inhibitory relationship between stimuli when the second stimulus is aversive, the first stimulus becomes more likely to elicit a response. In a study by Del Russo (1975), rats observed demonstrators rewarded for running from one side of a shuttlebox to the other whenever a tone sounded ~~in order to avoid~~ by delaying the onset of shock. When subsequently tested for their response to the tone, these animals made more avoidance responses than rats that were exposed to the tone but not to a demonstrator running during training, or to a demonstrator running but not to the tone. ~~Unfortunately, whether rats~~ If the rats in this experiment had previously experienced tone-shock pairings, either directly or vicariously, ~~is not known. However, if they did~~, then these results would suggest that rats that observed demonstrator running in response to the tone learned that the tone signalled shock would not occur.

The effect of exposure to a relationship among events cannot only be detected through changes in response evocation, but also through changes in the animal's ability to learn other relationships. Overshadowing occurs when exposure to an S_1-S_2 relationship at the same time as an S_3-S_2 relationship reduces the degree to which the animal learns about the S_3-S_2 relationship. Blocking, on the other hand, refers to those instances in which previous experience of an S_1-S_2 relationship reduces the degree to which the animal learns about an S_3-S_2 relationship when it is presented at the same time as the S_1-S_2 relationship. Overshadowing and blocking are characteristic of classical conditioning. Therefore, if observational conditioning and classical conditioning are mediated by similar mechanisms, one would expect to find examples of overshadowing and blocking in the social learning literature.

Beauchamp & Kacelnik (1991) placed naive zebra finches in an operant chamber with a conspecific demonstrator (S_1). Periodically, a light was turned on (S_3) and food was delivered into a food tray (S_2). Half of the demonstrators had previously learned that the light was a reliable signal of food, and approached the food tray whenever it was switched on. The other half had learned that it was an unreliable signal of food, and were just as likely to approach the food tray when the light was switched on as when it was switched off. Beauchamp & Kacelnik (1991) found that zebra finches paired with knowledgeable demonstrators were less likely to approach the food tray when the light was switched on than zebra finches paired with unknowledgeable demonstrators, both when tested in the presence of their demonstrator and when tested alone. In this experiment, zebra finches paired with knowledgeable demonstrators were exposed to two different relationships: that between a demonstrator approaching the food tray and the delivery of food (S_1-S_2) and illumination of the light and the delivery of food (S_3-S_2). It is likely that the demonstrator was the more salient stimulus, and therefore exposure to the S_1-S_2 relationship overshadowed learning about the S_3-S_2 relationship.

Blocking, on other hand, has yet to be demonstrated in experiments on social learning. Galef & Durlach (1993) allowed rats to interact with demonstrators that had recently been fed a distinctively flavoured diet. Rats that were exposed to the odour and/or flavour of marjoram-flavoured diet (S_1) on a demonstrator's breath (S_2), followed by cinnamon-flavoured diet (S_3) on a demonstrator's breath, subsequently consumed the same amount of cinnamon flavoured diet as rats that had been exposed to the S_3-S_2 relationship, but not to the S_1-S_2 relationship. Therefore, there is no evidence of blocking in this experiment. However, this does not mean that blocking is not a characteristic of observational conditioning because these effects are not always found in experiments on classical conditioning and may depend on the administration of multiple trials rather than the single trial used by Galef & Durlach (1993).

In discussing most, if not all, of the foregoing experiments two assumptions were made. First, animals learned an S-S relationship through conspecific observation because they vicariously experienced the sensory properties of the reinforcer that was delivered to, or withheld from, their demonstrator (Bandura, 1965). Second, any change in the observers' behaviour following exposure to an S-S relationship was a result of learning about that relationship. The results of a study by Groesbeck & Duerfeldt (1971) are relevant to the first of these two assumptions. They placed naive rats in an observation box at the end of a Y-maze while a demonstrator knocked down one of two different cue cards and drank from a water bottle. One group of rats were allowed to observe their demonstrator drinking, while another group were prevented from doing so by means of a piece of cloth draped in front of the bottle. Groesbeck & Duerfeldt (1971) found that while both groups learned to knock down the demonstrator's cue card faster than rats that had not been given the opportunity to observe any aspect of a demonstrator's performance, they did not differ from each other. This suggests that vicarious reinforcement did not exert an important influence on the observers' behaviour. However, it is likely that the observers could hear their demonstrators drinking, and that the sounds which accompanied drinking acquired reinforcing properties of their own during the observers' previous experience in the apparatus. If this is correct, then response acquisition may have been facilitated in both groups by a process depending on secondary, rather than on vicarious reinforcement.

In order to investigate the second assumption, it would be necessary to vary or abolish the contingency between demonstrators' responses and their consequences. If any change in an animal's behaviour following exposure to an S_1-S_2 relationship is a result of learning about that relationship, then one would expect degrading the relationship to have an aversive effect on performance. This manipulation was attempted by Palameta & Lefebvre (1985). They allowed pigeons to observe demonstrators piercing a hole in the lid of a food bowl (S_1) and eating from within (S_2), and found that these birds acquired the same response faster and with fewer pecks than birds that observed either S_1 or S_2 alone.

In a similar study by Del Russo (1971), rats observed demonstrators pressing a lever (S_1) for food (S_2). One group of the rats was rewarded with food following each of the demonstrators' responses (contingent group), while another group was given an equivalent amount of food prior to the start of the demonstration session (non-contingent group). Del Russo (1971) found that the contingent, but not the non-contingent group, acquired lever-pressing faster than rats that had not been given the opportunity to observe a demonstrator.

1.2.1.4 Summary and conclusion

Nonimitative social learning consists of stimulus learning by observation. Animals that observe conspecific demonstrators interacting with an environmental stimulus may learn about: (i) the presence or location of that stimulus (stimulus enhancement), (ii) its dynamic properties (emulation learning), and/or (iii) its relationship to a second stimulus which may be attractive or aversive for the animal (observational conditioning). Finally, nonimitative social learning may facilitate acquisition of a response which resembles that exhibited by a demonstrator. However, it may also facilitate the acquisition of nonmatching behaviour.

1.2.2 Imitative social learning

1.2.2.1 Imitation or observational learning

Imitation (or observational learning) refers to acquisition of a topographically novel response through observation of a demonstrator making that response (Heyes, 1994). According to Galef (1988), imitation is an "onerous concept to be employed only when no other explanation of an observed social influence on behaviour is possible" (p. 10). Compelling examples of imitation in animals are rare, but one example may have been provided by Dawson & Foss (1965). They allowed naive budgerigars to observe demonstrators using either their feet or their beak to remove a card from a plastic bowl containing seed. When subsequently provided with a closed bowl on test, these birds showed a reliable tendency to remove the card using the same appendage as their demonstrator.

True imitation requires that conspecific observation is sufficient for acquisition of a novel response (Galef, 1988). This implies that imitation is goal-directed; or that when an observer copies the movements of a demonstrator, its actions are regulated by a representation of their potential outcome (Heyes, 1993). In order to determine whether imitation is regulated in this manner, it would be necessary to manipulate the value of the outcome of demonstrators' responses for the observer. If imitation is goal-directed, then one would expect it to occur only when the observer assigns a positive value to the outcome of the demonstrators' responses. If imitation occurs when the observer assigns a negative value to the outcome of the demonstrators' responses, then this would suggest that it is automatic rather than goal-directed.

However, there are no known experiments in which evidence of goal-directed imitation has been sought in this manner. Furthermore, even if imitative behaviour was shown to be goal-directed, it would not be the only behaviour to be regulated in this manner. In the study by Darby & Riopelle (1959), rhesus monkeys observed demonstrators displacing one of two different objects from above a hole in a tray. During a subsequent test session, the observers were rewarded regardless of the choice that they made. If the demonstrator's choice had been rewarded, the observers tended to displace the same object, and if the demonstrator's choice had been nonrewarded, they tended to displace the other object. This suggests that the observers' behaviour was sensitive to changes in the value of the outcome of demonstrators' responses, or that it was goal-directed.

Thus, imitation cannot be distinguished from other forms of social learning in terms of its goal-directedness. However, it may be distinguished in terms of the type of the information that is acquired (Heyes, 1993; Heyes & Ray, in press). Imitation involves the acquisition of information about responses (rather than stimuli), and should be regarded as a special case of observational learning in which exposure to a positive relationship between a demonstrator's responses and an appetitive reinforcer is sufficient to promote matching behaviour on the part of the observer (Heyes, 1994). This implies that observational learning is mediated by the same mechanisms as instrumental conditioning, except that in the case of observational learning it is the demonstrator, rather than the learner, that makes the response which is to be acquired.

If this is correct, and observational learning and instrumental conditioning are mediated by similar mechanisms, then one would expect there to be a number of observational learning phenomena in addition to imitation. In the case of imitation, learning occurs as a result of socially-mediated exposure to a positive relationship between a response and an appetitive reinforcer (a reward contingency). Thus, ~~it~~ observational conditioning might be expected to occur as a result of exposure to a positive relationship involving an aversive reinforcer (a punishment contingency), a negative relationship involving an appetitive reinforcer (an omission contingency), and a negative relationship involving an aversive reinforcer (an avoidance contingency).

As in the case of observational conditioning, the effect of exposure to these four possible types of contingency may be detected as a change in response evocation. Exposure to either a reward or an avoidance contingency is likely to lead to an increase in responsiveness, while exposure to either a punishment or an omission contingency may lead to a decrease. Furthermore, the response that the observer makes may or may not match that made by the demonstrator, and it may or may not form part of the observer's preexisting behavioural repertoire.

1.2.2.2 Summary and conclusion

Imitative social learning consists of response learning by observation. When permitted to observe the behaviour of a conspecific demonstrator, naive animals may learn: (i) what to do or how to behave (imitation), and/or (ii) the relationship between some aspect of the demonstrator's behaviour and a second event that may be either attractive or aversive for the observer (observational learning). Imitation increases the probability of matching behaviour. Observational learning, on the other hand, may lead to changes in an observer's behaviour that either do or do not match that of its demonstrator.

In the foregoing discussion of imitative social learning, two putative varieties were not considered: matched-dependent behaviour and vocal imitation (Galef, 1988). The term matched-dependent behaviour was first introduced by Miller & Dollard (1941) to explain the fact that rats can learn to follow a demonstrator into either the same arm of a T-maze or the opposite arm for food. In this instance, it was assumed that the demonstrator's behaviour served as a discriminative stimulus indicating to the observer which behaviour it would be rewarded for emitting. However, matched-dependent behaviour cannot conventionally be regarded as a form of social learning because once the demonstrator has been removed from the maze, all aspects of the observer's behaviour dependent on the demonstrator's behaviour are lost (Galef, 1988).

Despite the fact that matched-dependent behaviour cannot be regarded as a form of social learning, it may lead to learning. Church (1957) allowed rats to follow a demonstrator into either the left or the right arm of a T-maze for food. After 150 trials, two red lights were switched on above the arm of the maze that the demonstrator entered and 100 additional trials given. The demonstrator was then removed from the maze and observer rats tested on their own in the presence of the lights. Church (1957) found that these rats gradually learned to follow demonstrators, and continued to enter the same arm of the maze even after the demonstrator was removed, which suggests that matched-dependent behaviour promoted learning about the relationship between the red light and food (observational conditioning).

Finally, vocal imitation was also excluded from the foregoing discussion on the grounds that it may depend on a specialized process not seen in any other species of animal or in any other instance of social learning by birds (Galef, 1988).

1.3 Identifying Imitative Social Learning

1.3.1 Survey of imitation experiments

For over a century, psychologists and biologists have investigated whether animals are capable of imitation. The current section is a discussion of some of the most instructive and widely-cited studies from this period, organized to reflect the fact that research on imitation in animals has become increasingly more rigorous and sophisticated.

1.3.1.1 Shaping, non-exposed, and duplicate-cage control procedures

In early experiments on imitative learning, naive animals were given the opportunity to observe conspecific demonstrators operating a manipulandum for food. The rate at which these animals subsequently acquired the same response was then compared with that of control animals trained to make the response through standard shaping procedures, or the method of successive approximations. The results of these experiments were contradictory. On the one hand, Jacoby & Dawson (1969) found that observation of lever-pressing demonstrators facilitated response acquisition in rats relative to a shaping procedure. John, Chesler, Bartlett, & Victor (1968) obtained similar results when training cats to make either a signalled avoidance or a signalled appetitive response. On the other hand, Powell (1968) and Powell, Saunders, & Thompson (1968) both reported that a shaping procedure was a more effective than an observational learning procedure when training rats to press a lever for liquid reinforcement.

These discrepant findings are likely to reflect differences in the skill and speed of the individual that was shaping the animals (Zentall, 1996). Moreover, the use of a shaping control group means that it is not possible to isolate the critical variables that were influencing the observers' behaviour and thus to determine what they learned, because the two groups of animals were exposed to radically different kinds of experience. These criticisms of the use of shaping control groups in studies of imitative learning led to the development of a new method for studying imitation, the non-exposed control procedure.

In studies employing the non-exposed control procedure, response acquisition by animals that observed demonstrators operating a manipulandum for food is compared with that of animals that observed the manipulandum but not a demonstrator during training. Typically, the target response is acquired more rapidly by observers of demonstrator action than by control animals (e.g. Jacoby & Dawson, 1969; Chesler, 1969; Oldfield-Box, 1970; Gardner & Engel, 1971). This suggests that exposure to demonstrators' responses results in more rapid learning than trial-and-error alone. However, it does not provide unequivocal evidence of imitation, because it may be due instead to social facilitation. Observers of demonstrator action may have acquired the target response faster than the non-exposed control group, because the mere presence and/or behaviour of a conspecific increased the rate at which the animal performed those responses most appropriate to the current stimulus situation.

Experiments designed to assess the possible influence of social facilitation on response acquisition have involved exposing naive animals to the mere presence of a conspecific or to the presence of a feeding conspecific. Huang, Koski, & DeQuardo (1983) allowed naive rats to observe demonstrators pressing a lever for food, and found that they acquired the same response faster than a control group that were exposed to the mere presence of a passive conspecific. In the study by John *et al.* (1968), cats that observed demonstrators pressing a lever for food whenever a light was turned on acquired the same response faster than cats that observed demonstrators rewarded for approaching the food tray but not pressing the lever whenever a light was turned on.

These experiments indicate that social facilitation cannot account for the more rapid response acquisition shown by observers of demonstrator action in the non-exposed control procedure. However, they do not provide strong evidence of imitation because they may be due instead to local enhancement. The animals in these experiments were not tested in the presence of a demonstrator, although they were tested on the same object as that to which demonstrators responded. This raises the possibility that response acquisition was facilitated by products of the demonstrator's activity deposited on or near the object rather than response learning by observation.

Duplicate-cage procedures, in which demonstrators and observers contact numerically distinct objects, have been used to control for the effects of local enhancement (e.g. Warden & Jackson, 1935; Zentall & Levine, 1972; Zentall & Hogan, 1976). When the duplicate-cage procedure has been used, clear effects of social facilitation on behaviour have been isolated. For example, in the study by Zentall & Levine (1972) naive rats observed demonstrator rats pressing a lever and drinking water from a bottle. These rats acquired the lever-pressing faster than rats that were exposed to the mere presence of a conspecific. Furthermore, under these conditions, exposure to the mere presence of a conspecific was found to retard response acquisition relative to a non-exposed control group. However, social facilitation does not always impair performance.

When the target response is well-learned performance may be improved by the presence of another animal (e.g. Levine & Zentall, 1974).

Although the duplicate-cage procedure rules out all possibility of local enhancement, it introduces another potential confound into studies of imitative learning. In the duplicate-cage procedure a demonstrator's activity may increase the likelihood that an observer will be exposed to stimuli of the same physical type as that to which the demonstrator responded (stimulus enhancement).

1.3.1.2 Two-action procedures

The two-action procedure in which naive animals observe conspecific demonstrators performing one of two or more alternative actions on a single object has been used to control for stimulus enhancement. Dawson & Foss (1965) allowed budgerigars to observe demonstrators removing a square piece of card from the top of a plastic bowl containing seed. The demonstrators used one of three different techniques to remove the card: they either edged it off with their beak, lifted it off with their beak, or used their foot to dislodge it. When subsequently presented with a covered bowl on test, observer birds showed a reliable tendency to use the same technique as their demonstrator. Over twenty years after the original experiment, Galef, Manzig, & Field (1986) attempted to replicate this effect. However, they found it to be small and transitory, rendering Dawson & Foss' (1965) procedure an unsuitable paradigm for analytic experiments on imitation.

An apparently more reliable imitative effect was obtained by Heyes, Dawson, & Nokes (1992) using a variant of the two-action procedure, the bidirectional control procedure. In this experiment, naive rats were allowed to watch from the observation compartment of an operant chamber, while a demonstrator pushed a joystick either to the left or to the right. Once the demonstrator had made 50 reinforced responses it was removed from the chamber. Observer rats were transferred into the empty demonstration compartment and given a test session in which both left and right responses were rewarded. These rats showed a reliable tendency to push the joystick in the same direction, relative to their own bodies, as had their demonstrator.

This effect could not have been due to social facilitation, because observers of left- and right-pushing demonstrators were exposed equally to the mere presence, consummatory behaviour, and general activity of a conspecific. It is also unlikely that it was due to either local enhancement or stimulus enhancement, because the demonstrators were not present at the time of testing, and observation of left- and right-pushing should have rendered the joystick equally attractive.

However, left- and right-pushing demonstrators did move the joystick towards different side walls of the operant chamber and these side walls were constructed from different materials. Thus, it is plausible that rats acquired information about movement of the joystick with respect to cues within the chamber (emulation learning) or about the relationship between movement of the joystick and the delivery of food (observational conditioning). Heyes *et al.* (1992) attempted to exclude emulation learning and observational conditioning as potential explanations of the bidirectional control effect, by testing rats with a joystick that had been rotated through an angle of 90 degrees between observation and testing. These rats moved the joystick in the same direction as their demonstrator, even though this resulted in the joystick moving toward a different point in space to that in which it had moved during observation.

The results of this experiment were interpreted as providing strong evidence of imitative learning in rats, or response learning by observation (Heyes, 1996). However, subsequent studies have cast doubt on the magnitude and provenance of the bidirectional control effect. A meta-analysis of bidirectional control data has indicated that at current parameters, the effect size is small (Gardner, 1997), and there is evidence that rats in the bidirectional control procedure are influenced by odour cues deposited on the joystick by demonstrators (Mitchell, Heyes, Gardner, & Dawson, 1999). In the experiment by Mitchell *et al.* (1999), rats observed demonstrators pushing a joystick to the left or right for food. When subsequently allowed access to the joystick on test and rewarded for both left and right responses, these rats showed a reliable tendency to respond in the same direction as their demonstrator. However, when the joystick was rotated through an angle of 180 degrees within its mounting between observation and test, rats showed a reliable tendency to respond in the opposite direction to their demonstrator. This suggests that demonstrators deposited attractive odour cues on the side of the joystick contralateral to its direction of motion. When the joystick was in the standard position, exploration of these cues promoted demonstrator-consistent responding. However, when the joystick had been rotated through an angle of 180 degrees, exploration of odour cues promoted a demonstrator-inconsistent response bias.

More recent studies using the two-action procedure have attempted to rule out observed differences in movement of the demonstrators' manipulandum (e.g. Zentall, Sutton, & Sherburne, 1996; Akins & Zentall, 1996). Naive birds were given the opportunity to manipulate a treadle after they had observe demonstrators either pecking at or stepping on that treadle for food. Zentall *et al.* (1996) found that of the ten pigeons that observed pecking, five pecked at the treadle and five stepped on it. Of the ten pigeons that observed stepping, nine stepped on the treadle and none pecked at it. Similarly, Akins & Zentall (1996) reported that when Japanese quail observed pecking demonstrators they made more pecking than stepping responses, and when they observed stepping demonstrators they made more stepping than pecking responses. However, only the former effect was reliable.

In these experiments, pecking and stepping demonstrators had the same effect on the treadle. Therefore, the results cannot be attributed to the observers learning the dynamic properties of the treadle or a treadle movement-food relationship. However, while these experiments provide good evidence that observation of pecking promotes pecking in both pigeons and quail, evidence for a similar effect of stepping is not strong. Furthermore, since pecking forms part of a bird's innate behavioural repertoire it is plausible that it was acquired via contagion acting in concert with stimulus enhancement. The sight of a pecking demonstrator may have acted as a releaser of pecking in an observer. If, in addition, the demonstrator's activity increased the probability that the observers would be exposed to the treadle, then this might result in the observers directing the majority of their pecking towards the treadle on test.

Unfortunately, two further studies which could have provided evidence against this interpretation yielded ambiguous results. First, Kaiser, Zentall, & Galef (1997) allowed pigeons to observe a conspecific either sitting passively in the treadle compartment or eating from a feeder. They found that these birds were less likely to step on the treadle than those birds that observed stepping demonstrators in the study by Zentall *et al.* (1996). However, this contrast does not provide evidence that stepping was acquired via imitation because it may be due instead to stimulus enhancement. In the study by Kaiser *et al.*, the observers did not see demonstrators contact the treadle and presumably found it less attractive than the observers in Zentall *et al.*'s study that did see demonstrators contact the treadle. In the second study, Akins & Zentall (1998) found that when quail observed nonrewarded stepping, they made fewer stepping responses than when quail observed demonstrators stepping on a treadle and being rewarded with food. However, this effect was not reliable.

In a study by Lefebvre, Templeton, Brown, & Koelle (1997), Carib grackles observed either a conspecific or a Zenaida dove demonstrator using its beak to remove a plug from an opaque inverted test tube containing seed. Grackle demonstrators used an open beak probing and pulling technique to manipulate a horizontal stick that protruded from the base of the plug and open the tube, while dove demonstrators used a closed beak pecking technique. Lefebvre *et al.* (1997) found that when grackles observed conspecific demonstrators, they were more likely to remove the plug using an open beak technique than when they observed dove demonstrators. Unfortunately, the two types of demonstrator used in this study manipulated different regions of the stick. Grackle demonstrators probed and pulled the tip of the stick, and dove demonstrators pecked at the base of the stick. Thus, it is plausible that stimulus enhancement rather than imitation was responsible for the observers' bias. A possibility that Lefebvre *et al.* attempted to exclude by showing that there was no effect of demonstrator type on where the observers directed their responses.

Finally, the two-action procedure has also been used to study imitative learning in several species of primate such as the chimpanzee. Whiten, Custance, Gomez, Texidor, & Bard (1996) allowed chimpanzees to observe a human demonstrator using one of two alternative actions to remove a pair of bolts from the rings through which they passed on the lid of a plastic box, and taking a piece of food from inside the box. When subsequently provided with a closed box on test, chimpanzees showed a reliable tendency to use the same action as their demonstrator. In this experiment, the bolts could be removed using either a twisting or a poking action. Twists caused the bolts to rotate in a clockwise direction and move towards the demonstrator's body. Pokes did not cause the bolts to rotate, but did result in them moving away from the demonstrator's body. This raises the possibility that the chimpanzee in this experiment did not learn about their demonstrator's behaviour. Rather, they may have learned about the way in which the bolts moved as a result of observing their demonstrator's behaviour (emulation learning).

1.3.2 Summary and conclusion

The foregoing survey indicates that the two-action procedure is important in two respects. First, it has substantially increased both the rigour and sophistication of research investigating imitation in animals. Second, it is potentially the most powerful method of isolating imitative from nonimitative social learning, or stimulus learning from response learning by observation.

1.4 Identifying Simultaneous Imitative and Nonimitative Social Learning

1.4.1 The two-object/two-action procedure

Use of the two-action procedure is based on the assumption that in any given context it is possible to manipulate precisely the events to which animals are exposed in order to make strong inferences about which factors led to any change in the animals' behaviour (Zentall, 1996). It is likely that in natural and experimental environments, providing animals with the opportunity to observe demonstrators performing an action on an object for food will result in learning about both stimuli and responses. Therefore, by excluding from the outset all possibility of detecting nonimitative social learning, two-action procedures may be creating conditions which are not conducive to learning.

Ray (1997) has suggested that the problems faced by psychologists and biologists attempting to demonstrate imitation in animals are similar to those encountered by investigators of asocial learning when determining whether an instrumental conditioning procedure involves learning about responses (instrumental conditioning) or learning about stimuli (classical conditioning). Prior to the 1970s, it was widely believed that all learning consisted of the association of a particular response with a particular outcome. However, this view was challenged by the results of a number of studies in which the importance was recognised of S-S relationships in controlling behaviour which had previously been regarded as instrumental.

In a study by Brown & Jenkins (1968), pigeons learned to peck a key, the illumination of which signalled the delivery of grain, even though keypecking had no effect on the probability of reward. Similarly, Williams & Williams (1969) found that pigeons learned to peck the key and continued to do so at a high rate, even though in this experiment keypecking postponed the delivery of grain. These "autoshaping" effects suggest that in those cases where pigeons are trained to peck a key through standard shaping procedures, or the method of successive approximations, this response was actually established by classical conditioning. The pigeons did not learn that keypecking resulted in the delivery of grain (instrumental conditioning). Rather, they learned that illumination of the key signalled the delivery of grain (classical conditioning), and as a consequence of which directed the majority of their foraging behaviour towards the key.

Classical conditioning may also account for changes in an animal's behaviour following exposure to a punishment contingency. Rats that are trained to press a lever for food and then punished for lever-pressing show a reduction in their rate of responding. This may be because rats learned a response-shock relationship (instrumental conditioning), or it may be because they learned a lever-shock relationship (classical conditioning). In order to distinguish these possibilities, Bolles, Holtz, Dunn, & Hill (1980) trained rats to respond in two different directions on two different levers. Rats were trained to lift a left lever up, press a left lever down, lift a right lever up, and press a right lever down. Once the rats were responding reliably, one of the four possible combinations of lever and direction was punished with foot shock.

According to Bolles *et al.* (1980), if rats learn a response-shock relationship, then rats punished for lifting the left lever, for example, should avoid lifting the left and the right lever, but press with equal frequency on both levers. If, on the other hand, rats learn a lever-shock relationship, then they should avoid the left lever and respond indiscriminately with lifts and presses on the right lever. In fact, evidence of both types of learning was obtained. From the start of training, rats responded less on the punished than on the unpunished lever, but responded equally in the punished and the unpunished direction. However, towards the end of training, rats began to respond less in the punished than in the unpunished direction.

The two-object/two-action procedure used by Bolles *et al.* (1980) to distinguish the effects of classical conditioning and instrumental conditioning on a punished animal's behaviour, can be readily modified to distinguish imitative and nonimitative social learning. Ray (1997) allowed naive rats to observe, from one side of an operant chamber, while a conspecific demonstrator manipulated one of two different levers in one of two different directions. The demonstrators had been trained to lift a left lever up, press a left lever down, lift a right lever up, or press a right lever down 50 times for food. Once the demonstrators finished responding, they were removed from the chamber and the observers were transferred into the empty demonstration compartment and given a test session in which all responses, regardless of location and direction, were rewarded with food. Observer rats showed a reliable tendency to manipulate the same lever in the same direction as their demonstrator, results which were interpreted as evidence that the rats in this procedure acquired information about both a stimulus and a response through conspecific observation.

Social facilitation cannot account for either of these effects because, regardless of which demonstrator rats observed, each rat was exposed equally to the mere presence, general activity, and consummatory behaviour of a conspecific. Local enhancement is also an unlikely explanation, because the demonstrators were not present when the observers were tested. However, the results of a recent experiment (Mitchell *et al.*, 1999) raise the possibility that demonstrators deposited attractive odour cues on or around the surface of the manipulandum which they operated, and that exposure to these cues on test was sufficient to bias the observers towards responding on the same lever and in the same direction as their demonstrator.

In order to test the hypothesis that lever choice by rats is the result of scent-mediated local enhancement rather than stimulus learning by observation, Heyes, Ray, Mitchell, & Nokes (1999) used a screening procedure. Naive rats were present in the observation compartment of an operant chamber while a conspecific demonstrator pressed either a left or a right lever. Half of the rats were allowed to observe demonstrator's responses, while the other half were prevented from doing so by an aluminium screen. When rats observed demonstrators' responses, they showed a reliable preference for the lever on which demonstrators responded. However, when rats had not been allowed to observe demonstrators' responses they distributed their responses equally between the two levers. These results suggest that mere exposure to demonstrator-deposited odour cues is insufficient to bias lever choice. However, they do not show what affect, if any, demonstrator-deposited odour cues have on lever choice when accompanied by compatible visual cues.

In a second experiment employing a box-swapping procedure, Heyes *et al.* (1999) examined the independent effects of visual cues and odour cues on lever choice in rats. Naive rats observed a conspecific (the 'viewed' demonstrator) pressing either a left or a right lever. The rats were then transferred into the demonstration compartment of a second operant chamber and given a test session in which responses on either the viewed demonstrator's lever (Group SAME) or the opposite lever (Group DIFFERENT) were rewarded. The demonstration compartment in which the observers were tested had just been vacated by another conspecific (the 'box' demonstrator), that had been pressing the reinforced lever during a demonstration session that had run concurrently with the one that the observers had viewed (Groups SAME+ and DIFFERENT+) or the nonreinforced lever (Groups SAME- and DIFFERENT-).

Heyes *et al.* (1999) predicted that if visual cues and odour cues affect lever choice , and if these effects are additive, rats rewarded for responding on their viewed demonstrator's lever should make more reinforced responses than rats rewarded for responding on the opposite lever. Furthermore, rats rewarded for responding on their box demonstrator's lever should make more reinforced responses than rats rewarded for responding on the opposite lever. It was found that at the start of the test session, rats rewarded for responses on the viewed demonstrator's lever (Group SAME) showed better discrimination than rats rewarded for responses on the opposite lever (Group DIFFERENT). Within Group SAME, rats rewarded for responses on the box demonstrator's lever showed better discrimination than rats rewarded for responses to the opposite lever. Within Group DIFFERENT, however, the reverse effect was found.

The finding that rats rewarded for responding on their viewed demonstrator's lever showed better discrimination than rats rewarded for responding on the opposite lever, provides evidence that lever choice is influenced by conspecific observation. This experiment also provided evidence that lever choice in rats is affected by demonstrator-deposited odour cues, although not in a manner as straightforward as originally predicted. Based on the assumption that demonstrators deposit more odour cues on or around the lever that they pressed, and that these odour cues are attractive to other rats, it was predicted that within Groups SAME and DIFFERENT rats rewarded for responding on their box demonstrator's lever would make more reinforced responses than rats rewarded for responding on the opposite lever. However, while this was found to be the case in Group SAME, the opposite effect was found in Group DIFFERENT.

Heyes *et al.* (1999) interpreted these results as evidence that rats are attracted to the lever on which they observed a demonstrator responding and on which a demonstrator deposited odour cues. However, in this example visual cues and odour cues served as discriminative stimuli indicating to the observer which lever it would be rewarded for pressing. In the case of Groups SAME+ and DIFFERENT-, visual cues and odour cues were biased towards the same lever making it easy for the observers to discriminate between the reinforced and the nonreinforced lever. In the case of Groups SAME- and DIFFERENT+, visual cues and odour cues were biased towards different levers making the discrimination more difficult to make.

Thus, there would appear to be sufficient grounds to suppose that both Ray (1997) and Heyes *et al.* (1999) have provided good evidence of stimulus learning by observation in rats. However, what is not clear is whether the rats in these experiments learned about the presence or location of the lever to which their demonstrator responded (stimulus enhancement), the dynamic properties of this lever (emulation learning), and/or its relationship to the delivery of food (observational conditioning). The extent to which the direction of observer rats' responses in the two-object/two-action procedure are influenced by their observation of a demonstrator's behaviour in addition to demonstrator-deposited odour cues also remains to be determined. Moreover, even if it could be shown that rats learned about the direction in which demonstrators responded, then this would still leave open the possibility that this effect was the result of stimulus learning by observation rather than response learning by observation.

1.4.2 Summary and conclusion

The two-object/two-action procedure, inspired by Bolles *et al.* (1980) and used by Ray (1997), forms the basis of the experiments reported in this thesis. In Chapter 2, Ray's (1997) two-object/two-action procedure was replicated in an attempt to distinguish imitative and nonimitative social learning in the rat, while follow-up studies assessed the extent to which visual cues and odour cues influence the direction of rats' responses. In Chapters 3 and 4, a series of experiments are reported in which the contingency between demonstrators' responses and food was abolished to elucidate the mechanisms underlying lever choice by rats in the two-object/two-action procedure. In Chapter 5, the results of an experiment in which a two-object/two-action procedure was used to test for imitative and nonimitative social learning in the European starling are presented. Finally, Chapter 6 is a discussion of the significance of the results reported in Chapters 2-5.

Chapter 2

Imitative and Nonimitative Social Learning In the Rat Using a Two-Object/Two-Action Procedure

2. Introduction

In a two object/two action procedure used by Ray (1997), naive rats observed, from one side of an operant chamber, while a conspecific demonstrator manipulated either a left or a right lever by lifting up or pressing down. Once the demonstrator had made 50 reinforced responses it was removed from the chamber. Observer rats were then transferred into the empty demonstration compartment and given a test session in which all responses were rewarded with food regardless of location and direction. Ray (1997) found that at the start of the testing, but not thereafter, the observers showed a reliable tendency to manipulate the same lever in the same direction as their demonstrator. These results were interpreted as evidence that the rats in this procedure acquired information about both a stimulus (nonimitative social learning) and a response (imitative social learning) through conspecific observation.

Since each rat was exposed equally to the mere presence, general activity, and/or consummatory behaviour of a conspecific, social facilitation cannot account for these results. Local enhancement is also an unlikely explanation because the demonstrators were removed from the apparatus before the observers were tested. However, it is possible that the demonstrators deposited odour cues on or around the surface of the lever which they operated, and that exposure to these cues on test biased both the location and the direction of observer rats' responses.

In order to examine the hypothesis that demonstrator-deposited odour cues affect lever choice by rats, Heyes *et al.* (1999) used both a screening and a box-swapping procedure. In the screening procedure, rats that were allowed to observe demonstrators pressing either a left or a right lever showed a reliable tendency to press the same lever on test, whereas rats that had been prevented from observing demonstrators' responses by an aluminium screen did not. In the box-swapping procedure, rats were allowed to observe viewed demonstrators pressing either a left or a right lever, and were then tested in a second chamber in which box demonstrators had pressed either the same lever as the viewed demonstrator or the opposite lever. These rats showed a bias in favour of the lever viewed demonstrators pressed, both when box demonstrators had pressed this lever and when they had pressed the opposite lever. Taken together, these experiments provide good evidence of stimulus learning by observation, or nonimitative social learning. This is because they show that rats are attracted to the lever on which they observed demonstrators responding, rather than that on which demonstrators deposited odour cues.

However, one question remains to be addressed and that is whether the direction effect detected by Ray (1997) provides evidence of imitative social learning, or response learning by observation. To provide a positive answer to this question, it would be necessary to rule out two alternative explanations. The first possibility is that demonstrators deposit odour cues asymmetrically on or around the lever which they operated, and that exposure to these cues on test is sufficient to bias the direction of observer rats' responses. The second possibility is that the direction effect was mediated by visual observation, but that rats learned about the effect of the demonstrator's behaviour on the lever rather than the demonstrator's behaviour *per se*.

The aim of the experiments reported in Chapter 2 was twofold: (i) to replicate the basic two object/two action effect obtained by Ray (1997) (Experiment 1), and (ii) to examine the outstanding interpretative problem described above (Experiments 2 and 3). Specifically, do visual cues arising from observation of a demonstrator's behaviour, instead or in addition to demonstrator-deposited odour cues, affect directional responding in rats?

2.1 Experiment 1

In Experiment 1, naive rats observed conspecific demonstrators manipulating either a left or a right lever by lifting up or pressing down. Once the demonstrator had made 50 reinforced responses it was removed from the operant chamber. Observers were then transferred into the empty demonstration compartment and given a test session in which all responses were rewarded with food irrespective of location and direction. Following the results obtained by Ray (1997), it was anticipated that these rats would show a reliable tendency to manipulate the same lever in the same direction as their demonstrator.

Method

Subjects

The subjects were 32 male hooded Lister rats obtained from Harlan Olac Ltd (Bicester, Oxon, UK). Of these rats, 16 had served as observers in a previous two object/two action procedure. These animals were assigned the role of demonstrator. The remaining 16 rats were experimentally naive and were the observers. Prior to the start of the experiment, both demonstrators and observers had an average free-feeding weight of 518 g.

Demonstrator and observer animals were housed separately in groups of four with water freely available. Several days before the start of the experiment all animals were reduced to 90%

of their free-feeding weight by scheduled feeding, and were maintained at this level throughout the experiment by being given a restricted amount of food each day.

Apparatus

All animals were trained and tested in four identical operant chambers (42 x 25 x 28 cm; see Figure 1) that were placed inside sound attenuating boxes. The walls and ceilings of each chamber were constructed from sheet metal, and the floor was made of parallel metal rods spaced 1 cm apart. Each chamber was divided, unequally, into two compartments by a 1 cm gauge wire-mesh partition. The larger of the two compartments (26 x 25 x 28 cm) was used for demonstration and testing, while the other compartment (16 x 25 x 28 cm) housed the observer. Both compartments could be accessed by way of separate doors located on the left of the chamber.

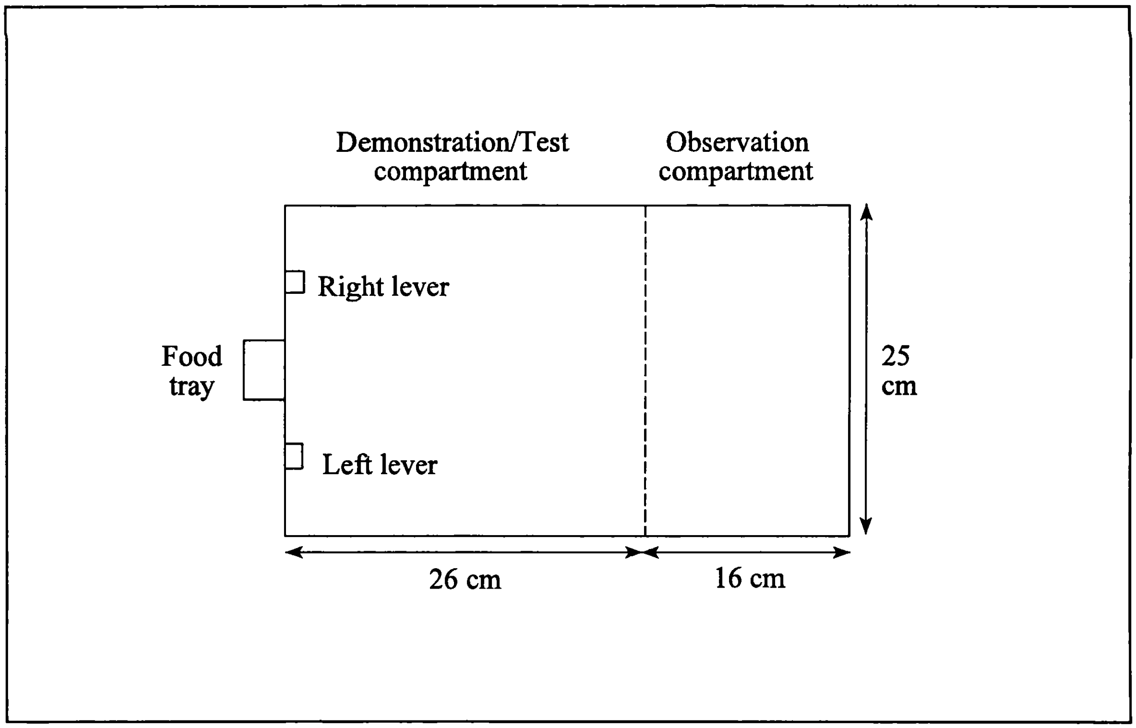

Figure 1. Plan of the two object/two action apparatus used in Experiments 1-7. The dashed line shows the position of the wire-mesh partition.

In the demonstration compartment, mounted on the wall directly opposite the wire-mesh partition, were two retractable levers constructed from sheet metal; one on the left and the other on the right. The levers, which were separated by a distance of 11 cm, were 1.5 cm wide, 0.9 cm deep, and extended 1 cm into the chamber. They were 14 cm above floor level and 5.5 cm from the adjacent side wall. Both of the levers could be moved either up toward the ceiling of the chamber or down toward the floor.

Microswitches were used to record lever movement, and these could be adjusted such that the extent of lever displacement necessary for a response to be registered could be varied. In Experiment 1 both demonstrators and observers had to displace the lever through a distance of 1.5 cm in order for a response to be registered.

The demonstration compartment also contained a recessed food tray (4.5 x 3.5 cm) located centrally between the two levers and 6 cm above floor level. Whenever the subject made a response designated for reinforcement, a 45 mg sucrose pellet was delivered into the food tray. A magazine responses was recorded whenever the rat's snout entered the food tray breaking a photocell beam.

The chamber was illuminated by a 24 V, 2.8 W house light located in the centre of the ceiling of the demonstration compartment. The observation compartment was featureless.

A BBC Master computer running on-line Spider language controlled the equipment and collected the data.

Procedure

Each session began with the illumination of the house light and finished after 50 reinforced responses had been made or 20-30 min had elapsed (variously defined below), at which point the house light was extinguished.

Demonstrator training

Initially each demonstrator received a single session of magazine training in the demonstration compartment from which the levers had been removed. During magazine training a total of 30 food pellets were delivered on a Random Time (RT) 60 sec schedule. The demonstrators were then trained, in 11 daily sessions, to manipulate either the left (n = 8) or the right (n = 8) lever. Within each group, half of the demonstrators were trained to lift the lever up and half were trained to press it down. Each of the demonstrator's training sessions lasted until the rat had made 50 reinforced responses or 20 min had elapsed.

Training was divided into two phases. During the first phase only the left or the right lever was available to the demonstrator. Responses made to this lever in the correct direction were rewarded with food, while responses in the opposite direction had no programmed consequences. Once each demonstrator had made 90% or more of its total responses in the correct direction in each of two consecutive sessions it entered the next phase of training. During the second phase of training both levers were available to the demonstrator, and only those responses on the correct lever and in the correct direction were rewarded with food. All other responses had no programmed consequences. Training continued until each demonstrator had made 90% or more of its total responses on the correct lever and in the correct direction over two consecutive sessions. This criterion was reached by all four groups after an average of ten sessions. One rat (a right up demonstrator) was excluded from the experiment because it failed to achieve the criterion level of performance after 11 sessions. Consequently, one of the remaining right up demonstrators was observed by two different rats. The behaviour of these observers did not differ detectably from that of the other observers on test.

During the final two sessions of training, a 'dummy' observer, of approximately the same age and weight as the demonstrator, was present in the observation compartment in order to ensure that demonstrator rats were accustomed to manipulating the lever in the presence of a conspecific. The demonstrators' performance was not found to be disrupted by the 'dummy' observer.

Observer training and testing

Equal numbers of rats observed a demonstrator that had been trained to manipulate the left or the right lever. Within each group, half of the rats observed a demonstrator lifting the lever up (Groups LEFT UP and RIGHT UP), while the other half observed a demonstrator pressing the lever down (Groups LEFT DOWN and RIGHT DOWN).

Before being allowed to observe a demonstrator for the first time, each rat received five daily sessions of training. On days 1, 3 and 5 observer rats were given a single session of magazine training in the test compartment as were the demonstrators. Context training, which occurred on days 2 and 4, consisted of placing a rat in the observation compartment of an operant chamber for a duration of 30 min with the house light on. At no point during magazine and context training did observers have access to the levers.

On day 6, the test day, each observer was placed in the observation compartment of an operant chamber for a 3 min acclimatization period. A demonstrator was then introduced into the adjacent compartment, and both animals were left for a further 3 min period. Following which, demonstrator rats were allowed to make 50 reinforced responses. Once a demonstrator had finished, it was removed from the operant chamber. Demonstration sessions lasted approximately 5 min. Observer rats were then transferred into the empty demonstration compartment and given a test session in which all responses were rewarded with food regardless of their location and direction. The interval between observation and testing was approximately 3 min, and the duration of the test session was 20 min.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 1. Accuracy was measured according to the percentage total responses each demonstrator made on the reinforced lever and in the reinforced direction. Owing to the fact that the largest variance (Group RIGHT UP) was approximately seven times greater than the smallest variance (Group RIGHT DOWN), a nonparametric test was used to analyse this data.

All four groups of demonstrators exhibited an equivalent level of accuracy and made in excess of 90% total responses on the reinforced lever and in the reinforced direction. Kruskal-Wallis one-way Analysis of Variance (ANOVA) performed on these data supported the impression that there were no reliable group differences (chi-square = 1.43, df = 3, p = 0.70, corrected for ties).

Group	LEFT UP	LEFT DOWN	RIGHT UP	RIGHT DOWN
Median Percentage Correct Responses	95.00	98.00	95.50	98.00
Interquartile Range	95.00, 97.50	96.00, 99.00	94.50, 98.00	97.00, 98.00
n	4	4	4	4

Table 1. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 1.

Observers' behaviour

Of the 16 observers tested, all responded on test. However, two (one belonging to Group LEFT UP and one belonging to Group RIGHT UP) made fewer than five responses and were excluded from the experiment. The total number of responses made over the course of the test session by the remaining observers is summarized in Table 2. It would appear that rats in Group LEFT UP made fewer responses than rats in the other three groups. However, this impression was not supported when the data were subjected to two-way (lever x direction) ANOVA. This revealed that neither the main effects were not reliable, nor was the interaction (F < 1 in all cases).

Sensitivity to the location and direction of demonstrators' responses was measured separately by means of a spatial discrimination ratio and a directional discrimination ratio. Discrimination ratios were computed using: (i) the first five responses and (ii) the total responses made by each observer. Spatial discrimination ratios were calculated by dividing the number of left responses by the total number of responses, and directional discrimination ratios were calculated by dividing the number of up responses by the total number of responses. The data relating to each measure were subjected to two-way ANOVA in which both lever (left, right) and direction (up, down) were factors.

Group	LEFT UP	LEFT DOWN	RIGHT UP	RIGHT DOWN
Mean Total Number of Responses	48.33	80.25	86.33	73.75
Standard Error of the Mean	30.15	25.94	37.19	23.46
n	3	4	3	4

Table 2. Mean total number of responses and standard error of the means for each group of observers in Experiment 1.

Spatial discrimination ratio

Figure 2a shows the spatial discrimination ratio for the first five responses made by each group of observers. As expected, exposure to the location of demonstrators' responses resulted in a tendency for demonstrator-consistent responding at the start of testing. Rats that observed demonstrators manipulating the left lever made proportionately more of their first five responses on the left lever (mean = 0.69, SEM = 0.10, N = 7) than rats that observed demonstrators manipulating the right lever (mean = 0.34, SEM = 0.08, N = 7). An effect which occurred both for those groups in which rats observed demonstrators lifting the lever up and for those groups in which rats observed demonstrators pressing the lever down. These impressions were supported by the results of two-way ANOVA which revealed a significant main effect of lever (F (1, 10) = 6.42, p = 0.03), but not of direction (F (1, 10) = 1.30, p = 0.28). The lever x direction interaction was not reliable (F < 1).

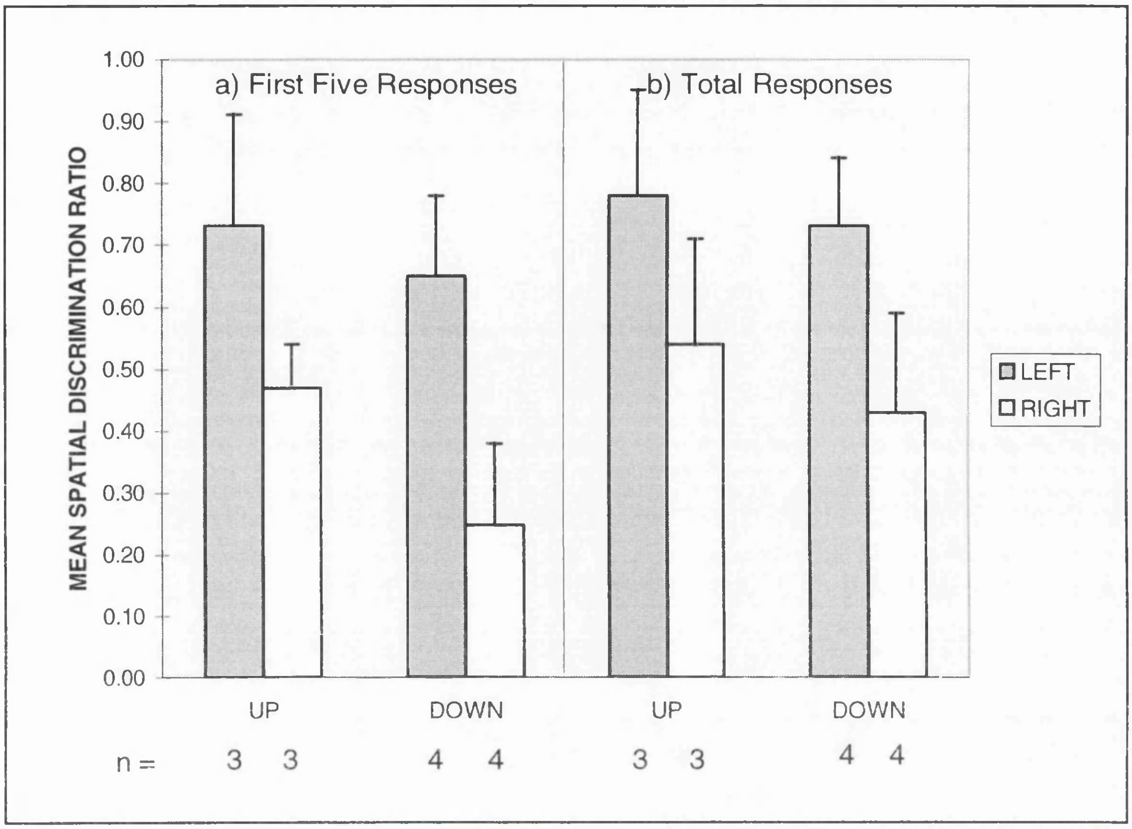

Figure 2. Mean spatial discrimination ratio (left responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 1. The black bars indicate the standard errors of the means.

Figure 2b shows the spatial discrimination ratio for the total responses made by each group of observers. It would appear that, by the end of testing, the observers still showed a preference for the lever which their demonstrator operated. Rats that observed demonstrators manipulating the left lever made proportionately more of their total responses on the left lever (mean = 0.75, SEM = 0.09, N = 7) than rats that observed demonstrators manipulating the right lever (mean = 0.48, SEM = 0.11, N = 7). However, this difference was not supported when the data were subjected to two-way ANOVA. This revealed that the main effect of lever (F (1, 10) = 2.97, p = 0.12), the main effect of direction (F < 1), and the lever x direction interaction were not reliable (F < 1).

Directional discrimination ratio

Figure 3a shows the directional discrimination ratio for the first five responses made by each group of observers. The data presented in this figure indicate that, overall, rats made fewer up than down responses. Furthermore, there is no evidence that exposure to the direction of demonstrators' responses resulted in a tendency for demonstrator-consistent responding at the start of testing. Rats that observed demonstrators lifting a lever up made an equivalent proportion of their first five responses in an upward direction (mean = 0.30, SEM = 0.09, N = 6) to rats that observed demonstrators pressing a lever down (mean = 0.25, SEM = 0.11, N = 8). Two-way ANOVA performed on these data revealed the main effects were not reliable, nor was the interaction (F < 1 in all cases).

The directional discrimination ratio for the total responses made by each group of observers is shown in Figure 3b. Again, there is an overall bias towards pressing the levers down except in the case of rats that observed demonstrators lifting the right lever up. Rats that observed demonstrators lifting the right lever up had made, by the end of testing, proportionately more up responses than rats that observed demonstrators pressing the right lever down. In contrast, rats that observed demonstrators lifting the left lever up did not make more up responses than rats that observed demonstrators pressing the left lever down.

These impressions were supported when the data were subjected to two-way ANOVA. This revealed a marginal main effect of direction (F (1, 10) = 3.67, p = 0.09), while simple effects confirmed that Group RIGHT UP made more up responses than Group RIGHT DOWN (F (1, 10) = 5.80, p = 0.04), whereas Groups LEFT UP and LEFT DOWN did not differ (F < 1). Furthermore, Group RIGHT UP made marginally more up responses than Group LEFT UP (F

(1, 10) = 5.00, p = 0.05), whereas Groups RIGHT DOWN and LEFT DOWN did not differ (F < 1). ANOVA also indicated that the main effect of lever (F (1, 10) = 2.57, p = 0.14) and the direction x lever interaction were not reliable (F (1, 10) = 2.86, p = 0.12).

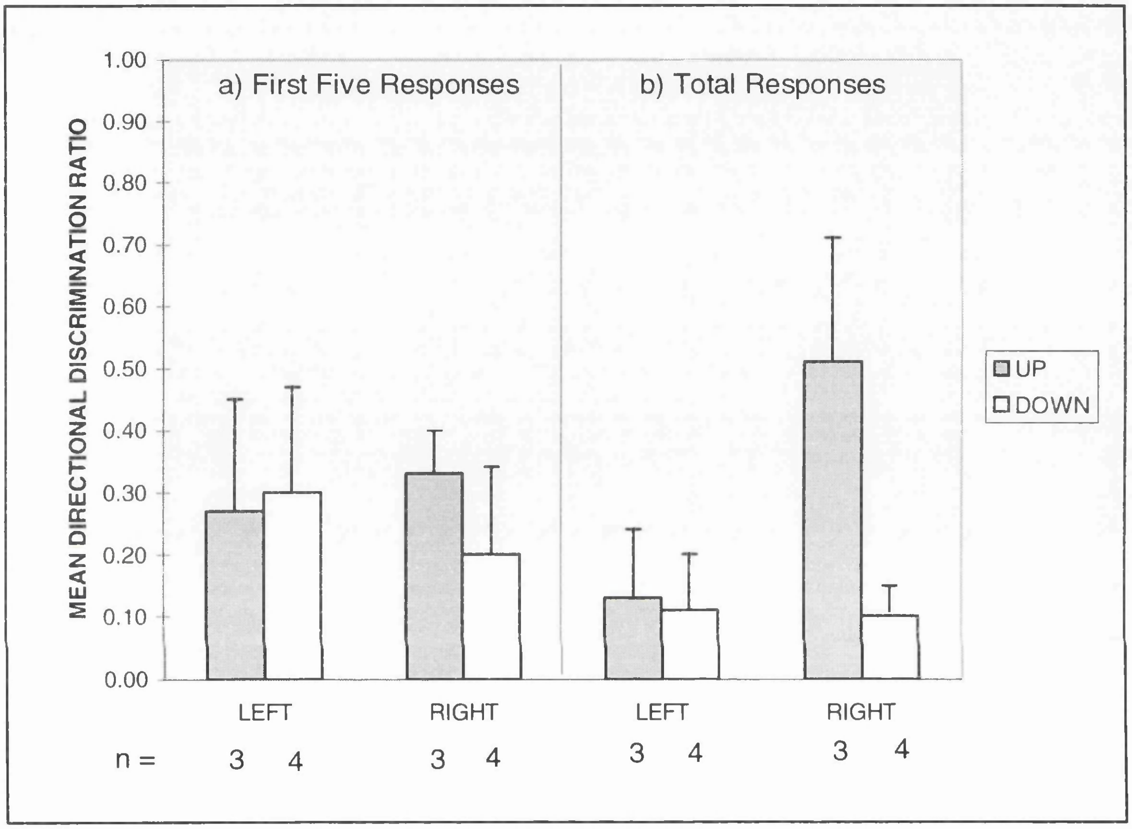

Figure 3. Mean directional discrimination ratio (up responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 1. The black bars indicate the standard errors of the means.

The finding that exposure to the direction of demonstrators' responses resulted in a tendency for demonstrator-consistent responding when demonstrators manipulated the right, but not the left lever, may have been associated with the fact that the left lever was situated next to the door. Rats are introduced into and removed from the chamber through this door. Therefore, it is possible that the observers, during their own previous experience in the demonstration compartment, associated the left side of the chamber with the aversive experience of being handled. An episode which might cause the observers to avoid looking at the left lever during a demonstration session. Alternatively, the observers may have been willing to look at the left lever during a demonstration session, but have been unable to detect the direction of a demonstrator's responses made on this lever because it was obscured by shadows or inadequate lighting.

Experiment 1 also indicated that while rats are influenced by exposure to demonstrators lifting the right lever up (i.e. Group LEFT UP vs Group RIGHT UP), there is no evidence for a similar effect of exposure to demonstrators pressing the right lever down (i.e. Group LEFT DOWN vs Group RIGHT DOWN). If Group RIGHT DOWN had been sensitive to the direction of demonstrators' responses, then one would of expected Group RIGHT DOWN to make fewer up responses (i.e. more down responses) than Group LEFT DOWN. In fact, the two groups did not differ. However, this does not mean that Group RIGHT DOWN were not influenced by the direction of demonstrators' responses. It is possible that they were, but that this effect could not be detected because the rats in this procedure show an unlearned bias towards down lever-pressing. This creates a ceiling effect that could not be modified by any learned bias.

In summary, Experiment 1 suggests that under certain conditions, rats in the two object/two action procedure are influenced by both the location and the direction of demonstrators' responses. However, these effects are not robust. Several further replications of Experiment 1 yielded either the direction effect, the spatial effect, or no reliable effect of observation. The reported experiment was the only one in which both effects were obtained simultaneously.

In addition, these replications employed various manipulations to increase the observers' level of up responding (i.e. raising the floors in the operant chambers, reducing the extent of lever displacement on test). Unfortunately, they were found to have no effect other than to shift the preference for the direction in which demonstrators responded from rats that observed demonstrators manipulating the right lever to rats that observed demonstrators manipulating the left lever. This seems to suggest that the failure to find an effect of the direction of demonstrators' responses when demonstrators manipulated the right but not the left lever in Experiment 1, was the result of an asymmetry within the chambers rather than an unwillingness on the part of the rats to look at the left side of the chamber.

The results obtained in Experiment 1 differ from those reported by Ray (1997) in two respects. First, Ray (1997) found that observer rats showed a tendency to respond in the demonstrators' direction at the start of testing, whereas Experiment 1 did not. However, initial test session effects are likely to be affected by extraneous variables associated with recent handling and placement which might explain why one was not detected here. Second, Experiment 1 found that by the end of testing rats showed a tendency to respond in the demonstrators' direction, whereas Ray (1997) did not. The test session employed by Ray terminated after each observer had made 50 reinforced responses, whereas in Experiment 1 it terminated after 20 min had elapsed and generated a much larger sample of behaviour. This raises the possibility that an effect of exposure to the direction of demonstrators' responses can only be detected when a rat has been given the opportunity to respond for a considerable period of time.

The fact that a demonstrator-consistent lever bias was found at the start of testing but not thereafter, while a demonstrator-consistent direction bias was found at the end of testing but not before, suggests that exposure to the direction of demonstrators' responses exerted a stronger effect on observer rats' behaviour than exposure to the location of demonstrators' responses. This effect may have occurred because direction is a more salient or visible cue than location, and thus resulted in the formation of an internal representations which persisted for longer in the rats' memory. Alternatively, it may have been easier for the observers to discriminate, on test, between the direction, rather than the location of their responses. For example, the difference between lifting a lever up or pressing it down may have been greater in terms of kinaesthetic feedback than the difference between manipulating a left or a right lever.

2.2 Experiment 2

In Experiment 1, by the end of testing, rats that observed demonstrators lifting a lever up or pressing it down showed a reliable tendency to respond in the same direction. According to Ray (1997), this effect may be due to response learning by observation. However, it may be due instead to local enhancement. It is possible that demonstrators deposited odour cues (e.g. food particles, saliva, fur) asymmetrically on or around the surface of the lever which they operated, and that exploration of these cues on test was sufficient to bias observer rats towards moving the lever in the same direction as their demonstrator.

The hypothesis that odour cues can influence the direction of rats' responses in an operant procedure is supported by a recent experiment. Mitchell *et al.* (1999) allowed rats to observe demonstrators pushing a joystick either to the left or to the right for food . When subsequently allowed access to the joystick for the first time and rewarded for both left and right responses, rats showed a reliable tendency to respond in the same direction as their demonstrator. However, when the joystick was rotated through an angle of 180 degrees within its mounting between observation and test, rats showed a reliable tendency to respond in the opposite direction to their demonstrator. These results were interpreted as evidence that demonstrators deposited attractive odour cues on the side of the joystick contralateral to its direction of motion. When the joystick was in the standard position, exploration of these cues promoted demonstrator-consistent responding. However, when the joystick had been rotated through an angle of 180 degrees, exploration of odour cues promoted a demonstrator-inconsistent response bias.

In Experiment 2, whether rats were permitted to observe the direction of their demonstrators' responses was manipulated to determine whether exposure to the products of a demonstrator's behaviour is sufficient to result in a tendency for demonstrator-consistent responding. Rats were present in the observation compartment of an operant chamber while a conspecific demonstrator moved a single lever either up or down. Half of the rats were allowed to observe their demonstrator's responses (Groups UP-NO SCREEN and DOWN-NO SCREEN), while the other half were prevented from doing so by an aluminium screen (Groups UP-SCREEN and DOWN-SCREEN). It was anticipated that rats assigned to the NO SCREEN groups would show a bias in favour of moving the lever in the same direction as their demonstrator. If this effect is due to response (or stimulus) learning by observation, then rats assigned to the SCREEN groups would not be expected to respond in the same direction as their demonstrator. If, on the other hand, the effect is due, instead or in addition to local enhancement, then one would expect rats assigned to the SCREEN groups to show a bias at least as strong as the rats assigned to the NO SCREEN groups.

Method

Subjects

The subjects were 48 male hooded Lister rats obtained from Charles River (Margate, Kent, UK). Of these rats, 16 had previously served as demonstrators in a two lever/two action observational learning procedure, and were used for the same purpose here. Prior to the start of the experiment, these animals had an average free-feeding weight of 342 g. The remaining 32 animals were experimentally naive and were the observers. These animals had an average free-feeding weight of 360 g.

Apparatus

The experiment was conducted in the same four operant chambers used in Experiment 1, to which two minor modifications were made in order to encourage up responding in the observers. The floors in each of the chambers were raised by 5 cm, and the distance through which the lever had to be moved on test in order for a response to be registered was reduced to 1.1 cm by adjusting the microswitches that recorded lever movement. Both of these modifications remained in effect throughout all subsequent experiments.

In the present experiment, only one lever, the left or the right, was available to the rat that occupied the demonstration/test compartment. Furthermore, an aluminium screen (24 x 27 cm) was secured, when appropriate (see below), to the wire-mesh partition that separated the observation compartment from the demonstration/test compartment.

A sponge, dampened with a warm, weak, detergent solution, was used to wash the interior of the operant chamber after each rat had completed either a training session, a test session, or both (see below). Once the operant chamber had been washed it was dried with absorbent tissue paper.

Procedure

Demonstrator training

Prior to the start of the experiment, equal numbers of rats had been trained to lift the left lever up, press the left lever down, lift the right lever up, or press the right lever down. Before being observed by the rats in this experiment, each demonstrator received a single session of training. This was to ensure that the demonstrators were accustomed to responding in the presence of an aluminium screen and one, rather than two, levers. Each demonstrator was observed by two different rats, and there was no evidence of a change in the demonstrators' performance during the first and the second demonstration session in which they were observed.

Observer training and testing

Equal numbers of rats were present in the observation compartment of an operant chamber while a demonstrator lifted a single lever up or pressed it down. Half of the rats were allowed to observe the direction of their demonstrators' responses (Groups UP-NO SCREEN and DOWN-NO SCREEN), while the other half were prevented from doing so by means of an aluminium screen (Groups UP-SCREEN and DOWN-SCREEN). Within each group, whether the demonstrator manipulated the left or the right lever was counterbalanced.

Before being placed in an operant chamber with a demonstrator for the first time, each rat received three daily sessions of training. Magazine training was administered on days 1 and 3, and context training on day 2.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 3. All four groups of demonstrators distributed nearly all of their total responses in the correct direction irrespective of the direction in which they had been trained to respond and the presence of a screen.

Group	UP- NO SCREEN	UP- SCREEN	DOWN- NO SCREEN	DOWN- SCREEN
Median Percentage Correct Responses	100.00	100.00	100.00	100.00
Interquartile Range	99.00, 100.00	100.00, 100.00	100.00, 100.00	100.00, 100.00
n	8	8	8	8

Table 3. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 2.

Observers' behaviour

Of the 32 observers tested, one (belonging to Group DOWN-SCREEN) failed to make any responses on test and was excluded from the experiment. Of the remaining observers, all made more than five responses on test. However, the first five responses made by three animals (two belonging to Group UP-NO SCREEN and one belonging to Group DOWN-NO SCREEN observer) were lost owing to apparatus fault. These rats, which were included in the analysis of the observers' total responses, could not be included in the analysis of the observers' first five responses.

The total number of responses made by each of the observers that responded on test is summarized in Table 4. Animals in all four groups made an equivalent total number of responses, an impression which was supported when the data were subjected to two-way (direction x screen) ANOVA. This revealed that neither of the main effects were reliable, nor was the interaction ($F < 1$ in all cases).

Group	UP- NO SCREEN	UP- SCREEN	DOWN- NO SCREEN	DOWN- SCREEN
Mean Number of Responses	70.63	70.13	64.13	81.29
Standard Error of the Mean	14.08	12.58	16.25	13.77
n	8	8	8	7

Table 4. Mean total number of responses and standard errors of the means for each group of observers in Experiment 2.

Figure 4a shows the directional discrimination ratio for the first five responses made by each group of observers. A preliminary three-way (lever x direction x screen) ANOVA performed on these data indicated that the main effect of, and interactions involving, lever were not reliable. Therefore, the data have been presented pooled across rats that observed demonstrators manipulating the left lever and rats that observed demonstrators manipulating the right lever.

It is evident that the manipulations employed in this experiment to increase the observers' up responding did not have the desired effect, since the observers still made more down than up responses. In addition to this bias, Figure 4a suggests that at the start of testing exposure to the products of demonstrators' behaviour was insufficient to result in a tendency for demonstrator-consistent responding. When rats were allowed to observe demonstrators' responses, those that observed demonstrators lifting a lever up made a greater proportion of their first five responses in an upward direction than those that observed demonstrators pressing a lever down. In contrast, when the rats' view of the demonstrators' responses was blocked by means of a screen, those that were paired with demonstrators lifting a lever up did not make more up responses than those that were paired with demonstrators pressing a lever down. However, these impressions could not be supported when the data were subjected to two-way (direction x screen) ANOVA. This revealed that the main effect of direction ($F < 1$), the main effect of screen ($F(1, 24) = 2.00$, $p = 0.17$), and the direction x screen interaction ($F < 1$) were not reliable.

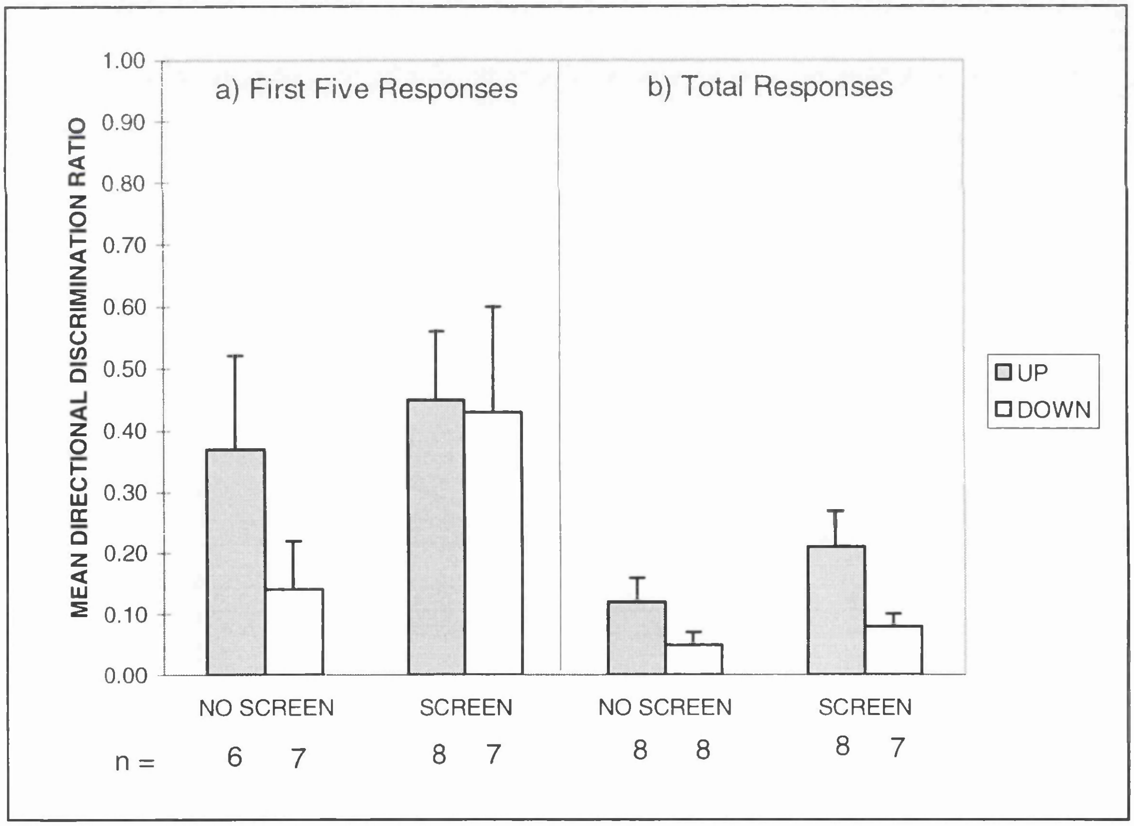

Figure 4. Mean directional discrimination ratio (up responses/total responses) of a) the first five and b) the total responses made by each group of observers in Experiment 2. The black bars indicate the standard errors of the mean.

The directional discrimination ratio for the total responses made by each group of observers is shown in Figure 4b. Again, the data have been presented pooled across rats that observed demonstrators manipulating the left or the right lever, because preliminary three-way (lever x direction x screen) ANOVA indicated that the main effect of, and interactions involving lever, were not reliable.

The data presented in this figure suggest that, by the end of testing rats made even fewer up relative to down responses than at the start of testing. However, in contrast to the start of testing, exposure to the products of demonstrators' behaviour now appears to be sufficient to result in a tendency for demonstrator-consistent responding. Rats that were paired with demonstrators lifting a lever up made proportionately more up responses (mean = 0.16, SEM = 0.04, N = 16) than rats that were paired with demonstrators pressing a lever down (mean = 0.06, SEM = 0.01, N = 15). This effect occurred both for those groups in which rats could observe the demonstrators' responses and for those groups in which they were prevented from doing so. Although, surprisingly, the tendency for demonstrator-consistent responding appears to be stronger among rats that could not observe the demonstrators' responses.

These impressions were supported when the data were subjected to two-way (direction x screen) ANOVA. This revealed a significant main effect of direction (F (1, 27) = 5.83, p = 0.02), while simple effects confirmed that Group UP-SCREEN made more up responses than Group DOWN-SCREEN (F (1, 27) = 6.00, p = 0.02), whereas Groups UP-NO SCREEN and DOWN-NO SCREEN did not differ (F (1, 27) = 2.00, p = 0.17). Furthermore, Group UP-SCREEN made marginally more up responses than Group UP-NO SCREEN (F (1, 27) = 3.00, p = 0.09), whereas Groups DOWN-SCREEN and DOWN-NO SCREEN did not differ (F <

1).ANOVA also indicated that the main effect of screen (F (1, 27) = 2.08, p = 0.16) and the direction x screen interaction (F < 1) were not reliable.

Thus, it would appear that preventing rats from observing the direction in which demonstrators moved a lever did not prevent them from responding in the same direction when subsequently allowed access to the lever on test. This suggests that demonstrators deposited attractive odour cues asymmetrically on or around the surface of the lever which they operated, and that exposure to these cues on test was sufficient to bias the direction of rats' responses. It would also appear that while rats are influenced by exposure to the cues deposited by demonstrators rewarded for lifting up (i.e. Group UP-NO SCREEN vs Group UP-SCREEN), there is no evidence of a similar effect of exposure to the cues deposited by demonstrators rewarded for pressing down (i.e. Group DOWN-NO SCREEN vs DOWN-SCREEN).

If demonstrators assigned to Group DOWN-SCREEN deposited odour cues on or around the lever which they operated, and if these cues were attractive to other rats, then one would of expected Group DOWN-SCREEN to make fewer up responses (i.e. more down responses) than Group DOWN-NO SCREEN. In fact, these two groups did not differ. However, this does not mean that the rats that demonstrated to Group DOWN-SCREEN did not deposit odour cues or that these cues were not attractive to other rats. It is more likely that Experiment 2 failed to detect an effect of exposure to odour cues deposited by down-pressing demonstrators, because of the bias towards pressing the lever down shown by the rats in this procedure.

In addition to an effect of exposure to demonstrator-deposited odour cues, Experiment 2 raised the possibility that there was an inverse effect of exposure to visual cues. In Experiment

2, rats that were prevented from observing the direction of demonstrators' responses showed a reliable bias in favour of the demonstrators' direction, whereas rats that had been allowed to observe demonstrators' responses did not. Since rats in the SCREEN groups had access to odour cues alone, while rats in the NO SCREEN groups had access to visual cues in addition to odour cues, this suggests that Groups NO SCREEN were influenced by their observation of a demonstrator's behaviour, and that this experience led to demonstrator-inconsistent responding effects.

One possible explanation to account for the fact that visual cues promoted demonstrator-inconsistent responding is as follows. Rats may have learned through visual observation about the return of the lever to its resting place, rather than the movement of the lever in the reinforced direction, either because the former event was more salient or because it was more contiguous with secondary reinforcement (i.e. the sound of magazine operation). For example, when the lever was being displaced the demonstrator was standing in front of it. When the lever was returning to its resting place, the demonstrator was in the process of moving towards the food tray.

However, this argument is weakened when one considers that in Experiment 1 and in the experiment by Ray (1997), simultaneous exposure to visual cues during observation training and odour cues on test resulted in reliable demonstrator-consistent responding effects. If visual cues and odour cues had opposite, although equal effects, one would have expected the rats in these experiments to distribute their responses equally between the demonstrator's direction and the opposite direction. Finally, although Experiment 2 was designed to distinguish scent-mediated local enhancement from response learning by observation, the fact that visual observation promoted demonstrator-inconsistent responding, suggests that this effect was due to stimulus learning by observation. In Chapter 1, it was shown that stimulus learning by observation could result in both matching and nonmatching behaviour on the part of an observer. The only outcome of response learning by observation is matching behaviour.

2.3 Experiment 3

Experiment 2 suggested that exposure to demonstrator-deposited odour cues was sufficient to bias rats' responses in favour of their demonstrator's direction. Visual observation, on the other hand, may have promoted demonstrator-inconsistent responding. However, since the latter effect is not consistent with the results of previous studies (e.g. Ray, 1997; Experiment 1), it must be corroborated. Experiment 3 used a box-swapping procedure with this objective. It was able to do so because box-swapping procedures are designed to manipulate, independently, the location of demonstrator-deposited odour cues and the visual information that is derived from the direction of lever movement.

In Experiment 3, each rat was allowed to observe a conspecific (the viewed demonstrator) moving a single lever either up or down. Observers were then transferred into the test compartment of a second operant chamber in which another rat (the box demonstrator) had been moving the lever either up (Groups UP-UP and DOWN-UP) or down (Groups UP-DOWN and DOWN-DOWN) during a demonstration session that had run concurrently with the one that the observers had viewed.

Following the results obtained in Experiment 2, it was anticipated that rats would show a bias in favour of moving the lever in the same direction as their box demonstrator (i.e. a main effect of box demonstrator). It was also anticipated that, if the effect of conspecific observation is to result in a tendency for observation-inconsistent responding, then rats would be expected to show a bias in favour of moving the lever in the opposite direction to their viewed demonstrator (i.e. a main effect of viewed demonstrator). One would not, however, expect any interaction between box demonstrator and viewed demonstrator.

Method

Subjects

The subjects were 80 male hooded Lister rats obtained from Charles River (Margate, Kent, UK). Of these rats, 16 had previously participated in a two object/two action observational learning procedure: eight as demonstrators and eight as observers. These animals, which at the start of the experiment had a free-feeding weight of 345 g, were assigned the role of demonstrator. The remaining 64 animals were naive and were the observers. These animals had a free-feeding weight of 401 g.

Apparatus

The experiment was conducted in the same four operant chambers used in Experiment 1. However in Experiment 3, only the left lever was made available to the rat that occupied the demonstration compartment.

Procedure

Demonstrator training

Prior to the start of Experiment 3 equal numbers of rats had been trained to lift the left lever up or press the left lever down. Before being observed by the rats in this experiment, each demonstrator received three sessions of training in which only correct responses were rewarded with food. Incorrect responses had no programmed consequences. Each demonstrator was viewed by four different rats. There was no evidence to suggest that the performance of the demonstrators changed from the first to the fourth demonstration session in which they were observed.

Observer training and testing

Equal numbers of rats observed a conspecific (the viewed demonstrator) moving a single lever either up or down. The rats were then transferred into the test compartment of a different operant chamber in which another rat (the box demonstrator) had manipulated the lever either up or down during a demonstration session that had run concurrently with the one that the observer had viewed. Thus there were four groups of observers: Group UP-UP, DOWN-UP, UP-DOWN, and DOWN-DOWN. For each group, the first coding element refers to the direction of the viewed demonstrators' responses, while the second coding element refers to the direction of the box demonstrators' responses.

Before being allowed to observe a demonstrator for the first time, each rat received four daily sessions of training. Magazine training sessions were given on days 1 and 4, while context training sessions were given on days 2 and 3. The first two sessions of training occurred in the operant chamber in which the rat was eventually allowed to observe its viewed demonstrator, while the last two sessions of training occurred in the operant chamber in which the rat was to be tested.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 5. Demonstrators that had been trained to lift a lever up or press a lever down distributed all of their responses in the correct direction.

Group	UP	DOWN
Median Percentage Correct Responses	100.00	100.00
Interquartile Range	100.00, 100.00	100.00, 100.00
n	32	32

Table 5. Median percentage correct responses [number of correct responses/total number of responses) x 100%] for each group of demonstrators in Experiment 3.

Observers' behaviour

Of the 64 observers tested, all responded on test and all made more than five responses. However, the first five responses made by four observers (two belonging to Group UP-DOWN and two belonging to Group DOWN-UP) were lost owing to apparatus fault. These animals, which were included in the analysis of the observers' total responses, were excluded from analysis of the observers' first five responses.

The total number of responses made by all 64 observers is summarized in Table 6. It is apparent that the rats in all four groups made an equivalent total number of responses, and impression which was supported when the data were subjected to two-way (viewed demonstrator x box demonstrator) ANOVA. This revealed that the main effect of viewed demonstrator ($F < 1$), the main effect of box demonstrator ($F (1, 56) = 1.51$, $p = 0.22$) and the viewed demonstrator x box demonstrator interaction (F (1, 56) = 1.77, p = 0.19) were not reliable.

Group	UP-UP	UP-DOWN	DOWN-UP	DOWN-DOWN
Mean Total Number of Responses	77.25	80.31	85.25	77.63
Standard Error of the Mean	6.87	8.14	5.5	5.43
n	16	16	16	16

Table 6. Mean total number of responses and standard errors of the means for each group of observers in Experiment 3.

Figure 5a shows the directional discrimination ratio for the first five responses made by each group of observers. As in previous experiments, rats made many more down than up responses. In addition to this bias, Figure 5a suggests that relative to the rats that viewed demonstrators lifting up, those that viewed demonstrators pressing down made proportionately more up responses. However, this effect only occurred when rats were tested in compartments in which box demonstrators had lifted the lever up. When rats were tested in compartments in which box demonstrators had pressed the lever down, those that viewed demonstrators lifting up or pressing down did not differ. However, despite these impressions, two-way (viewed demonstrator x box demonstrator) ANOVA performed on these data revealed that the main effect of box demonstrator (F (1, 56) = 1.51, p = 0.22), the main effect of viewed demonstrator (F < 1), and the viewed demonstrator x box demonstrator interaction (F (1, 56) = 1.77, p = 0.19) were not reliable.

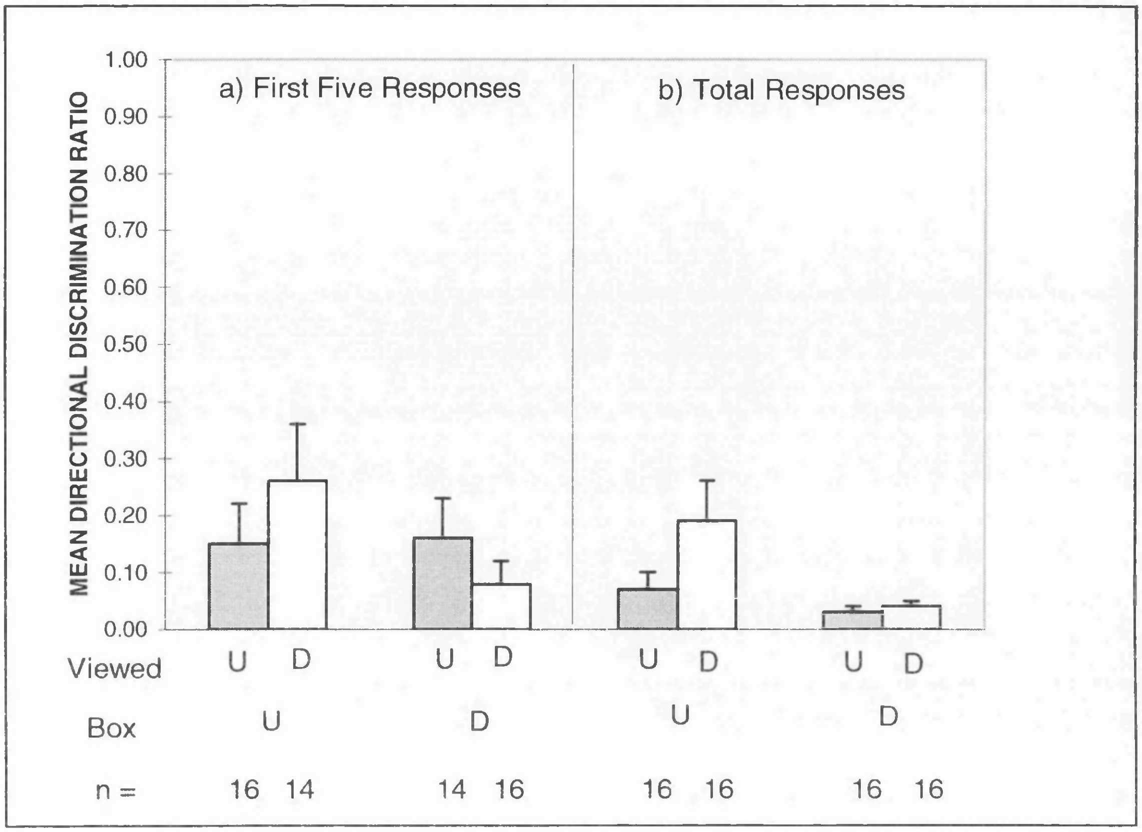

Figure 5. Mean directional discrimination ratio (up responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 3. The black bars indicate the standard errors of the means. U (Up) and D (Down) refer to the direction in which both the Viewed and the Box Demonstrator moved the lever.

The directional discrimination ratio for the total responses made by each group of observers is shown in Figure 5b. It is evident that the observers' behaviour by the end of testing resembled their behaviour at the start of testing. In addition to an overall bias towards down responding, Figure 5b suggests that exposure to the products of box demonstrators' behaviour resulted in a tendency for demonstrator-consistent responding, when the viewed demonstrators pressed down, and had no effect when the viewed demonstrators lifted up. Furthermore, observation of the direction of viewed demonstrators' responses appears to have resulted in a tendency for demonstrator-inconsistent responding, when the box demonstrators lifted up, and had no effect when the box demonstrators pressed down.

These impressions were supported when the data were subjected to two-way (viewed demonstrator x box demonstrator) ANOVA. This revealed a significant main effect of box demonstrator (F (1, 60) = 5.41, p = 0.02). The main effect of viewed demonstrator (F (1, 60) = 2.81, p = 0.10) and the box demonstrator x viewed demonstrator interaction (F (1, 60) = 1.47, p = 0.23) were not reliable. Simple effects performed on the data depicted in Figure 5b revealed that Group UP-UP made fewer up responses than Group DOWN-UP (F (1, 60) = 4.23, p = 0.04), whereas Groups UP-DOWN and DOWN-DOWN did not differ (F < 1). Furthermore, Group DOWN-UP made more up responses than Group DOWN-DOWN (F (1, 60) = 6.15, p = 0.02), whereas Groups UP-UP and UP-DOWN did not differ (F < 1).

Unfortunately, these results were not as straightforward as originally predicted. By the end of testing, exposure to the products of box demonstrators' behaviour resulted in a tendency for demonstrator-consistent responding when the viewed demonstrator pressed down (i.e. Group DOWN-UP vs Group DOWN-DOWN), while observation of viewed demonstrators' responses resulted in a tendency for demonstrator-inconsistent responding when the box demonstrators lifted up (i.e. Group UP-UP vs Group DOWN-UP).

One possible explanation of these results is as follows. First, exposure to odour cues deposited by box demonstrators rewarded for lifting up promoted up-responding, while exposure to odour cues deposited by box demonstrators rewarded for pressing down promoted down-responding. Second, observation of viewed demonstrators pressing down promoted up-responding, while observation of viewed demonstrators lifting up promoted down-responding. In both cases, the latter effect (i.e. that which promoted down responding) could not be detected owing to an extraneous bias towards pressing the lever down. The former effect (i.e. that which promoted up-responding), on the other hand, could be detected but only when accompanied by compatible observation or olfactory experience. For example, Group DOWN-UP was exposed to two factors favouring up-responding (viewed and box demonstrator). This would explain why the animals in this group made more up responses than the animals in Group UP-UP that were exposed to only one (box demonstrator). It would also explain why Group DOWN-UP, that was exposed to two factors favouring up responding (viewed and box demonstrator), made more up responses than Group DOWN-DOWN, that was exposed to only one (viewed demonstrator).

2.4 General Discussion

Taken together, the results of the experiments reported in this chapter are revealing. They suggest that in the context of a two-object/two-action procedure, a number of different social influences and social learning processes may facilitate acquisition of a novel response by naive rats.

In Experiment 1, naive rats observed conspecific demonstrators manipulating either a left or a right lever by lifting up or pressing down. When subsequently allowed access to the same levers on test, these rats showed an initial response bias in favour of the demonstrators' lever and an overall response bias in favour of the demonstrators' direction. Experiments 2 and 3 were designed to examine the possibility that odour cues deposited by demonstrators on a lever, instead or in addition to, visual cues arising from observation of the demonstrators' behaviour could result in demonstrator-consistent directional effects. Both experiments provided good evidence of an effect of exposure to demonstrator-deposited odour cues.

In Experiment 2, rats that were prevented from observing the direction of demonstrators' responses showed a reliable tendency to respond in the same direction when subsequently allowed access to the demonstrators' lever on test. In Experiment 3, rats observed viewed demonstrators lifting a lever up or pressing it down, and were then tested in compartments in which box demonstrators had moved the lever either up or down. These rats showed a reliable tendency to move the lever in the same direction as the box demonstrator.

In addition to obtaining evidence of an effect of exposure to odour cues, Experiments 2 and 3 also obtained evidence of an inverse effect of exposure to visual cues. In Experiment 2, rats that observed demonstrators moving a lever either up or down did not show a reliable response bias on test. Since these rats had access to odour cues in addition to visual cues, it was suggested that the failure to find an effect of the direction of demonstrators' responses was because observation promoted demonstrator-inconsistent responding which counteracted the effect of olfaction. More direct support for this hypothesis was provided by Experiment 3 in which rats that observed viewed demonstrators lifting a lever up or pressing it down showed a reliable tendency to respond in the opposite direction. One possible explanation of this effect is that the rats learned about the return of the lever to its resting place rather than the movement of the lever in the reinforced direction, either because this event was more visible or because it was more contiguous with the delivery of food.

Although the hypothesis that visual cues and odour cues have opposite, although equal effects, can account for Experiments 2 and 3, it fails to explain Experiment 1 or the results obtained by Ray (1997). In these experiments, rats that were exposed to both visual cues and odour cues exhibited a response bias in favour of the demonstrators' direction. The hypothesis outlined above might attempt to accommodate these findings by suggesting that although visual observation promotes demonstrator-inconsistent responding, it sometimes has no effect or promotes demonstrator-inconsistent responding. Which of these outcomes is observed depends on the influence of unknown variables.

This uncontrolled and unpredictable variation makes the two-object/two-action procedure unsuitable for the task of studying stimulus learning and response learning by observation in the rat. Furthermore, the fact that the rat relies heavily on olfactory information and has poor visual acuity renders it an inappropriate species to use in this procedure.

Chapter 3

Nonimitative Social Learning In the Rat: Sensitivity to the Consequences of Demonstrators' Responses I

3. Introduction

Experiment 1 sought evidence of nonimitative social learning by providing rats with the opportunity to observe demonstrators manipulating either a left or a right lever. When subsequently allowed access to the same levers on test, these rats exhibited a reliable preference for the demonstrator's lever. The results of two studies (Heyes *et al.*, 1999) have provided evidence that this effect was not due to odour cues deposited by demonstrators on or around the lever which they operated. First, rats that were prevented, by means of an aluminium screen, from observing whether demonstrators pressed either a left or a right lever, responded equally on both levers (Experiment 1: Heyes *et al.*, 1999). Second, rats that observed viewed demonstrators pressing either a left or a right lever responded predominantly on this lever, both when it had been pressed by a box demonstrator and when the opposite lever had been pressed (Experiment 2: Heyes *et al.*, 1999).

In Experiment 1, and in both of the experiments by Heyes *et al.* (1999), each of the demonstrators' responses was followed immediately by the delivery of a food pellet into a food tray in the demonstration compartment. It seems likely that this event was perceived by the observers and also that it was assigned a positive value, because during the observers' previous magazine training in the demonstration compartment, it signalled food was available. This raises the possibility that rats were attracted to the lever on which demonstrators responded as a result of learning a lever-food relationship, rather than by learning the static and/or dynamic properties of the lever alone.

Experiments showing that acquisition of an observed response is impaired by withholding demonstrator reward (e.g. Palameta & Lefebvre, 1985; Heyes, Jaldow, & Dawson, 1994; Akins & Zentall, in press), indicate that observation of the consequences of demonstrators' responses plays an important role in social learning. They have also been interpreted as evidence that vicarious reinforcement affects performance via an associative (observational conditioning) rather than a nonassociative (stimulus enhancement, emulation learning) process (Heyes, 1994). Following this example, each of the experiments reported in Chapter 3 manipulated whether rats were exposed to the delivery of food following each of their demonstrator's responses. The aim of these experiments was to determine whether vicarious reinforcement is necessary for producing demonstrator-consistent responding effects of the type detected in a two-object procedure.

3.1 Experiment 4

In Experiment 4, rats observed demonstrators pressing either a left or a right lever. Each of the demonstrators' responses was followed immediately by the delivery of a food pellet to the demonstrator (Groups LEFT-FOOD and RIGHT-FOOD) or had no significant consequences (Group LEFT-NO FOOD and RIGHT-NO FOOD). On the basis of previous findings, it was anticipated that observers in the FOOD groups would show a bias in favour of the demonstrators' lever. If this effect depends on observation of the consequences of demonstrators' responses, then one would not expect it to occur among observers in the NO FOOD groups. If, on the other hand, observation of the consequences of demonstrators' responses does not play an important role in demonstrator-consistent responding, then one would expect observers in the NO FOOD groups to show a bias as strong as that shown by the observers in the FOOD groups.

Method

Subjects

The subjects were 32 male hooded Lister rats. Of these rats, 16 had previously served as demonstrators in a two-object procedure and were used for the same purpose here. Prior to the start of this experiment, these animals had an average free-feeding weight of 444 g. The remaining 16 rats were experimentally naive and were the observers. These animals had an average free-feeding weight of 441 g.

Apparatus

All animals were trained and tested in four identical operant chambers, similar to the chambers used in Experiment 1 except in the following respects. The levers, which were constructed from Perspex and could only be pushed down, were 1 cm thick, 1 cm deep, and 4 cm wide. They were positioned 9 cm apart on either side of the food tray, and 2 cm above floor level. The food tray was located at floor level in the middle of the operant panel. Thus, the levers were larger, closer together, and nearer floor level than in previous experiments.

Procedure

Each session began with the illumination of the house light and finished once a variable number of food pellets had been delivered or responses made (variously defined below), at which point the house light was extinguished.

Demonstrator training

In a previous experiment, equal numbers of rats had been trained to press either the left or the right lever for food. Before being observed by the rats in this experiment, half of the left and half of the right lever-pressing demonstrators received 11 daily sessions of training. In the first session, each correct lever-press was followed by the delivery of a food pellet to the demonstrator. Incorrect lever-presses had no programmed consequences. This session terminated following the delivery of 30 food pellets. Over the next 10 sessions, each of which terminated following the delivery of 10 food pellets, discriminative lever-pressing was rewarded on a Variable Interval (VI) schedule in order to render responding resistant to extinction when being observed by rats in the NO FOOD groups. In Sessions 2 and 3, a VI-15 sec schedule was used. This was increased to a VI-30 sec schedule in Sessions 4 and 5, a VI-60 sec schedule in Sessions 6-10, and a VI-90 sec schedule in Session 11.

The remaining demonstrators received three daily sessions of training in which either left or right lever-pressing was continuously reinforced. These sessions terminated once 100 food pellets had been delivered. Following training, each of these rats demonstrated lever-pressing to an observer in the FOOD groups.

Observer training and testing

Initially, all of the observers received two daily sessions of magazine training in which a total of 20 food pellets were delivered on a RT-60 sec schedule. On day 3, these rats were confined in the observation compartment of an operant chamber. The demonstration compartment of this chamber contained a rat that was pressing either the left (n = 8) or the right (n = 8) lever. Within each group, half of the rats observed demonstrators pressing a lever and being rewarded with food (Groups LEFT-FOOD and RIGHT-FOOD), while the other half observed demonstrators pressing a lever but not being rewarded with food (Group LEFT-NO FOOD and RIGHT-NO FOOD).

Once a demonstrator had made 100 correct responses it was removed from the chamber. Group FOOD demonstrators took approximately 10 min to achieve this number of responses, while Group NO FOOD demonstrators took approximately 17 min. The observers were then transferred into the empty demonstration compartment and given a test session in which both left and right lever presses were rewarded with food. To standardize the observers' number of responses, test sessions terminated once 50 food pellets had been delivered. This modification remained in effect throughout all subsequent experiments reported in this chapter.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 7. For each demonstrator, accuracy was assessed by comparing the number of correct responses with the total number of responses. In the case of rats that demonstrated lever-pressing to the FOOD groups, correct responses were responses that were made on the reinforced lever. In the case of rats that demonstrated lever-pressing to the NO FOOD groups, correct responses were made on the lever that had previously been reinforced during demonstrator training.

The data presented in Table 7 indicate that while being observed by subjects, demonstrators responded predominantly on the correct lever. However, it would appear that the rats that demonstrated lever-pressing to the FOOD groups were more likely to press the correct lever than the rats that demonstrated lever-pressing to the NO FOOD groups. This effect was particularly pronounced for those demonstrators that pressed the right lever, and probably resulted from differences in the amount of partial reinforcement received by these animals during training.

Group	LEFT-FOOD	LEFT-NO FOOD	RIGHT-FOOD	RIGHT-NO FOOD
Median Percentage Correct Responses	100.00	94.50	100.00	88.50
Interquartile Range	100.00, 100.00	81.00, 97.50	98.50, 100.00	72.00, 99.00
n	4	4	4	4

Table 7. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 4.

Owing to the fact that the largest variance (Group RIGHT-NO FOOD) was almost 300 times greater than the smallest variance (Group LEFT-FOOD), a nonparametric test was used to analyse these data. Kruskal-Wallis one-way ANOVA yielded a reliable effect of group (chi-square = 8.36, df = 3, $p = 0.04$, corrected for ties), while follow-up tests indicated that Group RIGHT-FOOD demonstrators made more correct responses than Group RIGHT-NO FOOD demonstrators ($p < 0.05$). None of the other pairwise comparisons were reliable.

Observers' behaviour

The observers' behaviour was assessed by means of a spatial discrimination ratio, which was calculated for: (i) the first five responses made by each rat, and (ii) all 50 responses made by each rat over the course of the test session. Spatial discrimination ratios were computed, as in Experiment 1, by dividing the number of left responses by the total number of responses (i.e. five or 50). The data relating to each measure were subjected to two-way Analysis of Covariance in which lever (left, right) and reinforcement (food, no food) were both factors. There was one covariate in each analysis, and this was the demonstrators' percentage correct responses while being observed by subjects.

Of the 16 observers tested, all responded on test. However, one observer (belonging to Group LEFT-NO FOOD) failed to make 50 responses to complete the test session. This animal was excluded from the experiment.

The spatial discrimination ratio for the first five responses made by each of the remaining animals is shown in Figure 6a. Surprisingly, the data suggest that observation of nonrewarded lever-pressing was sufficient to result in a tendency for demonstrator-consistent responding at the start of testing, whereas observation of rewarded lever-pressing was not. When the demonstrators' responses had no significant consequences, rats that observed demonstrators pressing the left lever made proportionately more left responses than rats that observed demonstrators pressing the right lever. In contrast, when the demonstrators' responses were followed by food, rats that observed demonstrators pressing the left lever made an equivalent proportion of their first five responses on the left lever as rats that observed demonstrators pressing the right lever.

The results of two-way ANCOVA followed by simple effects went some way towards confirming these impressions. ANCOVA revealed that the main effect of lever (F (1, 10) = 3.34, p = 0.10) was not reliable. However, simple effects showed that while Groups LEFT-FOOD and RIGHT-FOOD did not differ (F < 1), Group LEFT-NO FOOD made marginally more left responses than Group RIGHT-NO FOOD (F (1, 10) = 4.30, p = 0.06). ANCOVA also indicated that the main effect of reinforcement (F < 1) and the lever x reinforcement interaction (F (1, 10) = 1.13, p = 0.31) were not reliable. In addition, there was no evidence to suggest that the demonstrators' percentage correct responses covaried with the observers' discrimination ratio (F < 1).

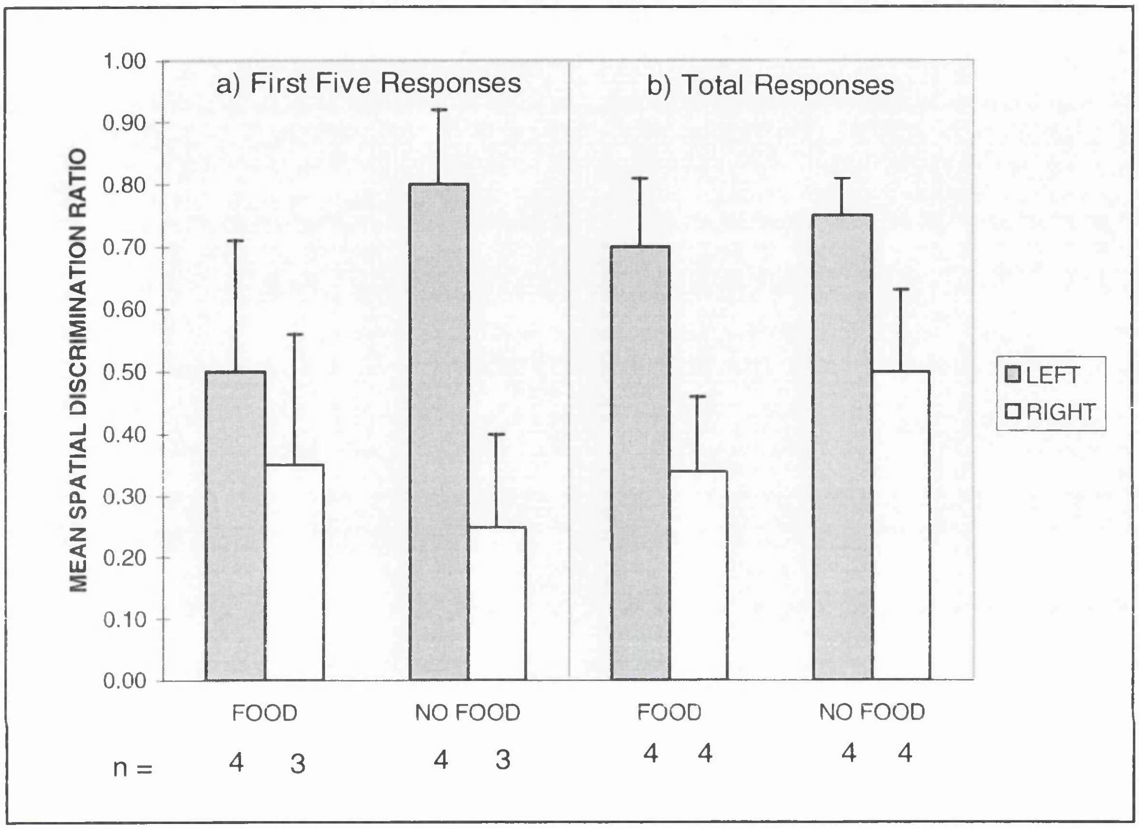

Figure 6. Mean spatial discrimination ratio (left responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 4. The black bars indicate the standard errors of the mean.

It is not particularly surprising that observation of rewarded lever-pressing was insufficient to support reliable demonstrator-consistent responding at the start of testing, . In only one of the experiments reported in Chapter 2 (Experiment 1), did observation training bias observer rats' first five responses. The poor replicability of these effects may be explained by the fact that variables associated with recent handling and placement exert an extraneous influence on initial test session performance.

The spatial discrimination ratio for the total responses made by each group of observers is shown in Figure 6b. In contrast to the start of testing, it would appear that observation of lever-pressing was sufficient to result in a tendency for demonstrator-consistent responding, both when the demonstrators' responses were rewarded with food and when the demonstrators' responses had no significant consequences. Rats that observed demonstrators pressing the left lever made proportionately more of their total responses on the left lever (mean = 0.72, SEM = 0.07, N = 7) than rats that observed demonstrators pressing the right lever (mean = 0.42, SEM = 0.09, N = 8). However, the data presented in Figure 6b does suggest that this effect may be stronger among the rats that observed rewarded demonstrators than among the rats that observed nonrewarded demonstrators.

These impressions were confirmed when the data were subjected to two-way ANCOVA followed by simple effects. ANCOVA yielded a significant main effect of lever (F (1, 10) = 6.57, p = 0.03), while simple effects confirmed that Group LEFT-FOOD made more left responses than Group RIGHT-FOOD (F (1, 10) = 6.57, p = 0.03), whereas Groups LEFT-NO FOOD and RIGHT-NO FOOD did not differ (F (1, 10) = 2.20, p = 0.17). ANCOVA also indicated that the main effect of reinforcement and the lever x reinforcement interaction were not reliable (F < 1 in both cases), nor was the covariate (F < 1).

That observation of rewarded lever-pressing resulted in reliable demonstrator-consistent responding by the end of testing, is again unsurprising. In Experiment 1, rats that observed demonstrators manipulating either a left or a right lever made, in total, more responses on the demonstrator's lever than on the opposite lever, although this effect was not reliable. It is possible that the effect was stronger in Experiment 4 because the levers were larger and therefore may have been more discriminable than in Experiment 1.

Experiment 4 does not satisfactorily resolve the question of whether demonstrator-consistent responding depends on observation of demonstrator-reinforcement in this paradigm. The FOOD groups did, and the NO FOOD groups did not, show a reliable demonstrator-consistent bias over 50 test responses, suggesting dependence on observation of demonstrator reward. However, contrary to this conclusion, the NO FOOD groups showed a trend in favour of demonstrator-consistent responding across the test session and a reliable effect over the first five responses.

3.2 Experiment 5

Experiment 4 failed to provide an unambiguous answer to the question of whether demonstrator-consistent responding depends on observation of the consequences of demonstrators' responses. In an attempt to resolve this issue, Experiment 5 replicated the method used in Experiment 4 to manipulate whether observer rats were exposed to the delivery of food following each of their demonstrator's responses. More specifically, it was hoped that a replication would provide a more reliable indication of whether the demonstrator-consistent bias detected among animals in the NO FOOD group over the first five test responses occurred by chance.

Method

The method used here differed from Experiment 4 in the following respects.

Subjects

The subjects were 32 male hooded Lister rats. Of these rats, 16 had previously served as demonstrators in a two-object procedure and were used for the same purpose here. Prior to the start of this experiment, these animals had an average free-feeding weight of 400 g. The remaining 16 animals were experimentally naive and were the observers. These animals had an average free-feeding weight of 350 g.

Apparatus

The experiment was conducted in the same four operant chambers used in Experiment 1. However, in this experiment the levers in each chamber were adjusted such that they could only be moved in a downward direction. This modification remained in effect throughout all subsequent experiments reported in this chapter.

Procedure

Each session began with the illumination of the house light, and finished once a variable number of responses had been made or 30 min had elapsed (variously defined below), at which point the house light was extinguished.

Demonstrator training

In a previous experiment, equal numbers of rats had been trained to press either the left or the right lever for food. Before being observed by the rats in this experiment, half of the left and half of the right lever-pressing demonstrators received 28 sessions of training over the course of 11 days. Each session terminated following the delivery of 50 food pellets to the demonstrator. In the first four sessions, each correct lever press was rewarded with food. Incorrect lever presses had no programmed consequences. Over the next 24 sessions, discriminative lever-pressing was rewarded on a VI schedule. In Sessions 5-8, a VI-5 sec schedule was used. This was increased to a VI-10 sec schedule in Sessions 9-12, a VI-20 sec schedule in Sessions 13-20, a VI-40 sec schedule in Sessions 21-24, and a VI-80 sec schedule in Sessions 25-28. Thus, the demonstrators were given more extensive VI training than in the previous experiment in an attempt to render responding even more resistant to extinction while being observed by rats in the NO FOOD groups.

The remaining demonstrators received ten sessions of training over six days. In each of these sessions either left or right lever-pressing was continuously reinforced. These sessions terminated once 50 food pellets had been delivered. Following training, these rats demonstrated lever-pressing to an observer in the FOOD groups.

Observer training and testing

Initially, all of the observers received four daily sessions of training. Magazine training consisted of the delivery of 30 food pellets on a RT-60 sec schedule, and was conducted on days 1 and 4. Context training was conducted on days 2 and 3.

On day 5, following the observers' fourth and final session of pretraining, each rat was allowed to observe a demonstrator pressing either the left or the right lever 50 times. Group FOOD demonstrators took approximately 3 min to achieve this number of responses, while Group NO FOOD demonstrators took approximately 7 min.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 8. While being observed by subjects, demonstrators responded predominantly on the correct lever. However, as in Experiment 4 rats that demonstrated lever-pressing to observers in the FOOD groups were more likely to press the correct lever than rats that demonstrated lever-pressing to observers in the NO FOOD groups. This effect occurred both when demonstrators pressed the left lever and when they pressed the right lever.

Group	LEFT-FOOD	LEFT-NO FOOD	RIGHT-FOOD	RIGHT-NO FOOD
Median Percentage Correct Responses	100.00	84.00	100.00	87.00
Interquartile Range	100.00, 100.00	76.50, 91.00	100.00, 100.00	78.50, 91.50
n	4	4	4	4

Table 8. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 5.

Kruskal-Wallis one-way ANOVA performed on these data yielded a reliable effect of group (chi-square = 12.91, df = 3, $p = 0.005$, corrected for ties), while follow-up tests indicated that Group LEFT-FOOD made more correct responses than Group LEFT-NO FOOD ($p < 0.05$) and Group RIGHT-FOOD made more correct responses than Group RIGHT-NO FOOD ($p < 0.05$). None of the other pairwise comparisons were reliable.

Observers' behaviour

Of the 16 observers tested, all responded on test and all made 50 responses to complete the test session.

The spatial discrimination ratio for the first five responses made by each of these animals is shown in Figure 7a. The data presented in this figure suggest that observation of lever-pressing was sufficient to result in a tendency for demonstrator-consistent responding at the start of testing when the demonstrators' responses were rewarded with food, but not when the demonstrators' responses had no significant consequences. However, these impressions could not be supported when they were tested using two-way ANCOVA. ANCOVA revealed that the main effect of lever (F < 1), the main effect of reinforcement (F < 1), and the lever x reinforcement interaction (F (1, 11) = 1.64, p = 0.23) were not reliable. In addition, the demonstrators' percentage correct responses did not covary with the observers' discrimination ratio (F (1, 11) = 1.74, p = 0.21).

The spatial discrimination ratio for the total responses made by each group of observers is shown in Figure 7b. This figure suggests that the observers' behaviour at the end of testing resembled their behaviour at the start of testing. Rats that observed demonstrators pressing either the left or the right lever and being rewarded with food, made proportionately more of their total responses on the demonstrator's lever. In contrast, rats that observed demonstrators pressing either the left or the right lever but not being rewarded with food, distributed their total responses equally between the two levers.

These impressions were tested when the data were subjected to two-way ANCOVA followed by simple effects. ANCOVA yielded a marginal main effect of lever (F (1, 11) 4.42, p = 0.06), while simple effects confirmed that Group LEFT-FOOD made more left responses than Group RIGHT-FOOD (F (1, 11) = 12.50, p = 0.005), whereas Groups LEFT-NO FOOD and RIGHT-NO FOOD did not differ (F < 1). None of the other simple effects were reliable. ANCOVA also indicated that the main effect of reinforcement (F < 1) and the lever x reinforcement interaction (F (1, 11) = 3.03, p = 0.11) were not reliable, nor was the covariate (F < 1).

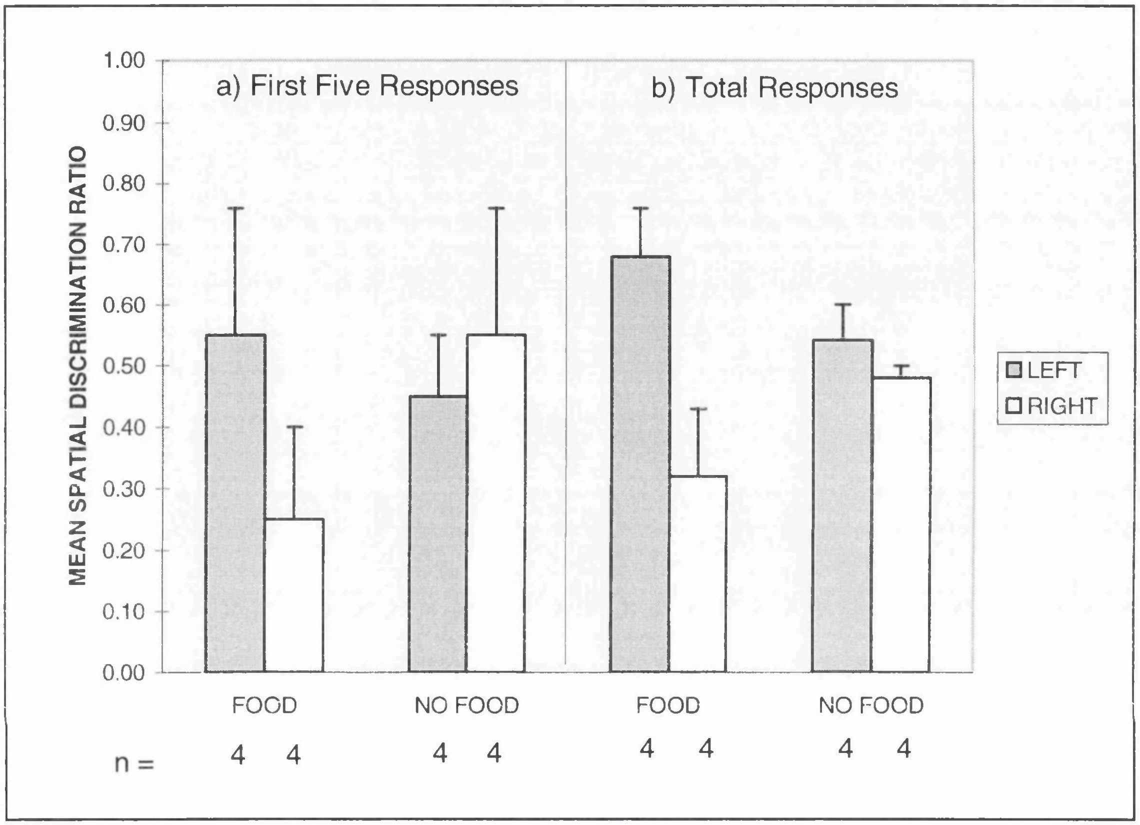

Figure 7. Mean spatial discrimination ratio (left responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 5. The black bars indicate the standard errors of the mean.

To corroborate these findings, the total responses from Experiments 4 and 5 were combined. Preliminary three-way (lever x reinforcement x replication) ANOVA performed on these data indicated that the main effect, and interactions involving, replication were not reliable. Therefore, the data from rats that observed lever-pressing in Experiments 4 and 5 were pooled for further analysis. Two-way ANOVA yielded a reliable main effect of lever (F (1, 26) = 14.25, p = 0.001), while simple effects confirmed that Group LEFT-FOOD made more left responses than Group RIGHT-FOOD (F (1, 26) = 16.67, p = 0.0004), whereas Groups LEFT-NO FOOD and RIGHT-NO FOOD (F (1, 26) = 2.67, p = 0.11) did not differ. Finally, the main effect of reinforcement (F < 1) and the lever x reinforcement interaction (F (1, 26) = 2.63, p = 0.12) were not reliable, nor was the covariate (F < 1).

These results are important for two reasons. First, they imply that there is a stronger tendency toward demonstrator-consistent responding when rats observe demonstrator reinforcement than when they observe demonstrator nonreinforcement. Further support for this conclusion is provided by the results of three unreported experiments that replicated the conditions under which animals in the NO FOOD groups were tested. Irrespective of whether these experiments were analysed independently or in combination, observer rats did not make more responses on the demonstrator's lever than on the opposite lever. Second, they confirm that there is a reliable effect of exposure to rewarded lever-pressing at 50 test responses. Experiment 1 could only find a similar effect across the first five test responses. The reason for this contrast is unclear. However, it is unlikely to have been due to differences in lever size, because in Experiments 1 and 5 the levers were identical.

Originally, it was anticipated that if vicarious reinforcement plays an important role in nonimitative social learning, then rats in the FOOD groups would show more demonstrator-consistent responding than rats in the NO FOOD groups. In line with current thinking (e.g. Palameta & Lefebvre, 1985; Heyes *et al.*, 1994; Akins & Zentall, 1998), such an effect might support the hypothesis that rats' preference for the lever on which demonstrators responded for food was a result of learning a lever-food relationship. However, there are at least three alternative explanations of the same results that do not rely on an associative learning mechanism.

The first possibility is that demonstrators deposit more odour cues on or around the lever to which they responded, and that these cues are attractive to other rats. If, in addition, attractive odour cues are a byproduct of consumption (e.g. food particles, saliva), then this would explain why exposure to the lever pressed by a FOOD demonstrator biased rats' responses, whereas exposure to the lever pressed by a NO FOOD demonstrator did not. However, the results of an experiment in which an aluminium screen prevented rats from observing which of two levers demonstrators pressed for food (Heyes *et al.*, 1999) makes this unlikely, since these rats failed to show a reliable preference for their demonstrator's lever.

The second possibility is that rats are attracted to levers by observing them pressed, both when demonstrators' responses are followed by reward and when they have no significant consequences. However, if NO FOOD demonstrators deposit odour cues that are aversive to other rats, exposure to these cues on test could inhibit the tendency toward demonstrator-consistent responding generated by visual observation. This hypothesis may be substantiated by a study in which rats experienced a double-alternation schedule of reward and nonreward (e.g. RRNNRRNN) in a runway (Ludvigson & Sytsma, 1967). There were two groups, both of which were rotated through their daily trials such that each rat received Trial 1 before Trial 2 was administered, and so forth. In one group (the patterned group), all rats received the same goal event on any given trial. In the other (the nonpatterned group), half the rats were rewarded on any given trial while the other half were nonrewarded. Ludvigson & Sytsma found that rats assigned to the patterned group ran faster on rewarded trials than on nonrewarded trials, while rats assigned to the nonpatterned group ran with the same speed on both types of trial.

These results were interpreted as evidence that rats exude quantitatively and/or qualitatively different odours when food is available than when it is withheld. However, the same effects could be explained if rats deposited odour cues on rewarded trials, but did not deposit any odour cues on nonrewarded trials. Unfortunately, the results of studies designed to resolve this issue were ambiguous. For example, Taylor & Ludvigson (1980) reported that patterned responding established under conditions of consistent reward and nonreward could be abolished by washing the runway following both types of trials. Patterned responding established under the same conditions was, however, unaffected by: (i) washing the runway following rewarded trials while leaving it undisturbed following nonrewarded trials, and (ii) washing the runway following nonrewarded trials while leaving it undisturbed following rewarded trials.

Although these results indicate that rewarded and nonrewarded trials differ in some important respect, they cannot be used to determine the nature of this difference. This is because Taylor & Ludvigson (1980) used as a baseline measure of performance, running speed under a condition in which any odours had presumably been eliminated by washing the runway. However, it seems unlikely that washing the runway would have provided an odour-free environment. On the contrary, it is more likely that it provided rats with important odour cues by which they could discriminate other types of trial.

Further evidence that rats deposit odour cues following an attractive experience but do not deposit any odour cues following an aversive experience, comes from a study of food aversion learning. Galef & Beck (1985) gave rats a choice between two food bowls each containing the same novel diet, and found that these rats avoided the bowl out of which demonstrators had fed and then been injected with poison (Experiment 1). This suggests that poisoned demonstrators deposited aversive odour cues on or around the toxic food bowl so as to dissuade other rats from feeding. However, follow-up experiments (Galef & Beck, 1985; Experiments 2-4) failed to confirm this interpretation. Instead, they showed that demonstrators deposited attractive odour cues on food bowls that they had visited without suffering any ill-effects, thus inducing other rats to approach these bowls. If this is correct, then it is unlikely that rats in the NO FOOD groups failed to show a demonstrator-consistent response bias because of unattractive odour cues deposited by demonstrators on or around the lever that they pressed.

This leaves the third possibility, that stimulus enhancement was responsible. According to Heyes (1994), stimulus enhancement occurs when observation of a demonstrator's activity exposes an observer to the stimulus with which the demonstrator interacted. An experience which may lead to either a decrease (habituation) and/or an increase (sensitization) in responsiveness to that stimulus. Although, it is more likely that when the demonstrators' responses are rewarded with food, increases in responsiveness will occur.

Dual-process theory (Groves & Thompson, 1970), the most widely accepted model of habituation and sensitization suggests that different types of neurological processes underlie these two types of behaviour. Habituation occurs in the stimulus-response (S-R) system, which consists of the neural pathway connecting the sense organs that are activated by a stimulus to the muscles involved in making a response to that stimulus. Sensitization, on the other hand, occurs in the animal's state system and involves those parts of the nervous system that determine the organism's level of responsiveness. Whether the repeated presentation of a stimulus elicits either a decrease or an increase in responsiveness depends on which of these two processes are activated, and if both are, which of the two is stronger.

If sensitization is mediated by the animal's state system, then it seems likely that any factor which alters the animal's level of arousal would have a corresponding effect on responsiveness to a repeatedly presented stimulus. For example, Davis (1974) measured the startle response of rats to a series of brief, loud tones (110 decibels). Rats were tested under two different conditions: one in which a noise generator provided reasonably quiet background noise (60 db), and the other in which the background noise was moderately loud (80 db). Davis found that depending on the test conditions, the rats' behaviour underwent different changes. When the background noise was quiet, repeated tone presentation elicited increasingly smaller startle responses. In contrast, startle responses became progressively larger with repetition of the tone when the background noise was loud.

It seems likely that when rats were tested in the presence of quiet background noise, the rats were relatively unaroused. Thus, only the S-R system underlying habituation was activated resulting in a decline in responsiveness to the tone. When the background noise was loud, the state system underlying sensitization was also activated producing an increase in responsiveness to the tone. Furthermore, since the net behavioural change was an increase in startle response magnitude, the sensitization process appears to have been strengthened more than the habituation process.

Dual-process theory provides an adequate account of the results of Experiments 4 and 5. Rats were exposed to levers as a result of observing them pressed, and this experience led to a decline in responsiveness to that lever. However, since the presence of a conspecific is arousing there was also an increase in responsiveness to the demonstrator's lever. When the demonstrators' responses were followed by reward, the presence of an additional arousing stimulus (i.e. food) strengthened the processes underlying sensitization more than the processes underlying habituation. Thus, rats showed a reliable tendency to approach the demonstrator's lever. When the demonstrators' responses had no significant consequences, the processes underlying habituation and sensitization were strengthened equally. This would explain why, in this condition, rats did not show a reliable tendency to either avoid or approach the demonstrator's lever.

3.3 Experiment 6

In Experiments 4 and 5, rats that observed rewarded lever-pressing exhibited a reliable tendency for demonstrator-consistent responding, while rats that observed nonrewarded lever-pressing did not. This contrast suggests that demonstrator reinforcement mediates nonimitative social learning effects in this procedure. However, it does not provide conclusive evidence that rats in the FOOD groups were attracted to the lever on which demonstrators responded as a result of learning a lever-food relationship, because it may be due instead to stimulus enhancement.

Observation of the demonstrators' behaviour may have exposed rats to the lever on which demonstrators responded, thereby promoting a decline in responsiveness to that lever. However, since rats were aroused by the presence of the demonstrator, there was also an increase in responsiveness to the demonstrator's lever. When the demonstrators' responses were followed by reward, the processes underlying sensitization were strengthened more than the processes underlying habituation resulting in a reliable tendency for demonstrator-consistent responding. In contrast, when the demonstrators' responses had no significant consequences rats did not exhibit a response bias. This was because the processes underlying sensitization and habituation were strengthened equally in this condition.

As a test of this hypothesis, Experiment 6 replicated the method used in Experiment 5, but introduced a 10 min delay between the demonstrators' final lever-press and the observers' first opportunity to respond. Available evidence suggests that sensitization is a temporary phenomenon, that lasts from between 3 sec (Groves & Thompson, 1970) and 10 min (Davis, 1974). Habituation, on the other hand, may persist for up to 24 hours (Leaton, 1974). This suggests that increasing the observation-test interval would have little effect on habituation of responsiveness to the demonstrator's lever, but would cause sensitization to decay. If sensitization effects are already stronger than habituation effects, as in the case of the FOOD groups, than an observation-test interval should result in rats distributing their responses equally between the two levers. If, on the other hand, sensitization and habituation effects are equal, as in the case of the NO FOOD groups, then an observation-test interval should result in rats avoiding their demonstrator's lever.

Method

The method used here differed from Experiment 5 in the following respects.

Subjects

The subjects were 32 male hooded Lister rats. Of these rats, 16 had previously served as demonstrators in a two-object procedure and were used for the same purpose here. Prior to the start of this experiment, these animals had an average free-feeding weight of 377 g. The remaining 16 rats were experimentally naive and were the observers. These animals had an average free-feeing weight of 206 g.

Apparatus

The experiment was conducted in the same four operant chambers used in Experiment 1.

Procedure

Observer training

After observing its demonstrator making 50 responses on either the left or the right lever, each observer was removed from the operant chamber and returned to its home cage. The home cages remained in the experimental cubicle for approximately 10 min, at which point the observers were returned to the empty demonstration compartments for testing.

Results and Discussion

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 9. While being observed by subjects, demonstrators responded predominantly on the correct lever. As in previous experiments, the demonstrators that were observed by rats in the FOOD groups were more likely to press the correct lever than the demonstrators that were observed by rats in the NO FOOD group. This effect was particularly pronounced for those groups in which the demonstrators pressed the left lever.

Kruskal-Wallis one-way ANOVA performed on this data revealed a reliable effect of group (chi-square = 13.82, df = 3, p = 0.003, corrected for ties), while follow-up tests indicated that Group LEFT-FOOD made more correct responses than Group LEFT-NO FOOD ($p < 0.05$). None of the other pairwise comparisons were reliable.

Group	LEFT-FOOD	LEFT-NO FOOD	RIGHT-FOOD	RIGHT-NO FOOD
Median Percentage Correct Responses	100.00	84.00	100.00	94.00
Interquartile Range	100.00, 100.00	78.50, 89.00	100.00, 100.00	89.50, 96.50
n	4	4	4	4

Table 9. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 6.

Observers' behaviour

Of the sixteen observers tested, one (belonging to Group RIGHT-NO FOOD) did not respond on test. Of the remaining rats, two (one belonging to Group LEFT-FOOD and one belonging to Group LEFT-NO FOOD) failed to make 50 responses to complete the test session. All three animals were excluded from the experiment.

The spatial discrimination ratio for the first five responses made by each of the remaining animals is shown in Figure 8a. It would appear that delaying the onset of testing was sufficient to result in a tendency for demonstrator-inconsistent responding among rats that observed nonrewarded lever-pressing, but not among rats that observed rewarded lever-pressing. When the demonstrators' responses had no significant consequences, rats made proportionately less of their first five responses on the demonstrator's lever than on the opposite lever. In contrast, when the demonstrators' responses were rewarded with food, rats made proportionately more responses on the demonstrator's lever than on the opposite lever.

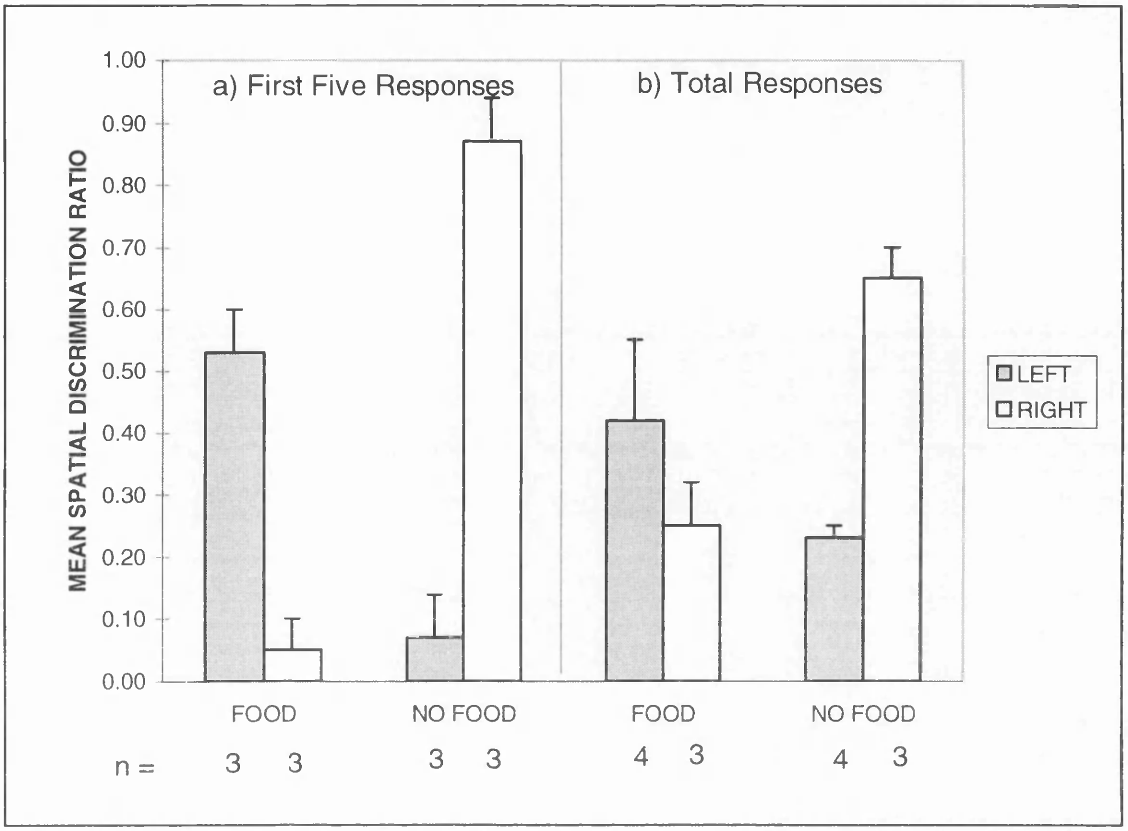

Figure 8. Mean spatial discrimination ratio (left responses/total responses) for a) the first five and b) the total responses made by each group of observers in Experiment 6. The black bars indicate the standard errors of the mean.

These impressions were confirmed when the data were subjected to two-way ANCOVA, which yielded a significant lever x reinforcement interaction (F (1, 8) = 66.91, p = 0.00004). Simple effects used to explore this interaction, indicated that Group LEFT-FOOD made more left responses than Group RIGHT-FOOD (F (1, 8) = 37.00, p = 0.0003), whereas Group LEFT-NO FOOD made fewer left responses than Group RIGHT-NO FOOD (F (1, 8) = 102.00, p = 0.000008). Furthermore, Group LEFT-FOOD made more left responses than Group LEFT-NO FOOD (F (1,8) = 34.00, p = 0.0004), and Group RIGHT-FOOD made fewer left responses than Group RIGHT-NO FOOD (F (1,8) = 107.00, p = 0.000007). ANCOVA also yielded a marginal main effect of lever (F (1, 8) = 5.00, p = 0.06). The main effect of reinforcement was not reliable

(F < 1), nor was the covariate (F < 1).

The spatial discrimination ratio for the total responses made by each group of observers is shown in Figure 8b. It would appear that the tendency for demonstrator-consistent responding detected among rats that observed rewarded lever-pressing, had diminished considerably by the end of testing. When the demonstrators' responses were followed by food, rats made an equivalent proportion of their total responses on the demonstrator's lever and on the opposite lever. In contrast, the tendency for demonstrator-inconsistent responding detected among rats that observed nonrewarded lever-pressing, persisted until the end of testing. When the demonstrators' responses had no significant consequences, rats made proportionately fewer responses on the demonstrator's lever than on the opposite lever.

Two-way ANCOVA followed by simple effects supported these impressions. ANCOVA revealed a significant lever x reinforcement interaction (F (1, 8) = 10.37, p = 0.01). While simple effects confirmed that Groups LEFT-FOOD and RIGHT-FOOD did not differ (F (1, 8) = 2.50, p = 0.15), whereas Group LEFT-NO FOOD made fewer left responses than Group RIGHT-NO FOOD (F (1, 8) = 14.00, p = 0.01). Furthermore, Groups LEFT-FOOD and LEFT-NO FOOD did not differ (F (1, 8) = 3.00, p = 0.12), whereas Group RIGHT-FOOD made fewer left responses than Group RIGHT-NO FOOD (F (1, 8) = 13.00, p = 0.01). ANCOVA also indicated that the main effect of lever (F (1, 8) = 2.50, p = 0.15) and of reinforcement (F < 1) were not reliable, nor was the covariate (F < 1).

The finding that delaying the onset of testing resulted in a tendency for demonstrator-inconsistent responding among the rats that observed nonrewarded lever-pressing, suggests that stimulus enhancement was occurring among these animals. Rats were exposed to the lever on which demonstrators responded during observation training, and this led to both a decrease and an increase in responsiveness to the demonstrator's lever. After the demonstrators' final lever-press, the processes underlying habituation and sensitization were equally strong. However, during the interval prior to testing, the processes underlying sensitization began to decay whereas the processes underlying habituation persisted. Thus, when returned to the demonstration compartment for testing, observer rats showed a tendency to avoid their demonstrator's lever.

This effect could not have been due to attractive odour cues, because if the NO FOOD demonstrators deposited attractive odour cues on or around the lever that they pressed, one would have expected rats to make more responses on this lever than on the opposite lever. If, instead, rats deposited aversive odour, then this might promote demonstrator-inconsistent responding. However, evidence to support the existence of an odour of nonreward is not strong (e.g. Ludvigson & Sytsma, 1969; Taylor & Ludvigson, 1980), and it is unclear why aversive odour cues, or attractive odour cues for that matter, would promote demonstrator-inconsistent responding with a delay between demonstration and testing, but have no detectable effect on performance without a delay.

Finally, Experiment 6 also found that delaying the onset of testing did not affect the tendency for demonstrator-consistent responding shown by rats that observed rewarded lever-pressing. Since rats in the FOOD groups were exposed to both a demonstrator and food during observation training, while rats in the NO FOOD were exposed to the former only, it is possible that the processes underlying sensitization were rendered more resistant to decay in the FOOD group. However, it is also possible that rats in the FOOD groups did not exhibit a tendency for demonstrator-inconsistent responding because when demonstrators' responses are followed by reward, rats learn a lever-food relationship.

3.4 General Discussion

Three experiments examined the role played by vicarious reinforcement (Bandura, 1965), or observation of the consequences of demonstrators' responses, in lever choice by rats. These experiments were designed to test the hypothesis that rats are attracted to the lever on which demonstrators responded as a result of learning a lever-food relationship (observational conditioning), against an alternative account based on nonassociative learning. According to this alternative account, observation of demonstrators' responses alone is sufficient to render attractive the lever on which demonstrators responded, and thereby promote learning about either the static (stimulus enhancement) and/or dynamic (emulation learning) properties of that lever.

In all three experiments, rats that observed demonstrators' responses followed by reward exhibited a reliable tendency for demonstrator-consistent responding. In contrast, when demonstrators' responses had no significant consequences, rats either failed to exhibit a reliable response bias (Experiments 4 and 5) or exhibited a reliable response bias in favour of the lever that the demonstrator did not press (Experiment 6). These results, which cannot be explained by either attractive or aversive demonstrator deposited odour cues, suggest that rats are attracted to the lever on which demonstrators responded as a result of observing the demonstrators' responses rewarded with food. However, the fact that exposure to nonrewarded lever-pressing was sufficient to bias rats' responses in Experiment 6 where there was a delay between demonstration and testing, raises doubts about whether demonstrator reinforcement affects performance via associative learning. Rats may have exhibited a tendency for demonstrator-consistent responding following exposure to rewarded lever-pressing, because they learned a lever-food relationship. Alternatively, exposure to rewarded lever-pressing may strengthened the processes underlying sensitization to the demonstrator's lever more than the processes underlying habituation.

One way in which associative learning theory could accommodate the results of Experiment 6 would be by suggesting that demonstrator reinforcement exerts two independent effects on behaviour. One effect is associative and refers to the learning of a lever-food relationship. The other is nonassociative and occurs when reinforcement increases the probability that rats will be attracted to the lever to which they were exposed by their demonstrator's behaviour.

Thus, the present series of experiments does not completely resolve the issue of whether demonstrator reinforcement affects lever choice via associative, in addition to, nonassociative learning. However, they are of considerable interest in their own right. First, Experiments 4-6 provides the first evidence of the interaction of socially mediated habituation and sensitization processes, and Experiment 6 provides a clear example of a case in which social learning results in non-matching behaviour.

Chapter 4

Nonimitative Social Learning In the Rat: Sensitivity to the Consequences of Demonstrators' Responses II

4. Introduction

The experiments reported in Chapter 3 do not completely exclude the possibility that rats are attracted to the lever on which demonstrators responded for food as a result of learning a lever-food relationship. In Experiment 6, where the onset of testing was delayed in an attempt to disassociate the effects of habituation and sensitization, rats that observed rewarded lever-pressing exhibited a tendency for demonstrator-consistent responding, while rats that observed nonrewarded lever-pressing exhibited a tendency for demonstrator-inconsistent responding. This contrast may have occurred because the presence of an appetitive reinforcer renders the processes underlying sensitization more resistance to decay caused by the passage of time. Alternatively, it may have occurred because rats in the FOOD groups learned a lever-food relationship.

One strategy that may be used to resolve this issue was suggested by Heyes, Jaldow, & Dawson (1993). According to Heyes *et al.* (1993), if rats are able to learn a response-food relationship through conspecific observation (e.g. Heyes & Dawson, 1990; Heyes *et al.*, 1992), then they should also be able to learn a response-no food relationship. This prediction was tested by training rats to push a joystick either to the left or to the right of its vertical starting position for food. The rats were then allowed to observe a conspecific demonstrator either sitting passively in the joystick compartment (Group NONE) or making 50 nonreinforced responses in the direction which had previously been reinforced during observer training (Group SAME) or in the opposite direction (Group DIFFERENT). After observation, the rats were given an extinction test in which neither left nor right responses were rewarded.

Heyes *et al.* (1993) found that during extinction testing, Group SAME made fewer previously reinforced responses than Group DIFFERENT, which made fewer than Group NONE. It was also found that although Groups SAME and DIFFERENT made an equivalent number of previously nonreinforced responses, both made fewer than Group NONE. These results suggest that observation of nonreinforced responding affects resistance to extinction in rats. They also suggest that observation of nonreinforced same responding results in less resistance to extinction than observation of nonreinforced different responding.

It is possible that inhibitory conditioning, or learning a response-no food relationship by observation (Mackintosh, 1974), was responsible for differences in resistance to extinction reported by Heyes *et al.* (1993). This account is based on two assumptions. First, instrumental pretraining resulted in rats expecting responses in one direction to be reinforced, and responses in the opposite direction to be nonreinforced. Second, during subsequent observation training, the rats in Groups SAME and DIFFERENT somehow equated the direction of their demonstrator's responses with the direction of their own. If this is correct, then Group SAME, which saw previously reinforced responses made in extinction, would have been subject to greater expectancy disconfirmation, and therefore would have been more likely to learn a response-no food relationship than Group DIFFERENT, which saw previously nonreinforced responses made in extinction. If, in addition, there was some generalization between left and right responses, then Group DIFFERENT would have been subject to greater expectancy disconfirmation, and therefore would have been more likely to learn a response-no food relationship than Group NONE, which did not observe responding in either direction prior to testing.

However, a recent experiment has raised doubts about whether the bidirectional control procedure provides evidence of observational learning. Mitchell *et al.* (1999) allowed naive rats to observe demonstrators pushing a joystick either to the left or to the right for food. When subsequently allowed access to the same joystick on test and rewarded for both left and right responses, these rats showed a reliable bias in favour of the demonstrator's direction. However, when the joystick was rotated within its mounting through an angle of 180 degrees between observation and testing, rats showed a reliable bias in favour of the direction in which the demonstrators did not push the joystick. These results suggest that demonstrators deposited attractive odour cues on the side of the joystick contralateral to its direction of motion, and that exploration of these cues on test biased observer rats' responses. When the joystick was in the standard position, exploration of odour cues promoted demonstrator-consistent responding. However, when the joystick had been rotated through an angle of 180 degrees, exploration of odour cues promoted a demonstrator-inconsistent bias.

The hypothesis that rats in the bidirectional control procedure are influenced by demonstrator-deposited odour cues rather than response learning by observation, is consistent with a number of studies (e.g. Heyes & Dawson, 1990; Heyes *et al.*, 1992). However, it cannot account for the results obtained by Heyes *et al.* (1993), since if the rats in this experiment had been attracted to the side of the joystick on which demonstrators deposited odour cues, one would of expected the rats in Group SAME to make more previously reinforced responses, or to be more resistant to extinction, than the rats in Groups DIFFERENT and NONE. In fact, the reverse effect was found.

If, instead, demonstrators deposited unattractive odour cues on the side of the joystick that they contacted, then this might have contributed to making Group SAME less resistant to extinction than Group DIFFERENT, and Group DIFFERENT less resistant to extinction than Group NONE. However, while rats appear to deposit odour cues following an attractive experience (e.g. Galef & Beck, 1985), evidence that rats deposit odour cues following an aversive experience is not strong (e.g. Ludvigson & Sytsma, 1967; Taylor & Ludvigson, 1980).

Irrespective of whether the bidirectional control procedure provides evidence of observational learning, the logic underlying the experimental manipulations used by Heyes *et al.* (1993) is sound and can be modified to determine whether rats in a two-object procedure engage in stimulus-reinforcer learning by observation in addition to single stimulus, exposure learning. This was the purpose of Experiment 7.

4.1 Experiment 7

In Experiment 7, each rat was trained to press either a left or a right lever for food, and then given the opportunity to observe a conspecific demonstrator either sitting passively in the lever compartment (Group NONE) or pressing a lever but not being rewarded with food. In the latter group, half of the rats observed demonstrators making 50 nonreinforced responses on the lever which had previously been reinforced during observer training (Group SAME), while the other half observed demonstrators responding on the opposite lever (Group DIFFERENT). After observation, the rats were given an extinction test in which neither left nor right responses were rewarded.

It was anticipated that if rats in a two-object procedure engage in stimulus-reinforcer learning by observation, then responding in the rats in Group SAME would be less resistant to extinction (i.e. would extinguish more quickly), than that of the rats in Groups DIFFERENT and NONE. If, on the other hand, single stimulus, exposure learning mediates lever choice by rats, one would expect responding in Group SAME to be more resistant to extinction (i.e. to extinguish more slowly) than the rats in Groups DIFFERENT and NONE.

Method

Subjects

The subjects were 48 experimentally naive male hooded Lister rats. Of these rats, 24 were assigned the role of demonstrator. Prior to the start of the experiment, these animals had an average free-feeding weight of 334 g. The remaining 24 rats were observers and had an average free-feeding weight of 355 g.

Apparatus

The experiment was conducted in the same four operant chambers used in Experiment 1.

Procedure

Each session began with the illumination of the house light and finished once a variable number of responses had been made or food pellets had been delivered (variously defined below), at which point the house light was extinguished.

Demonstrator training

Of the 24 rats assigned the role of demonstrator, 16 received two sessions of magazine training each day for two consecutive days. After magazine training, half of these rats were trained to press the left lever for food, while the other half were trained to press the right lever. Training consisted of 24 sessions, each of which terminated following the delivery of 50 food pellets to the demonstrator, and was conducted over the course of 14 days. In Sessions 1-16, each correct lever-press was rewarded with food. Incorrect lever-presses had no programmed consequences. In addition, the extent to which the lever had to be displaced in order for a response to be registered was gradually increased, such that from Session 4 onwards the demonstrators were required to move the lever through a distance of approximately 1.5 cm. In the final eight sessions, discriminative lever-pressing was rewarded on a VI schedule to render responding resistant to extinction. In Sessions 17-20, a VI-15 sec schedule was used. This was increased to a VI-30 sec schedule in Sessions 21-24.

After training, half of the left and half of the right lever-pressing demonstrators were observed by the rats in Group SAME. The remaining demonstrators were observed by the rats in Group DIFFERENT.

Finally, the eight demonstrators that had not received training to eat from a food tray or to press a lever, were given two daily sessions of context training before being observed by the rats in Group NONE.

Observer training and testing

Initially, all of the observers received four daily session's of magazine training. Equal numbers of rats were then trained, in the same way as were their demonstrators, to press either the left (Group LEFT, n = 12) or the right (Group RIGHT, n = 12) lever. Training was conducted in five daily sessions, each of which rewarded discriminative lever-pressing on a schedule of continuous reinforcement. Only those rats that made 90% or more of total responses on the reinforced lever during each of the two final sessions of training were permitted to enter the next phase of the experiment.

The next phase of the experiment, which consisted of observation training and testing, was conducted on the day after the observers' fifth and final session of conventional instrumental pretraining. Each rat was placed in the observation compartment of an operant chamber, the demonstration compartment of which contained either a passive conspecific (Group NONE, n = 8) or a conspecific demonstrator that was pressing a lever but not being rewarded with food. In the latter group, half of the rats observed demonstrators making 50 nonreinforced responses on the lever which had previously been reinforced during observer training (Group SAME, n = 8), while the other half observed demonstrators responding on the opposite lever (Group DIFFERENT, n = 8). Within Groups SAME, DIFFERENT and NONE, whether the rats had been pretrained to press either the left or the right lever was counterbalanced.

Once the demonstrator had made its final response, or an equivalent amount of time had elapsed if the demonstrator was being observed by a rat in Group NONE, it was removed from the chamber. Demonstrators took approximately 3 min to make 50 correct nonreinforced responses. The observers were then transferred into the empty demonstration compartment and given a test session in which neither left nor right responses were rewarded. Test sessions terminated once the observer had reached a criterion of 5 min without responding or 60 min had elapsed.

Results

Demonstrators' behaviour

The demonstrators' behaviour is summarized in Table 10. As in previous experiments, the demonstrators responded predominantly on the correct lever while being observed by subjects. Owing to unequal variances, a nonparametric test was used to analyse these data, and this confirmed that the rats that demonstrators of left and right lever-pressing made an equivalent percentage of their total responses on the correct lever (Mann-Whitney U test: $U = 20.50$, $N_1 = 8$, $N_2 = 8$, $p = 0.71$, corrected for ties).

Group	LEFT	RIGHT
Median Percentage Correct Responses	87.00	87.50
Interquartile Range	71.00, 92.50	81.50, 93.50
n	8	8

Table 10. Median percentage correct responses [(number of correct responses/total number of responses) x 100%] and interquartile range for each group of demonstrators in Experiment 7.

Observers' behaviour

Of the 48 rats assigned the role of observer, one (belonging to Group LEFT-NONE) failed to make 90% or more of total responses on the reinforced lever during each of the final two sessions of instrumental pretraining. This animal was excluded from the experiment. The behaviour of the remaining animals is summarized below.

Instrumental pretraining

Figure 9 shows the median percentage reinforced responses made by rats that were rewarded for pressing either the left or the right lever during each of the five sessions of instrumental pretraining. Owing to unequal variances, nonparametric tests were used to analyse these data.

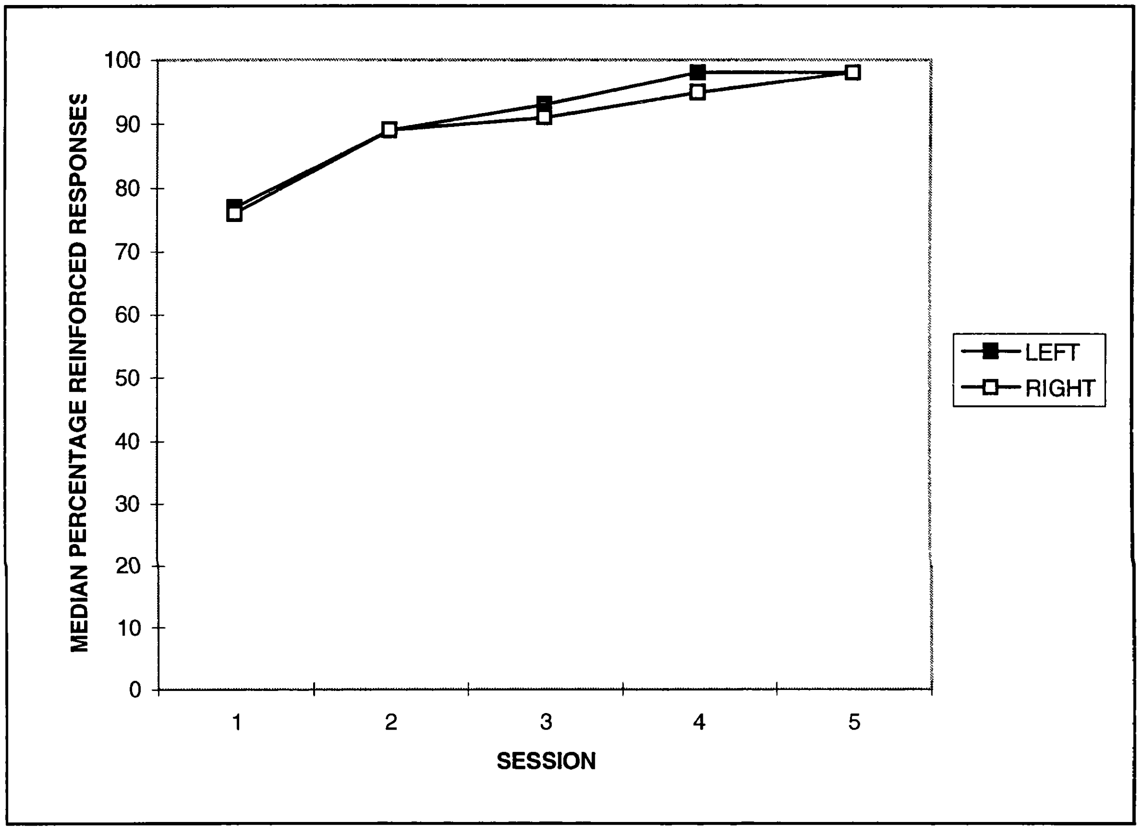

Figure 9. Median percentage reinforced responses [(number of reinforced responses/total number of responses) x 100%] for the observer rats that were rewarded for pressing either the left or the right lever during each of the five sessions of instrumental pretraining in Experiment 7. Interquartile range bars have been omitted for clarity.

It is apparent that across Sessions 1-5, rats that were rewarded for pressing the left lever made an equivalent percentage of their total responses on the reinforced lever (median = 92.00, interquartile range = 85.00 - 92.60, N = 11) as rats that were rewarded for pressing the right lever (median = 89.20, interquartile range = 88.00 - 92.60, N = 12). This impression was confirmed when a Mann-Whitney U test was performed on these data ($U = 54.50$, $N_1 = 11$, $N_2 = 12$, $p = 0.48$, corrected for ties).

However, the data presented in Figure 9 does suggest that left lever-pressing was acquired more rapidly than right lever-pressing. To test this, Friedman two-way ANOVA followed by multiple comparisons between treatments was performed. Friedman two-way ANOVA yielded a reliable effect of session for both Group LEFT (chi-square = 32.96, d.f. = 4, $p < 0.01$) and Group RIGHT (chi-square = 32.22, d.f. = 4, $p < 0.01$). While follow-up tests confirmed the impression that Group LEFT (Sessions 1 vs 4, Sessions 1 vs 5, and Sessions 2 vs 5: $p < 0.05$ in all cases) reached asymptote earlier in training than Group RIGHT (Sessions 1 vs 3, Sessions 1 vs 4, Sessions 1 vs 5, and Sessions 2 vs 5: $p < 0.05$). Since Groups LEFT and RIGHT were exposed to identical conditions during training, this effect was probably associated with the fact that the rats in this procedure show an unlearned bias towards left lever-pressing.

Observation testing

Resistance to extinction during observation testing was measured according to the number of previously reinforced responses that each observer made before reaching a criterion of 5 min without responding. Previously reinforced responses were responses that were made on the lever that had been rewarded for the observer during instrumental pretraining. To determine whether observation training exerted a more general influence on resistance to extinction, observer performance was also measured in terms of previously nonreinforced responses. Previously nonreinforced responses were responses that were made on the lever that had not been rewarded for the observer during instrumental pretraining.

The data relating to each measure were subjected to two-way ANCOVA in which instrumental pretraining (left, right) and observation training (same, different, none) were both factors. There were two covariates in each analysis, and these were: (i) the demonstrators' percentage correct responses while being observed by subjects, and (ii) the observers' percentage reinforced responses during the last two sessions of instrumental pretraining.

Previously reinforced responding

Figure 10 shows the mean number of previously reinforced responses made by each group of observers. Given that there were differences in acquisition of left and right lever-pressing, the data belonging to rats that were rewarded during pretraining for responses on either the left or the right lever are presented separately. This, it would appear, was necessary, since Figure 10 indicates that whether observation training influenced previously reinforced responding depends on the lever that was rewarded during instrumental pretraining. When the left lever was rewarded during instrumental pretraining, rats that observed nonreinforced responding on this lever made more previously reinforced responses than rats that observed nonreinforced responding on the opposite lever, which made more than rats that did not observe responding on either lever prior to testing. In contrast, when the right lever was rewarded, rats that observed nonreinforced responding on this lever made an equivalent number of previously reinforced responses as rats that observed nonreinforced responding on the opposite lever or did not observe responding on either lever prior to testing.

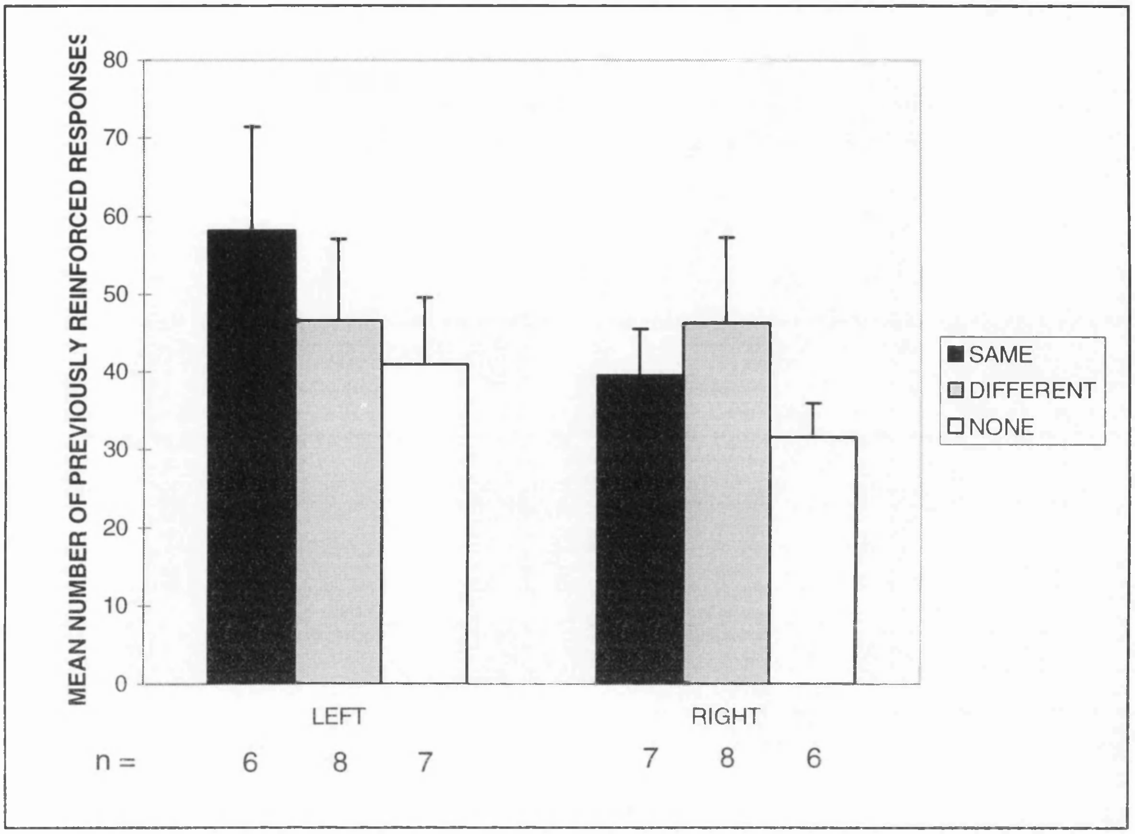

Figure 10. Mean number of previously reinforced responses made by the rats in Groups SAME, DIFFERENT, and NONE that were rewarded during instrumental pretraining for pressing either the left or the right lever. The black bars indicate the standard errors of the mean.

These impressions were tested when the data were subjected to two-way ANCOVA followed by simple effects. ANCOVA yielded a marginal main effect of instrumental pretraining (F (1, 15) = 4.43, p = 0.05). The main effect of observation training and the instrumental pretraining x observation training interaction were not reliable (F < 1 in both cases), nor were either of the covariates (demonstrators' percentage correct responses: (F (1, 15) = 1.67, p = 0.22); observers' percentage reinforced responses: (F (1, 15) = 2.53, p = 0.13). Simple effects performed on the data depicted in Figure 10 confirmed that there was a significant main effect of observation training when the left lever was rewarded during instrumental pretraining (F (2, 15) = 5.58, p = 0.02). When the right lever was rewarded the main effect of observation training was not reliable ($F < 1$). A Tukey test, used to identify the source of the observation training effect, indicated that Group LEFT-SAME made more previously reinforced responses than Group LEFT-NONE ($p < 0.05$). The difference between Groups LEFT-SAME and LEFT-DIFFERENT and between Groups LEFT-DIFFERENT and LEFT-NONE was, however, not reliable.

Finally, simple effects also showed that Group LEFT-SAME made more previously reinforced responses than Group RIGHT-SAME ($F(1, 15) = 8.42$, $p = 0.01$), whereas Groups LEFT-DIFFERENT and RIGHT-DIFFERENT ($F(1, 15) = 2.34$, $p = 0.15$), and Groups LEFT-NONE and RIGHT-NONE ($F < 1$), did not differ.

Previously nonreinforced responding

Figure 11 shows the mean number of previously nonreinforced responses made by each group of observers. As in the previous analysis, it would appear that observation training influenced responding when the left lever was rewarded during instrumental pretraining, but not when the right lever was rewarded. When the left lever was rewarded during instrumental pretraining, rats that observed nonreinforced responding on this lever made more previously nonreinforced responses than rats that observed nonreinforced responding on the opposite lever, which made more than rats that did not observe responding on either lever prior to testing. In contrast, when the right lever was rewarded, rats that observed nonreinforced responding on this lever made an equivalent number of previously nonreinforced responses on this lever than rats that observed nonreinforced responding on the opposite lever or did not observe responding on either lever prior to testing.

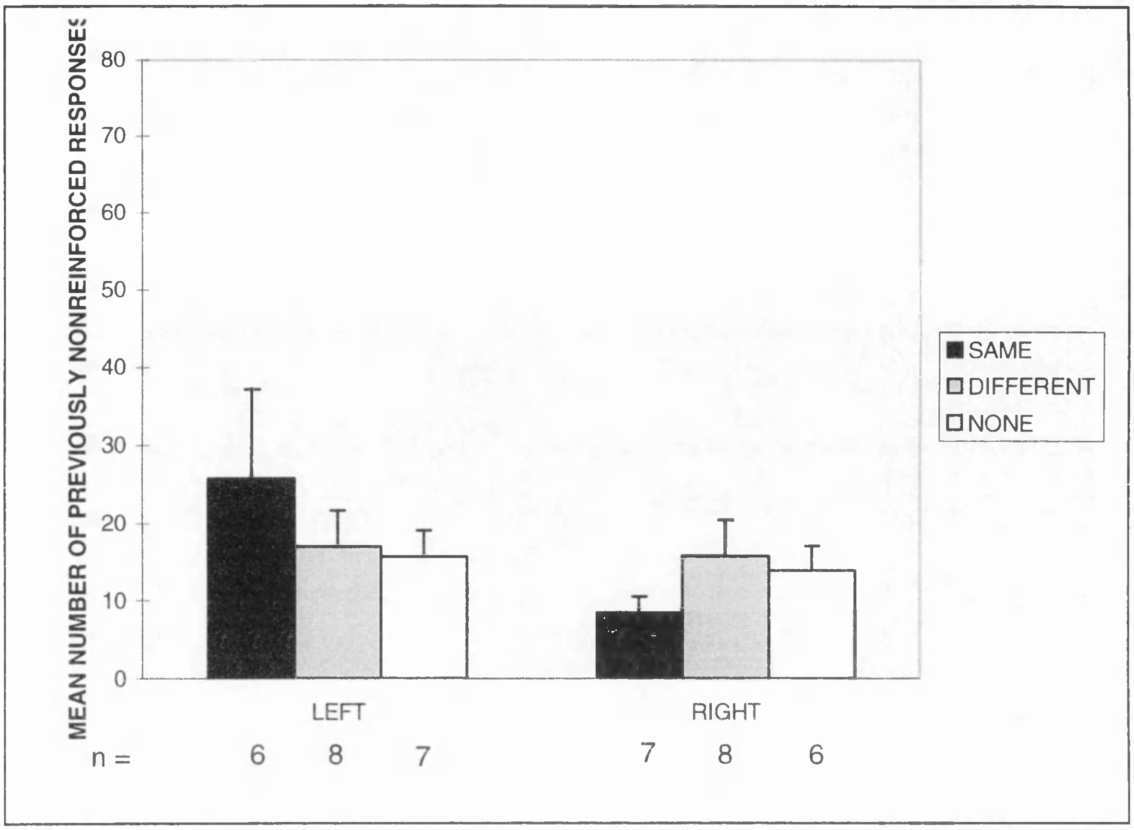

Figure 11. Mean number of previously reinforced responses made by the rats in Groups SAME, DIFFERENT, and NONE that were rewarded during instrumental pretraining for pressing either the left or the right lever. The black bars indicate the standard errors of the mean.

These impressions were tested when the data were subjected to two-way ANCOVA followed by simple effects. ANCOVA yielded a marginal main effect of instrumental pretraining (F (1, 15) = 4.42, p = 0.05). The main effect of observation training and the instrumental pretraining x observation training interaction were not reliable (F < 1 in both cases). In addition, although the demonstrators' percentage correct responses did not covary with the observers' previously nonreinforced responding (F < 1), the observers' percentage reinforced responses did (F (1, 15) = 5.75, p = 0.03). Simple effects confirmed that there was a significant main effect of observation training when the left (F (2, 15) = 3.78, p = 0.05), but not the right (F < 1), lever was rewarded during instrumental pretraining. A Tukey test, used to isolate the source of the observation training effect, indicated that Group LEFT-SAME made more previously nonreinforced responses than Group LEFT-NONE ($p < 0.05$). The difference between Groups LEFT-SAME and LEFT-DIFFERENT and between Groups LEFT-DIFFERENT and LEFT-NONE was, however, not reliable.

Finally, simple effects showed that Group LEFT-SAME made more previously nonreinforced responses than Group RIGHT-SAME ($F(1, 15) = 8.94, p = 0.01$), whereas Groups LEFT-DIFFERENT and RIGHT-DIFFERENT ($F(1, 15) = 1.16, p = 0.30$) and Groups LEFT-NONE and RIGHT-NONE ($F < 1$) did not differ.

Discussion

In a two-object procedure, resistance to extinction was a function of both observation experience and instrumental pretraining. Rats that observed responding without reinforcement on the lever that had been rewarded during observer pretraining (Group SAME), were more resistant to extinction (i.e. extinguished more slowly) than rats that were confined in the apparatus for the same period with a passive conspecific (Group NONE). However, this effect was confined to those rats that were rewarded, during pretraining, for responses on the left lever. When responses on the right lever were rewarded during pretraining, rats that observed nonreinforced responding on this lever extinguished at the same rate as rats that observed a passive conspecific.

The first effect is relatively straightforward and implies that rats are attracted to a lever as the result of observing it pressed, and that this experience interfered with subsequent acquisition of a lever-no food relationship. During an extinction test immediately following conspecific observation, rats in Group LEFT-SAME made more previously reinforced responses than rats in Group LEFT-NONE. This effect cannot be accounted for by attractive odour cues deposited by demonstrators on or around the lever that they pressed (Heyes *et al.*, 1999). Furthermore, had demonstrators deposited aversive odour cues on the lever that they pressed, one would of predicted the reverse effect. Thus these results, like those reported in Chapter 3, are more consistent with the hypothesis that rats in a two-object procedure engage in single stimulus, exposure learning rather than stimulus-reinforcer learning by observation.

Experiment 7 also found that the rats in Group LEFT-SAME made more previously nonreinforced responses than the rats in Group LEFT-NONE, suggesting that there was some generalization between responses that were either observed and/or made on the left and the right lever. However, if this is correct, and if, in addition, rats are attracted to levers as the result of observing them pressed, one would have expected Group LEFT-DIFFERENT to extinguish at a faster rate than Group LEFT-SAME, but at a slower rate than Group LEFT-NONE. Experiment 7 did in fact show a trend in this direction, but it was not reliable.

The second effect, that of instrumental pretraining, is also straight forward. Rats that were rewarded for pressing the left lever during instrumental pretraining showed an effect of conspecific observation, while rats that were rewarded for pressing the right lever did not. However, Group LEFT also required fewer trials to reach asymptote during observer pretraining, and therefore may have formed a stronger representation of the lever-food relationship by the end of pretraining. This would explain why Group LEFT-SAME extinguished more slowly on test than Group RIGHT-SAME, and, more speculatively, may have made Group LEFT more sensitive to the effects of observation experience.

Finally, Experiment 7 is also of interest because it has uncovered two previously unknown facts about the performance of rats in a two-object procedure. Although the rats in this procedure had extensive direct experience of lever-pressing, and were tested in extinction, they were still attracted to the lever on which a demonstrator responded. This suggests that observation experience has a powerful effect on the behaviour of rats, and illustrates the fact that social learning does not always lead to the transfer of locally adaptive information.

Chapter 5

Imitative and Nonimitative Social Learning In the European Starling Using a Two-Object/Two-Action Procedure

5. Introduction

The results of Experiments 1-3 suggested that the two-object/two-action procedure cannot be used effectively to study imitative and nonimitative social learning in the rat. Rats in this procedure may acquire information about the presence or location of stimuli through conspecific observation. However, there is no evidence that they acquire information about responses in a similar manner. This may be because rats are highly sensitive to the effects of odour cues. A fact which makes it extremely difficult to prove that any behavioural change following exposure to a conspecific demonstrator is the result of response learning by observation. Alternatively, rats may not possess the visual acuity necessary to discriminate complex patterns of behaviour and therefore to imitate a conspecific.

This suggests that if, instead, the two-object/two-action procedure was used with an animal for which visual cues provide the primary source of information, then better evidence of imitation might be obtained. For example, Galef *et al.* (1986) following an original experiment by Dawson & Foss (1965), allowed naive budgerigars to observe demonstrators removing a square piece of card from the top of a plastic bowl containing seed. The demonstrators used one of three different techniques to remove the card: they either edged it off with their beak, lifted it off with their beak, or used their foot to dislodge it. When subsequently presented with a covered bowl on test, observer birds showed a reliable tendency, but only when the first two test sessions were combined, to remove the card using the same technique as their demonstrator.

There are two reasons why this effect is unlikely to have been due to scent cues deposited by demonstrators on the card. First, birds are relatively insensitive to odour cues, and, second, food is digested inside the body cavity rather than inside the mouth. Stimulus enhancement is also an unlikely explanation, because the published report suggests that the demonstrators contacted the same region of the card. However, the demonstrators did not cause the card, when it was removed, to follow an identical trajectory, which raises the possibility that the observers learned the dynamic properties of the card or a card movement-food relationship.

However, recent experiments have reported apparently more reliable imitative effects in both pigeons (Zentall *et al.*, 1996) and Japanese quail (Akins & Zentall, 1996). In each of these experiments, naive birds observed conspecific demonstrators either pecking at or stepping on a treadle for food. When subsequently allowed access to the treadle on test, observer birds exhibited either an exclusive or a proportional response bias in favour of the demonstrator's topography. In Zentall *et al.*'s study, five of the ten pigeons that observed pecking pecked at the treadle and five stepped on it. Of the ten pigeons that observed stepping, nine stepped on the treadle and none pecked at it. In Akins & Zentall's study, quail that observed pecking made more pecking than stepping responses, while quail that observed stepping made more stepping than pecking responses, although the latter effect was not reliable.

The demonstrators in these experiments contacted the same part of the treadle when making a response, and the two alternative response topographies had an identical effect upon the environment (i.e. movement of the treadle followed by food). Therefore, the results are unlikely to be due to the observers learning either the static and/or dynamic properties of the treadle or a treadle movement-food relationship. However, while these experiments provide good evidence that observation of pecking facilitated acquisition of pecking in both pigeon and quail, evidence for a similar effect of stepping is not strong. Furthermore, since pecking forms part of a bird's innate behavioural repertoire, it is possible that it was acquired via nonimitative processes such as contagion acting in concert with stimulus enhancement. For example, the sight of a pecking demonstrator may have acted as a releaser for pecking in the observer. If, in addition, the observers were exposed to the treadle as a result of seeing it moved, then this would explain why they directed their pecking behaviour towards this object on test.

Unfortunately, two further studies that could have provided evidence against this interpretation yielded ambiguous results. First, Kaiser *et al.* (1997) allowed pigeons to observe a conspecific either sitting passively in the treadle compartment or eating from a food tray. They found that these birds were less likely to step on the treadle than the birds that observed rewarded stepping in Zentall *et al.*'s (1996) study. This contrast suggests that observation of a stepping demonstrator facilitated acquisition of the same response. However, it does not provide unambiguous evidence of response learning by observation, because it may be due instead to stimulus enhancement. More specifically, if birds were exposed to the treadle as a result of observing it moved, then birds that observed a passive conspecific would not have found the treadle attractive.

In the second study, Akins & Zentall (1988) allowed quail to observe demonstrators that were stepping on a treadle. The demonstrators' responses were either followed by food or had no significant consequences (i.e. the demonstrators were performing in extinction). They found that quail that observed rewarded stepping made more stepping responses than quail that observed nonrewarded stepping. However, this effect was not reliable. Thus, although these results are least consistent with the hypothesis that stepping can be acquired through conspecific observation, further studies are required to completely resolve this issue.

Finally, Lefebvre *et al.* (1997) gave Carib grackles the opportunity to observe either a conspecific or a Zenaida dove demonstrator using its beak to remove a plug from an opaque inverted test-tube containing seed. Grackle demonstrators used an open beak, probing and pulling technique, while dove demonstrators used a closed beak, pecking technique. When subsequently presented with a closed tube on test, grackles that observed conspecific demonstrators were more likely to displace the plug using an open beak technique, while grackles that observed heterospecific demonstrators used a closed beak technique. However, the two types of demonstrator used in this study contacted different regions of the apparatus. Grackle demonstrators probed and pulled at the tip of the stick that protruded from the base of the stopper, while dove demonstrators pecked at the base of the stick. This raises the possibility that stimulus enhancement, rather than response learning by observation, was responsible for the observers' bias. A possibility that Lefebvre *et al.* (1997) attempted to eliminate by showing that the location of demonstrators' responses had no effect upon the subsequent location of observers' responses.

In comparison with studies of imitation in rats, experiments with bird provide reasonably strong evidence of response learning by observation. The budgerigar and grackle studies did not completely exclude the possibility of nonimitative social learning. However, the avian data can still be regarded as strong for two reasons (Heyes & Ray, in press). First, there is no independent evidence that birds can discriminate the complex dynamic properties of objects under the conditions described above (e.g. Galef *et al.*, 1986; Lefebvre *et al.*, 1997). Second, the fact that pigeon and quail show demonstrator-consistent responding effects under conditions that control for nonimitative social learning (e.g. Zentall *et al.*, 1996; Akins & Zentall, 1996), raises the possibility that stimulus learning by observation was not entirely responsible for the effects reported in the budgerigar and grackle studies.

Consequently, the experiment reported in Chapter 5 used a two-object/two-action procedure in an attempt to distinguish imitative and nonimitative social learning in the European starling. This species was chosen because it adapts well to conditions in captivity. Furthermore, it has a poorly-developed sense of smell, and relies heavily on visual cues while foraging. For example, when probing for invertebrates in the surface soil or turf, the starling pushes its closed beak into the substrate which it then opens by means of an upward movement of the upper mandible (Feare, 1984). The starling's eyes then move forward in the eye sockets to provide a better view. If an item of prey is detected it is grasped between the mandibles and withdrawn when the starling's head is raised. Finally, the starling is a suitable species for a study of social learning because it is highly gregarious, typically foraging and roosting in groups of between two and 300 individuals.

5.1 Experiment 8

In Experiment 8, each of the subjects observed a conspecific demonstrator using its bill to remove one of two distinctively coloured objects, a red or a black plug, from a hole in the lid of a plastic box. Half of the subjects observed demonstrators that had been trained to remove the plug by pulling up on a loop of string inserted through the centre, while the other half observed demonstrators pushing down on the plug. It was anticipated that birds would provide evidence of stimulus learning by observation by removing the same plug as their demonstrator, and of response learning by observation by removing the plug in the same direction as their demonstrator.

Method

Subjects

The subjects were 48 juvenile starlings decoy-trapped on a pig farm in Somerton, Somerset (UK). Of these animals, 16 were randomly assigned the role of demonstrator and 34 were observers. The experiment was conducted in two replications, and four of the observers in Replication 1 were subsequently trained as demonstrators for Replication 2.

Throughout the experiment, demonstrator and observer birds were housed separately in groups of eight in 2 cm-gauge wire-mesh cages (41 x 60 x 66 cm), with free access to water. One hour prior to the start and during the course of experimental sessions, all animals were food deprived. At all other times, food (high-protein chick crumbs) was freely available. The birds were maintained on a 16:8 hours light:dark cycle (light onset 0600 hours).

Apparatus

All animals were trained and tested in two identical cages, similar in all respects to the cages in which the birds were housed. Each cage was divided into two chambers of equal size (60 x 41 x 66 cm) by a wooden partition, and each chamber (see Figure 12) was further subdivided by a 2 cm gauge wire-mesh partition to form two compartments (30 x 66 x 41 cm). The left compartment was used for demonstration and testing, and the right housed the observer. Both could be accessed by way of separate doors located at the front of the cage. A single perch, extending from the front to the back of the cage (6 cm from the ceiling, 3 cm from the right wall) was provided in each compartment.

In the demonstration compartment, a clear plastic box (14.5 x 9.5 x 5.5 cm) was placed on the floor next to the wall directly opposite the wire-mesh partition (see Figures 12 and 13). The position of the box was such that its long axes ran parallel to the adjacent side wall. A piece of white card (19 x 14 cm) was secured to the lid of the box, which was placed inside an open-top, white cardboard container (19 x 14 x 6 cm). This container was also used to cover the plastic box when it was not required.

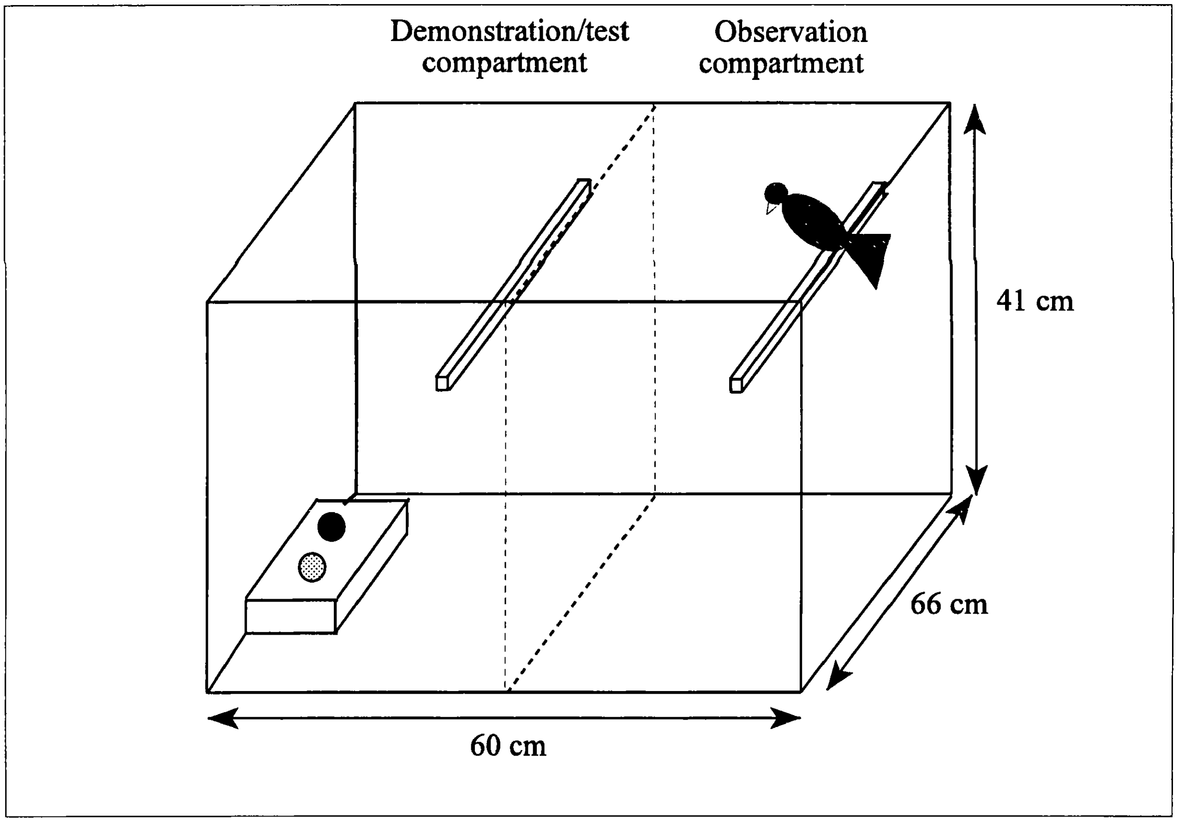

Figure 12. Plan of the apparatus used in Experiment 8 showing the position of the food-finding task. The filled circle indicates the black plug, and the stippled circle the red plug. The dashed line shows the wire-mesh partition that separated the demonstration/test compartment from the observation compartment.

The plastic box was divided by a sheet metal partition into two halves measuring 7.25 x 9.5 x 5.5 cm, such that either or both halves could be filled with live mealworms. The mealworms could be accessed via two separate holes (diameter 3.5 cm) in the lid of the food box, one directly above the centre of each half. These holes served as receptacles for the plugs, which were made using inverted bottle caps, 1.3 cm deep. The inside of each bottle cap was lined with a section of ping-pong ball to create a concave surface, and the entire bottle cap and lining was coloured with either a red or a black odourless marker pen. A loop of string, 2 cm long, was inserted through a small hole in the centre of the bottle cap and secured with a knot. When in place, the red plug was always in the hole nearest the front of the cage, and the black plug in the hole nearest the back of the cage. Both plugs could be removed from their receptacle by either pulling up on the loop of string inserted through the centre of the plug, or by pushing down on the plug.

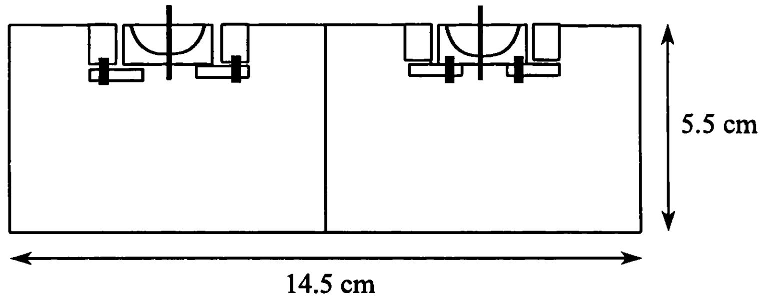

Figure 13. Plan of the food-finding task used in Experiment 8 showing the position of the plugs and the brackets that were used to restrict movement of the plugs. The plug blocking entrance to the left feeding compartment was used to train up-pulling demonstrators, while the plug blocking entrance to the right feeding compartment was used to train down-pushing demonstrators.

The plugs were held in place by a 1 cm deep metal ring, that surrounded the circumference of the hole on the lower surface of the lid. The inside of this ring was lined with a thin layer of sponge. For the purposes of demonstrator training, three brackets positioned equidistant from one another were secured to the free end of the metal ring and could be moved directly underneath the hole such that the plug could not be pushed downwards. Three metal brackets were also secured to the base of the plug, so that when the plug was in place and the brackets were positioned pointing away, it could not be pulled upwards.

The equipment was controlled and the data collected manually by the experimenter, who was positioned, at all times, approximately 30 cm from the front of the cage and visible to the subjects. Demonstrator and observer birds rapidly habituated to the presence of the experimenter over the course of training. Their behaviour in the presence of the experimenter was not detectably different from their behaviour when observed from behind a door through a peephole. All experimental sessions were recorded using a JVC camcorder (Model number GR-AX60E), supported on a tripod immediately in front of the experimenter.

Procedure

Each session began when the cardboard container covering the food box was removed, and finished once a bird had made 10 rewarded responses or after a predetermined interval had elapsed (variously defined below), at which point the food box was covered.

Demonstrator training

Initially, each of the demonstrators were given three daily sessions of training to feed from the plastic box. Session 1 was conducted in the demonstrator's home cage in the presence of its cage mates, while Sessions 2 and 3 were conducted with each bird, on its own, in the demonstration compartment of the experimental chamber. During Session 1, demonstrators were allowed to feed from the plastic box, from which the lid had been removed, for 240 min. The lid was replaced during Sessions 2 and 3, and each bird was allowed to feed through the holes for a period of 30 min. During each of the last two sessions of training, both halves of the food box were filled with mealworms and the birds were not exposed to the plugs.

After learning to eat from the box, eight of the birds were trained by the method of successive approximation to remove the red plug from the food box. Half of these animals were trained to remove the plug by pulling up on the loop of string inserted through the centre, and half by pushing down on the plug. The remaining eight animals were trained to remove the black plug, half by pulling up and half by pushing down. Thus, there were four groups of demonstrators: RED UP, RED DOWN, BLACK UP, and BLACK DOWN. Instrumental training sessions were conducted at a rate of one per day and each session lasted until a bird had made 10 rewarded responses or 20 min had elapsed.

During the initial phases of this instrumental training, only the red or the black plug was available, and, only the compartment below this plug was filled with mealworms. The amount of displacement necessary to remove the plug from its receptacle was gradually increased until each demonstrator was removing a plug that was flush with the lid of the box. If the plug was removed using the correct response topography, demonstrators were allowed to take between one to three mealworms from the box. The plug was then retrieved and replaced by the experimenter. Once demonstrators were reliably removing the plug in the correct direction, either the black or the red plug was placed in the empty hole. Initially, demonstrators were prevented from removing this plug by means of brackets. However, as training progressed the use of brackets became unnecessary and both compartments were filled with mealworms.

Training continued until each bird made 10 correct, reinforced responses in 5 min or less during each of two consecutive training sessions. The majority of demonstrators reached criterion after eight sessions in the case of birds trained to pull the plug up, and after five sessions in the case of birds trained to push the plug down. Thus, in this procedure the demonstrators learned faster to push the plug down than to pull it up. Those demonstrators that did not reach criterion by this point (one belonging to Group RED UP, one belonging to Group RED DOWN, and two belonging to Group BLACK UP), were excluded from the experiment. An additional demonstrator (belonging to Group RED UP) died during the course of training.

At the start of the experiment, it was intended for each demonstrator to be observed by two different birds in Replications 1 and 2. However, following the exclusion of five demonstrators from the experiment, some of the remaining birds demonstrated plug removal to more than four different observers. There was no evidence to suggest that the demonstrators' performance changed across demonstration sessions or across replications.

The four birds that served as observers in Replication 1 and then as demonstrators in Replication 2 received five sessions of training before demonstrating plug removal for the first time. During training, these birds were rewarded for removing the same plug in the same direction as the demonstrator they had observed in Replication 1.

Observer training and testing

All of the observers received five daily sessions of pretraining. The birds were trained to feed from the plastic box in the same way as were their demonstrators on days 1, 3, and 5. Habituation training was conducted on days 2 and 4 and consisted of placing each bird in the observation compartment of an experimental chamber for 30 min. During this period, the bird's demonstrator was present in the adjacent test compartment, although the food box was not.

Following pretraining, equal numbers of birds were allowed to observe a conspecific demonstrator using its beak to remove either a red or a black plug from a hole in the lid of a food box by pulling up on the loop of string inserted through the centre (Groups RED UP and BLACK UP) or by pushing down (Groups RED DOWN and BLACK DOWN). Each bird observed one demonstration session per day for seven consecutive days. Before the demonstration session began, the bird was removed from its home cage and introduced into the observation compartment of a chamber. A 2 min habituation period followed, after which a demonstrator was introduced into the adjacent compartment. Each observer was paired with the same demonstrator throughout the experiment. Demonstrator and observer birds were permitted a further 2 min habituation period, before the food box was uncovered and the demonstration session commenced. Each session lasted until a demonstrator had made 10 correct, rewarded responses or 10 min had elapsed. Once the session had finished the food box was covered and both animals were removed from their respective compartments.

Each observer was tested a total of three times. Test sessions were conducted immediately after the fifth, sixth, and seventh demonstration sessions. The demonstrator was removed from the chamber and the observer allowed to enter the empty test compartment by sliding back the wire-mesh partition. Once the observer was in place, the food box was uncovered and the test session commenced. Test session duration was 10 min. During this period, observers were allowed to take between one to three mealworms from the plastic box following each plug removal regardless of the plug, and the direction, in which it was removed. Not every removal attempted by an observer was successful. In those cases in which the plug was only partially removed, the bird was given 60 sec in which to complete the response. If the bird failed to respond it was not rewarded, and the plug was returned to its correct position.

Videotapes of the observers' test sessions were scored by two independent raters blind to the viewed animal's group assignment. The raters agreed about both the object and direction of the observers' responses on 100% of a randomly selected 30% of test sessions.

Results

Demonstrators' behaviour

Demonstrators employed distinct response topographies when pulling the plug up out of the food box and when pushing it down into the food box. Standing on the lid of the box or on the floor of the cage, the demonstrator moved its head towards the plug and opened its beak. If the demonstrator had been trained to pull the plug up, its mandibles were closed over the loop of string and its head thrust backwards carrying the plug away from the box. Once the plug had been removed it was dropped to the floor of the cage. If the demonstrator had been trained to push the plug down, its open mandibles were thrust against the concave lining of the plug causing it to drop down into the box. Up and down responses showed minimal variation and were always made with open and closed beaks respectively.

Demonstrators showed perfect discrimination while being observed by subjects. However, Figure 14 indicates that there were differences between groups in rate of reinforced responding.

Across Sessions 1-7, demonstrators that pushed the plug down made more reinforced responses than demonstrators that pulled the plug up. This effect occurred both when demonstrators removed the red plug and when they removed the black plug. In addition, while the number of responses made by down-pushing demonstrators did not change over the course of the experiment, the number of responses made by up-pulling demonstrators gradually increased.

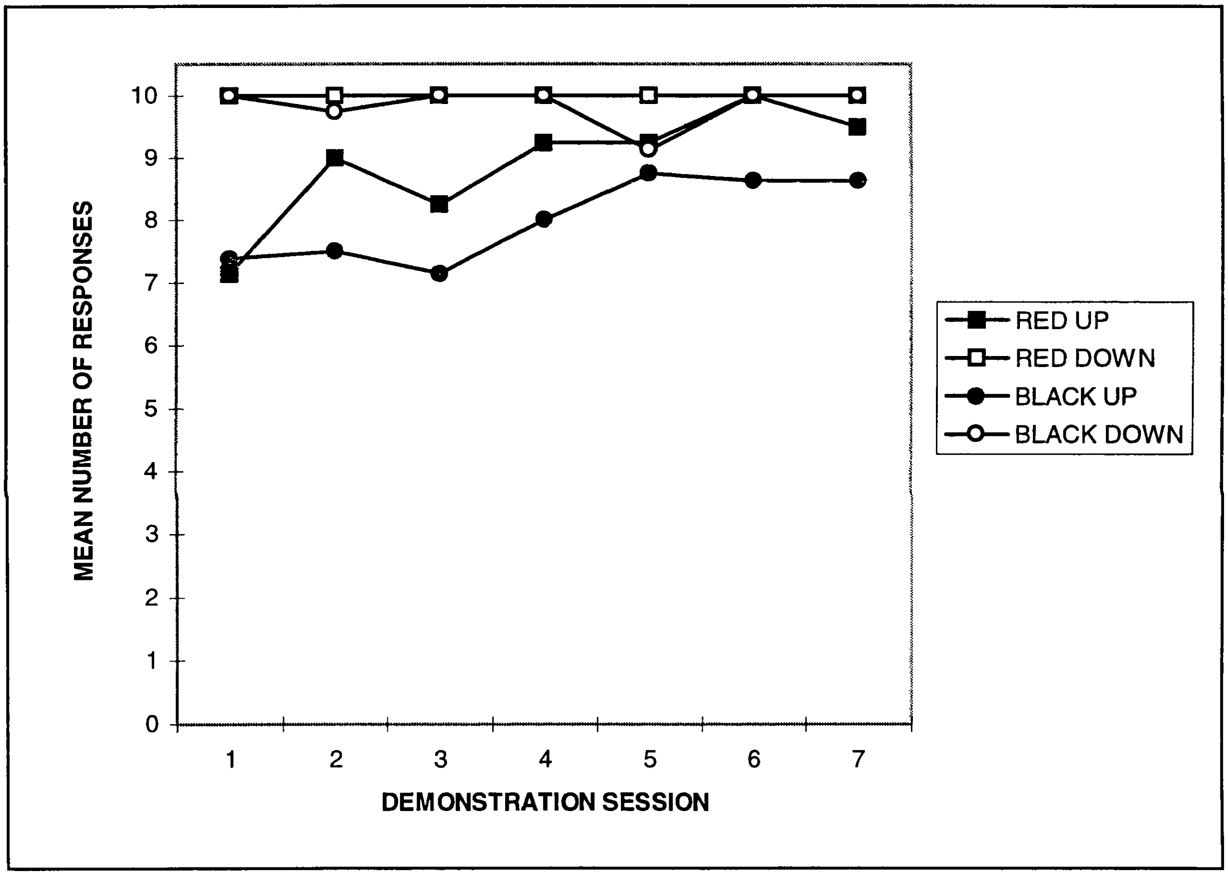

Figure 14. Mean number of responses made by the demonstrators during each of the seven demonstration sessions in Experiment 8. Standard error of the mean bars have been omitted for clarity.

These impressions were supported when the data were subjected to mixed-model ANOVA in which location (red, black) and direction (up, down) were the between-subject factors, and demonstration session (1-7) was the within-subject factor. This revealed a significant main effect of direction ($F (1, 28) = 11.49$, $p = 0.002$) and a significant interaction involving direction and session ($F (6, 168) = 2.92$, $p = 0.01$). None of the other main effects or interactions were reliable ($F < 1$ in all cases).

To examine more closely the direction x session interaction, simple effects analysis was performed. When comparing up-pulling and down-pushing demonstrators in each session, an error term comprising the weighted average of the between- and the within-subject error mean squares from the original ANOVA was used. When comparing Sessions 1-7 at each level of demonstrator direction, the error term was simply the within-subject mean squares. To control for family-wise error rate, the chosen level of significance was $\propto = 0.007$ (i.e. 0.05 / 7).

In the first analysis, differences were found between up-pulling and down-pushing demonstrators during Session 1 ($F (1, 101) = 19.52$, $p = 0.00003$), but not during Sessions 2 ($F (1, 101) = 6.82$, $p = 0.01$), 3 ($F (1, 101) = 13.80$, $p = 0.01$), 4 ($F (1, 101) = 4.88$, $p = 0.03$), 5 ($F < 1$), 6 ($F (1, 101) = 1.22$, $p = 0.27$), and 7 ($F (1, 101) = 2.27$, $p = 0.14$). In the second analysis, there was a significant main effect of session among demonstrators that pulled the plug up ($F (1, 168) = 4.98$, $p = 0.0001$). Tukey's HSD test used to isolate the source of this effect, indicated reliable differences between the following sessions: 1 and 5 ($p < 0.001$), 1 and 6 ($p < 0.001$), 1 and 7 ($p < 0.001$). Finally, the main effect of session among demonstrators that pushed the plug down was not reliable ($F < 1$).

Observers' behaviour

The observers used the same response topography as their demonstrators to pull the plug up or to push it down. Of the 32 observers tested, 13 (four RED UP, one RED DOWN, five BLACK

UP, and four BLACK DOWN observers) failed to respond, i.e. to remove a plug during any of the three test sessions, and were excluded from the experiment. A chi-square test used to analyse these data, indicated that whether a bird responded on test was independent of the demonstrator it observed. Of the 19 birds that did respond, 11 (three RED UP, five RED DOWN, two BLACK UP, and one BLACK DOWN observer) responded on all three test sessions; five (two RED UP and three BLACK DOWN observers) responded on two test sessions; and three (two RED DOWN and one BLACK UP observer) responded on one test session. Thus the sample sizes were: RED UP = 5, RED DOWN = 7, BLACK UP = 3, and BLACK DOWN = 4.

The number of responses made by these birds during each of the three test sessions is shown in Figure 15. It is apparent that while there was an increase in the number of responses made between Sessions 1 and 2, there was no change in the number of responses made between Sessions 2 and 3. This impression was tested when the data were subjected to mixed-model ANOVA in which location and direction were the between-subject factors, and test session (1-3) was the within-subject factor. This analysis revealed a significant main effect of session (F (2, 30) = 77.26, p = 0.002). None of the other main effects or interactions were reliable ($F < 1$ in all cases). Tukey's HSD test used to isolate the source of the session effect, indicated reliable differences between Sessions 1 and 2 ($p < 0.01$) and between Sessions 1 and 3 ($p < 0.01$).

Sensitivity to the location of demonstrators' responses was assessed for each bird by means of a spatial discrimination ratio. Spatial discrimination ratios were calculated by dividing the number of left responses (i.e. the number of times the red plug was removed) by the total number of responses. A directional discrimination ratio assessed sensitivity to the direction of demonstrators' responses, and was calculated for each bird by dividing the number of up responses (i.e. the number of times a plug was removed by pulling up) by the total number of responses. Owing to low within-group variability, the data relating to each measure were subjected to nonparametric tests .

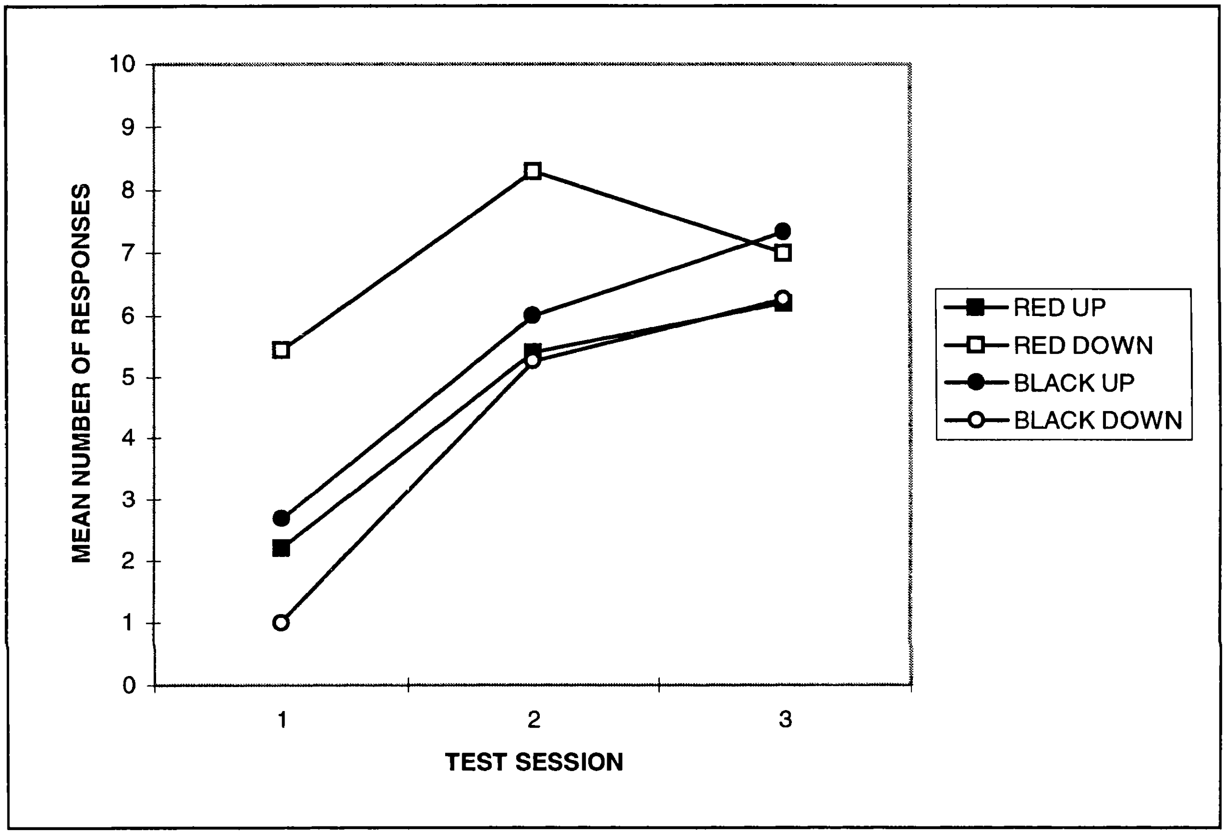

Figure 15. Mean number of responses made by the observers during each of the three test sessions in Experiment 8. Standard error of the mean bars have been omitted for clarity.

Figure 16 shows the spatial discrimination ratio for the responses made by birds that observed demonstrators removing either the red or the black plug. As anticipated, exposure to the location of demonstrators' responses resulted in a reliable tendency for demonstrator-consistent responding. Birds that observed demonstrators removing the red plug were themselves more likely to remove the red plug than birds that observed demonstrators removing the black plug during each of the three test sessions. However, while this effect was significant during Sessions 1 (Mann-Whitney U test: $U = 4$, $N_1 = 8$, $N_2 = 4$, $p = 0.03$) and 3 (Mann-Whitney U test: $U = 10$, $N_1 = 12$, $N_2 = 6$, $p = 0.01$), it was only marginal during Session 2 (Mann-Whitney U test: $U = 13$, $N_1 = 10$, $N_2 = 6$, $p = 0.06$).

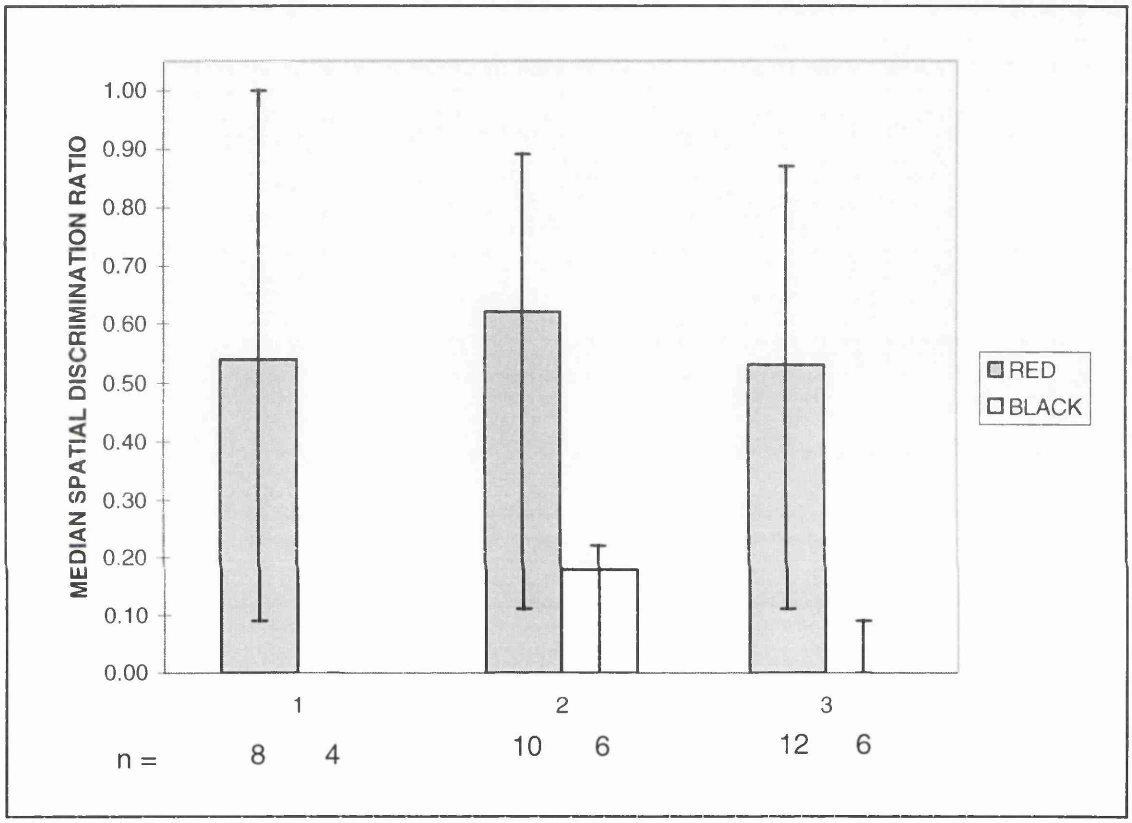

Figure 16. Median spatial discrimination ratio (left responses/total responses) for the birds in Groups RED and BLACK during each of the three test sessions in Experiment 8. The black bars show the interquartile ranges.

To verify that the tendency for demonstrator-consistent responding persisted across test sessions, the data from the 16 birds that responded during at least two test sessions were analysed. A Wilcoxon signed-ranks test comparing the spatial discrimination ratio for the first (median = 0.17, interquartile range = 0.00 - 0.86) and the last (median = 0.13, interquartile range = 0.00 -

0.53) test session on which these birds responded, confirmed the impression that there was no difference (Wilcoxon signed-ranks test: T, $N = 16$, $p = 0.55$).

Therefore, the spatial discrimination ratios relating to the 16 birds that responded during at least two test sessions were pooled and analysed. This revealed that birds that observed demonstrators removing the red plug were themselves more likely to remove the red plug (median = 0.48, interquartile range = 0.22 - 0.77) than birds that observed demonstrators removing the black plug (median = 0.09, interquartile range = 0.00 - 0.13; Mann-Whitney U test: $U = 4.0$, $N_1 = 10$, $N_2 = 6$, $p = 0.005$). However, the spatial discrimination ratios of birds that observed demonstrators pulling the plug up (median = 0.46, interquartile range = 0.10 - 0.77) or pushing it down (median = 0.16, interquartile range = 0.09 - 0.26), did not differ (Mann-Whitney U test: $U = 23.5$, $N_1 = 7$, $N_2 = 9$, $p = 0.40$).

Figure 17 shows the directional discrimination ratio for responses made by birds that observed demonstrators removing a plug by pulling it up or pushing it down. It is apparent that exposure to the direction of demonstrators' responses resulted in considerable demonstrator-consistent responding effects. During Sessions 1 (Mann-Whitney U test: $U = 3.5$, $N_1 = 5$, $N_2 = 7$, $p = 0.006$) and 2 (Mann-Whitney U test: $U = 4.5$, $N_1 = 7$, $N_2 = 9$, $p = 0.007$), birds responded exclusively in the same direction as their demonstrator. During Session 3 (Mann-Whitney U test: $U = 10$, $N_1 = 8$, $N_2 = 10$, $p = 0.001$), birds made proportionately more responses in their demonstrator's direction than in the opposite direction.

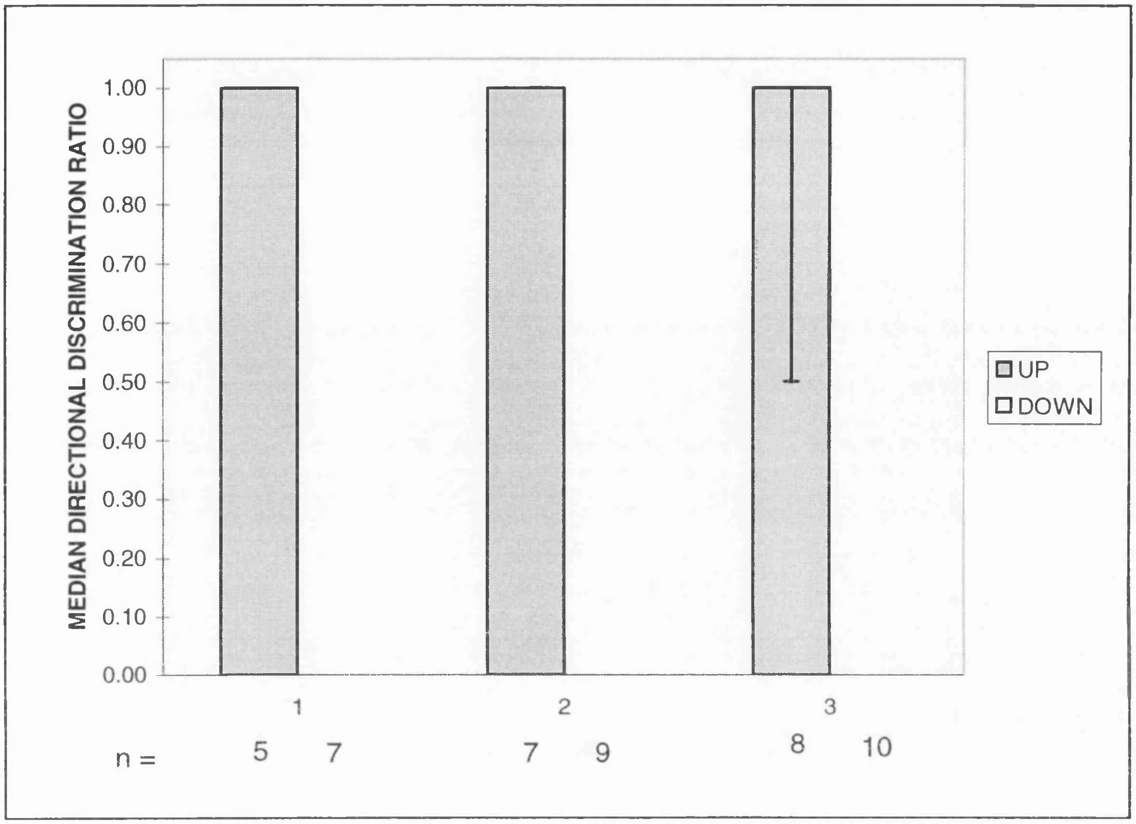

Figure 17. Median directional discrimination ratio (up responses/total responses) for the birds in Groups UP and DOWN during each of the three test sessions in Experiment 8. The black bars show the interquartile ranges.

A Wilcoxon signed-ranks test was used to analyse the directional discrimination ratio for the first (median = 0.00, interquartile range = 0.00 - 1.00) and the last (median = 0.00, interquartile range = 0.00 - 1.00) test session in which responses were made by the 16 birds that responded during at least two sessions. This confirmed that the tendency for demonstrator-consistent responding did not change over testing (Wilcoxon signed-ranks test: T, N = 16, p = 1.00). Furthermore, when all responses were analysed, birds that observed demonstrators pulling a plug up made proportionately more up responses (median = 1.00, interquartile range = 1.00 - 1.00) than birds that observed demonstrators pushing a plug down (median = 0.00, interquartile range = 0.00 - 0.00; Mann-Whitney U test: U = 4.5, $N_1 = 7$, $N_2 = 9$, p = 0.0007). However, birds that observed demonstrators removing either a red (median = 0.50, interquartile range = 0.00 - 1.00) or a black plug (median = 0.00, interquartile range = 0.00 - 0.00), made an equivalent proportion of up responses (Mann-Whitney U test: $U = 20$, $N_1 = 10$, $N_2 = 6$, $p = 0.20$)..

Although up-lifting and down-pushing demonstrators exhibited different rates of reinforced responding, it is unlikely that this influenced the behaviour of their observers. Birds that observed demonstrators lifting a plug up or pushing it down: (i) made an equivalent number of responses during each of the three test sessions, (ii) distributed their responses equally between the red and the black plug, and (iii) responded, almost exclusively, in their demonstrator's direction.

Discussion

Experiment 8 provided evidence that starlings are influenced by both the object and the direction of demonstrators' responses. Birds that observed demonstrators removing one of two distinctively coloured plugs from a hole in the lid of a plastic box by pulling up or pushing down, showed a reliable tendency to remove the same plug in the same direction as their demonstrator.

The fact that exposure to the object of demonstrators' responses promoted reliable demonstrator-consistent responding provides good evidence of stimulus learning by observation. This effect could not have been due to social facilitation because, regardless of whether birds observed demonstrators removing either the red or the black plug, each observer was exposed equally to the mere presence, general activity, and consummatory behaviour of a conspecific. Local enhancement is also an unlikely explanation because the demonstrators were not present at the time of testing, although they may have deposited odour cues on the manipulated plug so as to render it more attractive than the plug that was not manipulated. However, this possibility is unlikely since birds are relatively insensitive to odour cues and digest food internally rather than inside the mouth cavity.

Stimulus learning by observation akin to that found here has been reported elsewhere. In a study by Coleman & Mellgren (1997), zebra finches fed preferentially at the same location as a conspecific. A similar effect was detected by McQuoid & Galef (1992) in Burmese red jungle fowl, and in this experiment was shown to persist for many hours following observation of a conspecific's feeding behaviour. Finally, Turner (1964) found that newly hatched chicks were more likely to peck at grain that was the same colour as the grain at which a mechanical model hen was pecking.

These effects may be examples of either single stimulus, exposure learning (e.g. stimulus enhancement, emulation learning) or stimulus-stimulus associative learning by observation (e.g. observational conditioning). To distinguish these possibilities it would be necessary to elucidate the role played by observation of the consequences of demonstrators' responses in demonstrator-consistent responding. In an attempt to achieve this aim, Palameta & Lefebvre (1985) allowed pigeons to observe demonstrators that were either piercing a hole in the paper lid covering a food bowl and eating from within, or piercing a hole in the paper lid covering a food bowl but not eating from within. When subsequently provided with an intact bowl on test, observers of piercing-and-eating demonstrators solved the food-finding problem faster and with fewer pecks than observers of piercing-but-not-eating demonstrators. These results indicate that observation of demonstrators feeding was necessary for acquisition of a novel foraging technique in pigeons. However, they do not show whether demonstrator reinforcement influenced the pigeons' behaviour via either an associative (observational conditioning) or a nonassociative (stimulus enhancement, emulation learning) process.

It is apparent that the birds in Experiment 8 learned something about the plug to which demonstrators responded. However, what is not clear is whether they encoded the location and/or the colour of the plug. To determine whether location was sufficient for learning, it would be necessary to repeat Experiment 8 using two plugs of the same colour. Alternatively, the relative contribution of colour and location could be assessed by testing half of the birds with the plugs in the same position as they had been during observation (Group SAME), and testing the other half with the plugs in the opposite position (Group DIFFERENT). If observers learned the location and the colour of the demonstrator's plug, then both groups would be expected to remove the same coloured plug as their demonstrator, although this tendency would be stronger in Group SAME than in Group DIFFERENT.

The birds in this experiment not only displaced their demonstrator's plug, they also moved it in the same direction. Social facilitation and/or local enhancement cannot account for this effect. However, it does not provide unequivocal evidence of imitation, because it may be due instead to stimulus learning by observation. In Experiment 8, demonstrators that pulled up grasped the loop of string that protruded from the centre of the plug between their bills, while demonstrators that pushed down pressed their open bills against the plug's concave lining. If, as a result, up-pulling and down-pushing observers found different regions of the plug attractive (stimulus enhancement), then this may have been sufficient to result in reliable demonstrator-consistent responding effects. Furthermore, demonstrators that pulled the plug up caused it to move out of the food box, while demonstrators that pushed the plug down caused it to move into the food box. This raises the possibility that the observers learned the dynamic properties of the plug (emulation learning) or a plug movement-food relationship (observational conditioning).

Similar problems in studies of imitation in birds have been encountered elsewhere. Lefebvre *et al.* (1997), for example, allowed grackles to observe demonstrators using either an open beak, probing and pulling technique or a closed beak, pecking technique to remove the stopper from an opaque, inverted test-tube containing seed. When subsequently presented with a closed tube on test, observer birds displaced the stopper using the same technique as their demonstrator. However, since open and closed beak demonstrators contacted different parts of the apparatus, this effect does not provide unequivocal evidence of response learning by observation. It may be due instead to stimulus enhancement.

In another study, budgerigars observed demonstrators using either their beak or their feet to remove a square piece of card from the lid of a plastic bowl containing seed (Galef *et al.*, 1986). When presented with a covered bowl, these birds showed a reliable tendency to remove the card using the same appendage as their demonstrator. Since beak and feet demonstrators contacted the same region of the card, this effect could not have been due to stimulus enhancement. However, since the card followed different trajectories depending on whether it was edged off, lifted off, or displaced, emulation learning and/or observational conditioning may have been responsible for the observers' bias.

Despite these problems, experiments with starlings, grackles, and budgerigars still provided the most compelling evidence of imitation in animals to date (Heyes & Ray, in press). First, there is no evidence to support the hypothesis that under the conditions of a two-action procedure, birds may learn the complex dynamic properties of objects. Second, experiments with pigeons (Zentall *et al.*, 1996) and quail (Akins & Zentall, 1996) show that demonstrator-consistent responding effects occur even when there is no obvious opportunity for birds to learn the complex dynamic properties of objects.

Finally, avian paradigms are also likely to support analytic studies of imitation in animals because they yield effects that are relatively easy to replicate. For example, in the context of the present experiment, the effect of the direction of demonstrators' responses has been replicated more than once (Fawcett, Skinner, & Goldsmith, unpublished data).

Chapter 6

The Two-Object/Two-Action Procedure: Theoretical and Methodological Significance

6. Introduction

A two-object/two-action procedure was used with the aim of distinguishing the effects of imitative and nonimitative social learning on acquisition of an appetitively reinforced response in both the rat and the starling. The results of these experiments are important in two respects. First, they are consistent with the hypothesis that in most natural and experimental environments, providing naive animals with the opportunity to interact with conspecific demonstrators will result in a number of different social influences acting on the animal's behaviour. Second, it is easy to see how in some circumstances, these social influences could be manipulated in order to analyse both the psychological mechanisms of, and distinctive conditions favouring, imitative and nonimitative social learning.

Imitative social learning consists of response learning by observation (Heyes, 1993; Heyes & Ray, in press). It is the means by which animals, that are observing the behaviour of others, learn responses, actions, or patterns of behaviour; how to execute them and what are their consequences (observational learning or imitation). Nonimitative social learning, on the other hand, consists of stimulus learning by observation. It allows animals to acquire information about stimuli, objects, or events in the environment; their presence or location (stimulus enhancement), dynamic properties (emulation learning), and/or value (observational conditioning).

In Chapter 1, it was suggested that the two-object/two-action procedure inspired by Bolles *et al.* (1985) and used by Ray (1997), has the potential to distinguish these two forms of learning.

In the two-object/two-action procedure, naive animals are allowed to observe conspecific demonstrators manipulating one of two different objects in one of two different ways. During a subsequent test session in which the observers are given access to the objects for the first time, a record is made of their responses. If animals engage in nonimitative social learning, then one would expect the observers to show a response bias in favour of the demonstrator's object. If, instead or in addition, animals engage in imitative social learning, then one would expect the observers to show a bias in favour of the demonstrator's action.

The power of the two-object/two-action procedure lies in its ability not only to distinguish imitative from nonimitative social learning, but also from those processes that, although they do not constitute learning, may result in the behaviour of one animal resembling that of another. These processes, which have been given the generic name social enhancement by Galef (1988), can be assigned to one of three different categories. Contagious behaviour (Thorpe, 1963), for example, refers to those instances in which an observed behaviour acts as a releaser for the same behaviour in others, and is usually avoided in studies of social learning by training novel or sufficiently improbable responses (Thorpe, 1963; Zentall, 1988). Social facilitation (Zajonc, 1965, 1969; Clayton, 1978), on the other hand, is more difficult to circumvent.

Social facilitation occurs when the mere presence and/or behaviour of a conspecific increases the rate at which another animal performs those responses most appropriate to the current stimulus situation. The underlying mechanism may take one of several different forms. A conspecific may increase the rate at which another animal performs a target response either by acting as a motivational cue or by reducing the animal's level of isolation-induced fear or vigilance. It is likely that social facilitation plays some role in the two-object/two-action procedure.

However, it cannot offer a complete explanation of the predicted effects because, regardless of the object and form of demonstrators' responses, each observer is exposed equally to the mere presence, general activity, and consummatory behaviour of a conspecific.

The final category of social enhancement occurs when an animal is attracted to a site or an object by the current presence of a conspecific at that site (Thorpe, 1963). Local enhancement, as it is defined here, cannot generate effects of the type predicted, because the demonstrators are removed from the apparatus before the observers are tested. However, if the demonstrators bring about some change in the objects that they contact (e.g. odour cues, food particles; Galef, 1988), then it is possible that mere exposure to these changes will be sufficient to bias the responses of other animals.

This chapter is divided into two parts. Part 1 includes discussion of the different social influences that may act upon rats and starlings in the two-object/two-action procedure. Part 2 considers how, in some circumstances, these social influences might be manipulated in order to answer questions about the psychological mechanisms of, and distinctive conditions favouring, imitative and nonimitative social learning.

6.1 Theoretical Significance of the Two-Object/Two-Action Procedure

6.1.1 The rat

In Experiment 1, naive rats observed demonstrator rats manipulating one of two different levers (left, right) in one of two different directions (up, down). When subsequently allowed access to the same levers on test and rewarded for all responses, regardless of location and direction, these rats showed a reliable preference for the demonstrator's lever and the demonstrator's direction.

Unfortunately, these effects were not particularly robust. Several further replications of Experiment 1 yielded either the location effect, the direction effect, or no reliable effect of conspecific observation. Only in the reported experiment were both effects obtained simultaneously.

Available evidence suggests that rats are very sensitive to the effects of odour cues deposited by conspecifics (e.g. Galef & Beck, 1985). Therefore, additional studies were required in order to determine the extent to which the effect of demonstrator location and direction were the result of: (i) visual cues arising from observation of the demonstrators' behaviour, in addition to (ii) odour cues deposited by demonstrators on or around the lever which they operated.

This was the objective of an experiment by Heyes *et al.* (Experiment 1: 1999), in which rats were present in the observation compartment of an operant chamber while demonstrators pressed either a left or a right lever. When subsequently allowed access to the same levers on test, rats that observed demonstrators' responses exhibited a reliable bias in favour of the demonstrator's lever, whereas rats that were prevented from observing demonstrators' responses by an aluminium screen distributed their responses equally between the two levers. These results suggest that mere exposure to demonstrator-deposited odour cues is not sufficient to bias lever choice by rats. However, they do not show what role odour cues play when accompanied by compatible visual experience. Therefore, Heyes *et al.* (Experiment 2, 1999) allowed rats to observe viewed demonstrators pressing either a left or a right lever, before transferring them into the test compartment of another operant chamber in which box demonstrators had pressed either the left or the right lever. They found that these rats responded preferentially on the viewed demonstrator's lever, both when box demonstrators had pressed this lever and when box demonstrators had pressed the opposite lever.

Both experiments provide evidence of nonimitative social learning, or stimulus learning by observation, by showing that rats are attracted to the lever on which demonstrators were observed responding, rather than on which they deposited odour cues. However, it is less clear whether rats manipulated their demonstrator's lever because they learned either the static and/or dynamic properties of the lever, or because they learned a relationship between the lever and food. In Experiment 1 and in both of the experiments by Heyes *et al.* (1999), each of the demonstrators' responses was followed immediately by the delivery of a food pellet into a food tray in the demonstration compartment. It seemed likely that this event would be perceived by the observers and also that it would be assigned a positive value, because during the observers' previous magazine training in the demonstration compartment it signalled food was available. A possibility which, if correct, is consistent with the hypothesis that an associative learning process rendered attractive the lever on which demonstrators responded.

In an attempt to examine the mechanisms underlying lever choice by rats, Experiments 4 and 5 followed previous examples (e.g. Palameta & Lefebvre, 1985; Heyes *et al.*, 1994; Akins & Zentall, 1988) by manipulating whether rats were exposed to demonstrator reinforcement. Rats were given access to levers for the first time after they had observed demonstrators pressing either the left or the right lever. Each of the demonstrators' responses was rewarded with food or had no programmed consequences. It was found that when rats observed rewarded lever-pressing, they made more responses on the demonstrator's lever than on the opposite lever. In contrast, when rats observed nonrewarded lever-pressing, they failed to exhibit a reliable response bias.

These results suggest that rats are attracted to the lever demonstrators pressed as a result of observing the demonstrators' responses rewarded with food. However, they fail to provide unambiguous evidence that demonstrator reinforcement influenced observer rats' performance via an associative rather than a nonassociative process. Observation of rewarded lever-pressing may have resulted in a tendency for demonstrator-consistent responding because rats learned a lever-food relationship (observational conditioning). Alternatively, rats may have been exposed to the lever on which demonstrators responded as a result of observing it pressed (stimulus enhancement), and this experience may have led to both a decrease (habituation) and an increase (sensitization) in responsiveness to that lever. Which of these two processes was stronger would then determine the behavioural change that occurred (Groves & Thompson, 1970). If, for example, the processes underlying sensitization were strengthened more than those underlying habituation when the demonstrators' responses were followed by reward, then this would explain why rats in the FOOD groups approached their demonstrator's lever. If, when the demonstrators' responses had no significant consequences the two sets of processes were strengthened equally, then this would explain why rats in the NO FOOD groups did not approach their demonstrator's lever.

To test the stimulus enhancement hypothesis, Experiment 6 replicated the method used in Experiments 4 and 5, but introduced a delay between the demonstrators' final lever-press and the observers' first opportunity to respond. Available evidence suggests that sensitization leads to temporary changes in responsiveness (e.g. Groves & Thompson, 1970; Davis, 1974), while habituation may persist for longer (Leaton, 1974). If this is correct, and if in addition rats are exposed to levers as a result of observing them pressed, then one would expect that by delaying the onset of testing, Experiment 6 would cause sensitization of demonstrator-consistent responding effects to decay, but would have little, if any, effect on habituation of the same effects. More specifically, one would expect rats in the FOOD groups to distribute responses equally between the two levers, and rats in the NO FOOD groups to avoid responding on their demonstrator's lever. As in previous studies, Experiment 6 found that observation of rewarded lever-pressing resulted in a preference for the lever demonstrators pressed. Observation of nonrewarded lever-pressing, on the other hand, resulted in a preference for the lever demonstrators did not press.

The behaviour of rats in the NO FOOD groups is consistent with the hypothesis that stimulus enhancement was occurring among these animals. The behaviour of rats in the FOOD groups is, on the other hand, susceptible to at least two alternative interpretations. First, it is possible that when demonstrators' responses are rewarded with food, the processes underlying sensitization are rendered more resistant to decay than when demonstrators' responses have no significant consequences. Second, it is possible that when demonstrators' responses are rewarded with food, rats learn a lever-food relationship.

If the second interpretation is correct and rats acquire a lever-food relationship through conspecific observation, then they should also acquire a lever-no food relationship in a similar manner. This prediction was tested in Experiment 7 using an observational extinction procedure inspired by Heyes *et al.* (1993). Rats were trained to press a left or a right lever for food, and then given the opportunity to observe a conspecific demonstrator either sitting passively in the lever compartment (Group NONE) or making 50 nonreinforced responses on the lever that had previously been reinforced during observer training (Group SAME) or on the opposite lever (Group DIFFERENT). Following conspecific observation, the rats were given an extinction test in which neither left nor right responses were rewarded.

It was anticipated that extinction testing would result in acquisition of a lever-no food relationship, and that the strength of this relationship could be assessed by measuring the number of responses each rat made during the test session (Mackintosh, 1974). If, in addition, demonstrators expose rats to lever-outcome relationships, then Group SAME, which saw previously reinforced responses made in extinction, would be expected to make fewer responses on test, or acquire a lever-no food relationship more readily, than Group DIFFERENT, which saw previously nonreinforced responses made in extinction. Furthermore, if there was some generalization between left and right responses, then Group DIFFERENT would be expected to make fewer responses on test, or acquire a lever-no food relationship more readily, than Group NONE, which did not observe responding on either lever prior to testing. In fact, Group SAME made more responses on test than Group NONE, suggesting that rats are attracted to levers as a result of observing them pressed, and that this experience interferes with subsequent acquisition of a lever-no food relationship. Group DIFFERENT made an intermediate number of responses, but this effect was not reliable.

The remaining rat studies not yet summarized, were designed to examine the influence of visual observation and demonstrator-deposited odour cues on the direction of rats' responses in the two-object/two-action procedure. In Experiment 2, rats were present in the observation compartment of an operant chamber while a conspecific demonstrator lifted a single lever up or pressed it down. When subsequently allowed access to the same lever on test, rats that observed demonstrators' responses showed an unlearned bias towards down lever-pressing. Rats that were prevented from observing demonstrators' responses by an aluminium screen also showed this bias, but, in addition, moved the lever in the same direction as the demonstrator. In Experiment 3, rats observed viewed demonstrators lifting a lever up or pressing it down. They were then transferred into the test compartment of another chamber in which box demonstrators had moved the lever either up or down. As in previous experiments, these rats made many more down than up responses. However, they also showed a tendency to move the lever in the same direction as the box demonstrator, while responding in the opposite direction to the viewed demonstrator.

Thus, it would appear that directional responding in rats is influenced both by their observation of the demonstrators' behaviour, in addition to odour cues deposited by demonstrators on or around the lever which they operated. The former effect is the most surprising and apparently the most complex. In Chapter 1, it was maintained that imitation should be regarded as a special case of observational learning in which exposure to the positive relationship between demonstrators' responses and an appetitive reinforcer is sufficient to promote matching behaviour on the part of the observer. In Experiments 2 and 3, visual observation biased the direction of rats' responses in favour of the direction in which demonstrators did not respond. This is clearly not an example of imitation, but it may still be the result of observational learning which, according to Heyes (1994), need not always lead to matching behaviour. Nonmatching behaviour may also result from stimulus learning by observation. Rats may have acquired, during observation training, information about the return of the lever to its horizontal resting place rather than movement of the lever in its reinforced direction, either because the former event was more visible or because it was more contiguous with the delivery of food.

In contrast, the effect of demonstrator-deposited odour cues is relatively straightforward. It would appear that demonstrators deposit attractive odour cues asymmetrically on or around the lever which they operated, and that exposure to these cues on test was sufficient to promote reliable demonstrator-consistent responding effects. In the case of rats assigned to Group UP, an excess of odour cues would have been encountered on the ventral surface of the lever (i.e. that facing the floor of the chamber), resulting in a tendency to lift the lever up. In contrast, an excess of odour cues would have been encountered on the dorsal surface of the lever (i.e. that facing the ceiling of the chamber) in the case of rats assigned to Group DOWN, resulting in a tendency to press the lever down.

That exposing rats to demonstrator-deposited odour cues can give rise to acquisition of a novel response is consistent with the results of numerous studies. First, early attempts to demonstrate response learning by observation in rats usually involved providing naive animals with the opportunity to press a lever on which they had previously observed conspecifics responding for food. These animals acquired the target response faster or more efficiently than animals that observed either an empty lever compartment or a passive conspecific during training, and were therefore tested with a previously unmanipulated lever (e.g. Jacoby & Dawson, 1969; Gardner & Engel, 1971; Huang *et al.*, 1983). This effect, although consistent with the occurrence of imitation, does not provide unequivocal evidence of response learning by observation, because it may be due instead to scent-mediated local enhancement. Rats may have approached and contacted the lever as a result of changes brought about on it by the demonstrator's behaviour, and this may have facilitated subsequent acquisition of a lever-food relationship.

Second, attempts to examine the role played by demonstrator-deposited odour cues in imitative learning by rats have indicated that this factor exerts an important influence on behaviour. Heyes *et al.* (1992) allowed naive rats to observe demonstrators as they pushed a joystick either to the left or to the right for food. Half of these animals were then allowed access to the joystick from the position previously occupied by the demonstrator, and found to show a reliable tendency to respond in the same direction as their demonstrator. In this experiment, the joystick was suspended vertically between demonstrators and their observers. Therefore, it was viewed from a substantially different stimulus configuration during observation and on test; an arrangement which makes it unlikely that stimulus learning by observation was responsible. To completely exclude this possibility, Heyes *et al.* tested the remaining animals with a joystick that had been rotated, within the demonstration compartment, through an angle of 90 degrees. These rats showed a reliable tendency to respond in the same direction, relative to their own body, as had their demonstrator, even though this resulted in the joystick moving towards a different point in space as it had moved during observation.

This experiment appeared to provide good evidence that rats in the bidirectional control procedure can acquire a response through conspecific observation (Heyes, 1996). However, a recent study has raised doubts about this conclusion. Mitchell *et al.* (1999) allowed rats to observe demonstrators pushing a joystick either to the left or to the right. As in previous studies, these animals responded predominantly in the demonstrator's direction when allowed access to the joystick on test. However, since the same effect could have been obtained if demonstrators deposited attractive odour cues on the side of the joystick contralateral to its direction of motion, rats were also tested with a joystick that had been rotated, within its mounting, through an angle of 180 degrees. Under this condition, any odour cues deposited by demonstrators would have been on the side of the joystick ipsilateral to its observed direction of motion, and exploration of these cues might be expected to result in a tendency for demonstrator-inconsistent responding. This prediction was confirmed.

Finally, and more generally, rats rely on olfactory cues to provide important information about the environment and to regulate many aspects of interspecific social behaviour (Barnett, 1975). For example, rats will begin eating a novel food not only because of their tendency to approach conspecifics (Galef, 1971; Galef & Clark, 1971, 1972) or residual cues that conspecifics have deposited (Galef & Beck, 1985) and begin feeding in their presence, but also because of exposure to odour cues on a demonstrator's breath.

In an experiment by Galef & Wigmore (1983), naive rats were given the opportunity to interact with demonstrators that had recently been fed one of two distinctively flavoured diets. When subsequently offered a choice between these two diets, rats consumed more of the diet their demonstrator had eaten. This effect was not disrupted by placing a wire-mesh partition between the two animals during the period of interaction or by anaesthetizing the demonstrator. However, it was abolished by placing a plexiglass partition between the two animals and by rendering the observer anosmic. These results were interpreted as evidence that rats can communicate information to one another about ingested foods that are distant in time and space. Furthermore, it would appear that the necessary information is borne on olfactory and/or gustatory cues carried on the demonstrator's breath.

The hypothesis that in a two-object/two-action procedure conspecific observation promotes demonstrator-consistent directional responding, while odour cues have an inverse effect is appealing. However, it cannot account for Experiment 1 (see also Ray, 1997) where rats that had access to visual cues during demonstration sessions and to odour cues on test, responded in the same direction as their demonstrator. If, on the other hand, the current hypothesis included the possibility that conspecific observation did not always yield the same outcome then it could readily accommodate these findings. However, this is an unsatisfactory compromise since it is currently not known under which conditions stimulus (or response) learning by observation gives rise to matching behaviour and under which conditions it gives rise to nonmatching behaviour.

6.1.2 The starling

In Experiment 8, naive starlings observed conspecific demonstrators seizing live mealworms from one of two holes in the lid of an opaque plastic box. One of the holes was blocked by a red plug, while a black plug blocked the other hole. To gain access to the mealworms, demonstrators had to remove the plug, which they did either by pulling up on a loop of string inserted through the centre of the plug or by pushing down. Demonstrators were given the opportunity to remove the plug 10 times each day for five days, before the observers were given access to a sealed container for the first time on day 5. During this period, in which the observers were rewarded for removing either plug in either direction, they showed a reliable bias in favour of removing the same plug in the same direction as their demonstrator.

These results are striking not only because they suggest that starlings were influenced by both the location and direction of demonstrators' responses, but also because both effects persisted across two subsequent days of testing, and the latter effect has been replicated more than once (Skinner, Fawcett, & Goldsmith, unpublished data). Furthermore, it is difficult to see how local enhancement could have biased the birds' responses. This is because the demonstrators were removed from the apparatus before the observers were tested, and it is unlikely that they deposited food particles and/or other byproducts of consumption on or around the plug which they manipulated.

If this interpretation is correct, then there is a strong possibility that starlings in the two-object/two-action procedure engage in nonimitative social learning, or stimulus learning by observation. However, it remains to be determined whether the birds in Experiment 8 displaced their demonstrator's plug because they learned either the static and/or dynamic properties of the plug alone, or because they learned a relationship between movement of the plug and the availability of food.

Unfortunately, it is more difficult to interpret the effect of demonstrator direction as evidence of imitative social learning for two reasons. First, demonstrators contacted different parts of the plug depending on whether they pulled it up or pushed it down. When pulling up, demonstrators grasped the loop of string that protruded from the centre of the plug between their mandibles. When pushing down, demonstrators thrust their open mandibles against the surface of the plug. If, as a result, the observers assigned to Groups UP and DOWN directed their responses to different areas of the plug, then this would raise the possibility that stimulus enhancement, instead or in addition to, response learning by observation biased the direction of their responses. Second, demonstrators caused the plug to move in different directions with respect to the lid of the food box, which may have allowed the observers to learn either the dynamic properties of the plug or a plug movement-food relationship. For example, observers in the UP groups may have learned that the plug moved up and out of the food box, while observers in the DOWN groups may have learned that the plug moved down and into the food box.

Despite these problems, there is still good reason to suppose that starlings were influenced by their demonstrator's behaviour, rather than by the effect of their demonstrator's behaviour on the plug (Heyes & Ray, in press). First, there is no independent evidence that under the conditions provided by a two-action test, birds (or members of any other species) can learn to discriminate the complex, dynamic properties of objects. Second, recent studies have shown that both pigeons (Zentall *et al.*, 1996) and quail (Akins & Zentall, 1996) show demonstrator-consistent responding effects when observed differences in movement of the demonstrator's manipulandum have been controlled. A control procedure similar to that employed in experiments with pigeons and quail, was adopted in a pilot study with budgerigars.

6.1.2.1 The budgerigar

Naive budgerigars observed from one side of a wire-mesh cage (see Figure 18), while a conspecific demonstrator slid a stick either to the left or to the right. Each time demonstrators slid the stick through a distance of approximately 6 cm, seed was delivered via a dispenser to the left side of the cage and the stick was returned to its starting position by the experimenter. Initially, it was intended that the seed dispenser would occupy a neutral position with respect to the direction of stick movement, so as not provide to any salient cues for the observers. However, when seed was delivered to the back of the cage, demonstrators failed to acquire the target response, and when it was delivered from above the stick, it scattered throughout the cage inadvertently rewarding the observers.

The observers were allowed to watch a demonstrator make 10 rewarded responses every day for five days, before being allowed access to the stick for the first time on day 5, and then again on days 6 and 7. It was anticipated that budgerigars would provide evidence of imitative social learning by sliding the stick in the same direction as their demonstrator. Such an effect could not be due to stimulus enhancement, because demonstrators contacted the same part of the stick when sliding it to the left and when sliding it to the right. Emulation learning and/or observational conditioning are also unlikely explanations, because it was not possible for the observers to see the ends of the stick moving.

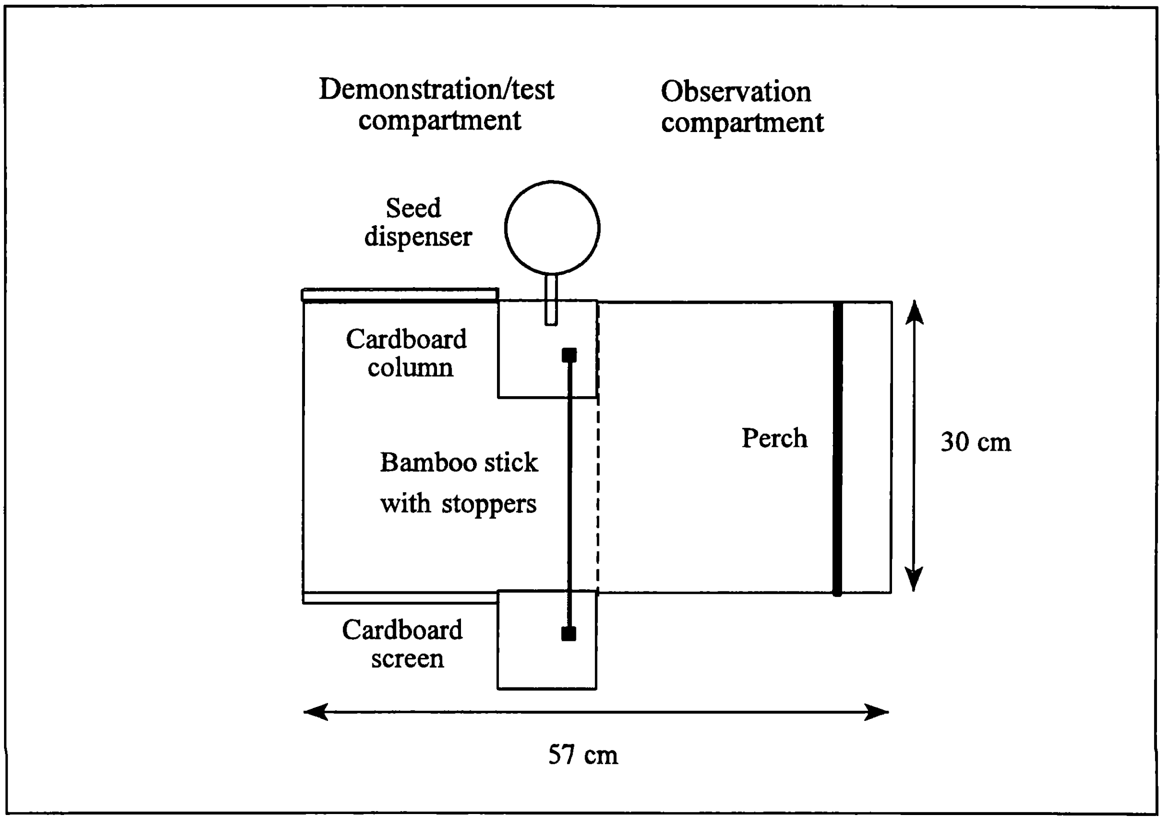

Figure 18. Plan of the apparatus used in the pilot study. The dashed line shows the position of the wire-mesh partition that separated the demonstration/test compartment from the observation compartment.

Of the 12 birds that were tested, nine failed to respond (i.e. did not slide the stick through a distance of approximately 1 cm in either direction on any of the three days of testing). However, of the three birds that did respond, all exhibited a substantial bias in favour of their demonstrator's direction. It is interesting that all three birds observed the same demonstrator, and that this demonstrator exhibited what was judged to be the most efficient method of stick-sliding. This raises the possibility that had demonstrators been required, during training, to slide the stick in one single, smooth movement, rather than to jerk it in a series of stages, a stronger imitative effect would have been obtained.

Although these results were disappointing, the budgerigar paradigm is still worth pursuing for a number of different reasons. Not only because it has the potential to provide an unambiguous demonstration of imitation, or response learning by observation, it can be readily modified to form a two-object/two-action procedure (i.e. by adding a second stick above that already present). However, before such a study could be embarked upon a number of procedural changes would have to be made in order to improve the size of any imitative effect which might be obtained. It would be advisable to train demonstrators to exhibit the most efficient method of stick sliding possible, and to reward sliding with seed delivered to a neutral position with respect to the direction of stick movement. In addition, the test criteria, or the distance through which the observers are required to move the stick, could be reduced.

6.1.3 Summary and conclusion

Taken together, the experiments outlined above are consistent with the hypothesis that in a two-object/two-action procedure, a number of different social influences and social learning processes may facilitate acquisition of a novel response by naive animals.

In Experiment 1, rats observed demonstrators manipulating either a left or a right lever by lifting up or pressing down. When subsequently allowed access to the same levers on test, these rats exhibited a reliable bias in favour of the demonstrator's lever and the demonstrator's direction. Follow-up studies provided evidence that rats were exposed to levers as a result of observing them pressed (stimulus enhancement), and that reinforcement of demonstrators' responses increased the probability that rats would approach and contact the lever demonstrators pressed (sensitization). Once in the vicinity of this lever, rats encountered odour cues deposited asymmetrically by demonstrators on or around the surface which they contacted. Exploration of these cues was found to be sufficient to bias rats' responses in favour of their demonstrator's direction (local enhancement).

In Experiment 8, starlings observed demonstrators displacing either a red or a black plug from above a hole in the lid of a plastic box by lifting up or pushing down. When presented with a sealed box on test, these birds displaced the same plug in the same direction as their demonstrator. It was suggested that observation of the demonstrators' behaviour exposed starlings to the plug (stimulus enhancement, observational conditioning), but whether demonstrator reinforcement exerted an important influence on the observers' performance remains to be determined. It was also suggested that exposure to the demonstrator's behaviour, rather than to the effect of the demonstrator's behaviour on the plug, increased the probability that the observer would remove the plug in the same direction as their demonstrator (imitation or observational learning).

6.2 Methodological Significance of the Two-Object/Two-Action Procedure

The previous section dealt with theoretical issues arising from use of the two-object/two-action procedure, while the current section addresses a related matter; what is the methodological significance of the two-object/two-action procedure? More specifically, what is the advantage of knowing that, in this paradigm, a number of different social influences and social learning processes facilitate acquisition of a novel response by naive animals?

It will be argued that the methodological significance of the two-object/two-action procedure is twofold. First, it can be used to elucidate the psychological mechanisms of social learning, and thereby to test hypotheses concerning the extent to which these are the same as those underlying asocial learning. Second, it can be used to investigate the distinctive conditions favouring imitative and nonimitative social learning, and consequently what role these two processes play in behavioural adaptation.

6.2.1 What are the psychological mechanisms of imitative and nonimitative social learning?

Since formal research on the subject began a century ago (Thorndike, 1898), a substantial amount of information has been gathered with respect to whether a given species of animal is capable of some form of social learning and what role social learning plays in the ontogeny of adaptive behaviour (Galef, 1988). Considerably less effort was made, during this same period, to study the psychological mechanisms of social learning. In contrast, research on asocial learning has largely ignored questions about function, concentrating instead on the mechanisms of learning; an effort which has culminated in animal learning theory.

According to animal learning theory, learning is a change in the animal that is caused by a specific experience at a certain time, t_1, and is detectable later, t_2, in the animal's behaviour (Rescorla, 1988). Categories of learning can be distinguished according to the type of experience which gave rise to any change in the animal's behaviour. If, for example, the experience was exposure to a single stimulus, then the category of learning would be habituation or sensitization depending on whether the animal exhibited a decrease or an increase in responsiveness to that stimulus. Changes in responsiveness may also result from exposure to the relationship among events; either between two stimuli (S-S: classical conditioning) or between a response and a reinforcer (R-S*: instrumental conditioning).

Exposure to the relationship among events not only leads to changes in responsiveness, it also affects the probability that animals will learn other relationships. Overshadowing occurs when exposure to an S_1-S_2 (or an R_1-S^*) relationship at the same time as an S_3-S_2 (or an R_2-S^*) relationship reduces the degree to which animals learn about the S_3-S_2 (or an R_2-S^*) relationship. Blocking, on the other hand, refers to those instances in which previous experience with an S_1-S_2 (or an R_1-S^*) relationship interferes with the animals' ability to learn about an S_3-S_2 (or an R_2-S^*) relationship when it is presented at the same time as the S_1-S_2 (or an R_1-S^*) relationship.

In Chapter 1, it was shown that most, if not all, social learning phenomena resemble asocial learning phenomena in terms of their conditions of occurrence, which favours the hypothesis that these two forms of behavioural change are mediated by common mechanisms. For example, providing naive animals with the opportunity to interact with conspecific demonstrators may facilitate exposure to the static (stimulus enhancement) and/or dynamic (emulation learning) properties of a stimulus, or to the relationship between that stimulus and another event which may be either attractive or aversive for the animal (observational conditioning). If, instead, the demonstrator's behaviour exposes the observer to an R-S* relationship by acting as the source of the target response, then this would be an example of imitation or observational learning. Finally, one might expect socially mediated exposure to the relationship between events, either between two stimuli or between a response and a reinforcer, to result in changes not only in responsiveness, but also in the observers' ability to learn other relationships.

6.2.1.1 Nonimitative social learning

The two-object/two-action procedure seeks evidence of nonimitative social learning by allowing animals to observe demonstrators manipulating one of two different objects. If, during a subsequent test session, the observers approach that object which demonstrators were observed to operate, then this may provide evidence of stimulus learning by observation. To determine whether the mechanism underlying this effect was either single stimulus, exposure learning (stimulus enhancement) or stimulus-stimulus associative learning by observation (observational conditioning) it would be necessary, but not sufficient, to abolish the contingency between demonstrators' responses and the delivery of food (e.g. Palameta & Lefebvre, 1985; Heyes *et al.*, 1994; Akins & Zentall, 1998).

If, for example, the observers approach that object which demonstrators operated when the demonstrators' responses were not followed by reward, then this would suggest that observation of the consequences of demonstrators' responses did not play an important role in this procedure and observational conditioning would be an inappropriate description of the mechanism underlying this effect. If, on the other hand, the observers in this condition did not approach that object which demonstrators operated, then this would suggest that demonstrator reinforcement was important. However, it would remain to be determined whether it exerted either an associative (observational conditioning) or a nonassociative (stimulus enhancement) influence on the observers' performance. Finally, if the observers' preference for the object demonstrators manipulated was mediated by observational conditioning, then one might expect it to be subject to both overshadowing and blocking.

6.2.1.2 Imitative social learning

The two-object/two-action procedure also seeks evidence of imitative social learning by allowing animals to observe demonstrators manipulating an object in one of two different ways. If it can be shown that the observers subsequently manipulate the object in the same way as a result of exposure to the demonstrator's behaviour, rather than to the effect of the demonstrator's behaviour on the environment, then this may provide evidence of response learning by observation.

It is seldom that investigators of imitation in animals offer any account of the underlying mechanisms. However, it is commonly assumed that imitation is unique among other forms of social learning in that it involves complex and poorly understood cognitive processes. It has been claimed that imitation occurs when the sensory input from a demonstrator's behaviour is transformed into a 'symbolic conception' (Bandura, 1986), an 'imaged representation' (Piaget, 1951), or a 'supramodal representation' (Meltzoff, 1985), all of which contain the information necessary for guiding the execution of matching behaviour on the part of the observer. These so-called 'transformational' theories provide a plausible account of imitation. However, they rely upon the existence of mental representations that cannot be measured directly and therefore cannot be tested (Heyes & Ray, in press).

It may, instead, be more appropriate to regard imitation as a special case of associative learning in which the underlying processes have become specialized to cope with the fact that responses may be acquired both directly by execution and indirectly by observation. If this is correct, then it suggests that the capacity to imitate may be derived from previous experience of simultaneously observing and executing an action. One example of a theory based on this assumption is Heyes & Ray's (in press) Associative Sequence Learning (ASL) theory.

According to Heyes & Ray (in press), imitation consists of acquisition of sequences of action units rather than unitary actions. When the animal observes, for the first time, a sequence of action units two sets of associative processes are activated which result in the formation of 'horizontal' and 'vertical' links. It is by the horizontal processes that associations are formed between sensory representations of each component in the sequence, enabling the animal to learn what the sequence looks like. However, observational sequence learning is not by itself sufficient to support imitative behaviour, which depends on a second set of processes that result in the formation of vertical associations between sensory representations of each individual action unit in a sequence and a motor representation of the same unit. These associations are established before the novel sequence is observed, during, for example, the course of self-observation or synchronized action; two experiences which provide the opportunity for contiguously observing and executing an action. To the extent that these vertical links have been established, exposure to a novel sequence of actions, or recollection of that sequence by the horizontal processes, will activate the appropriate motor representations in the order necessary for sequence reproduction.

The advantage of ASL theory is that it makes two predictions, both of which can be tested in a two-object/two-action procedure. ASL theory predicts that imitation will be possible only to the extent that the observer: (i) is capable of stimulus sequence learning, and (ii) has contiguous experience of seeing-and-doing components of the action sequence. The results of a study by Whiten (1998) may be relevant to the first of these two predictions. Whiten allowed four chimpanzees to observe a human demonstrator opening the lid of a plastic box and removing a piece of food from within. When closed, the lid was held in place by two different types of latch: a bolts latch and a barrel latch. The bolts latch consisted of two plastic rods, each of which passed through a metal ring on the lid of the box and could be opened by twisting and pulling or poking the rods out of their lodgings. The barrel latch consisted of a metal T-bar, which could be turned or spun and in this way removed from a hollow barrel on the side of the box.

In this experiment, all of the chimpanzees observed the demonstrator manipulating both of the latches before opening the box and removing the piece of food. However, while two of the chimpanzees observed the demonstrator manipulating the bolts latch before the barrel latch, the other two observed the demonstrator manipulating the barrel latch before the bolts latch. Within each condition, one of the chimpanzees observed the bolts twisted and pulled out of their lodgings and the T-bar turned or spun, while the other chimpanzee observed the bolts poked out of their lodgings and the T-bar turned or spun. When subsequently presented with a closed box on test, chimpanzees showed a reliable tendency to approach the latches in the same order as the demonstrator, although they did not open them in the same way.

These results suggest that chimpanzees possess the first necessary condition for imitation; they are capable of stimulus sequence learning. However, whether they also have the capacity to imitate is unclear. In fact, even if this experiment had found that chimpanzees opened latches using a demonstrated technique, it would not provide strong evidence of response learning by observation, because it may be due instead to emulation learning. The demonstrator had different effects upon the bolts depending on whether they were twisted and pulled or poked out of their lodgings. When the bolts were twisted and pulled, they rotated in a clockwise direction and moved towards the demonstrator's body. When they were poked, they did not rotate and moved away from the demonstrator's body.

The second prediction generated by ASL theory could be tested by exposing animals to a novel sequence of actions, while varying the degree to which they have correlated experience of seeing-and-doing each component of the sequence. For example, naive animals could be given the opportunity to observe demonstrators performing the following sequence of actions: AB. One group might have previously observed and executed both components of this sequence in the presence of a demonstrator (low combinatorial novelty), another group might have observed and executed only one component of the sequence in the presence of a demonstrator (medium combinatorial novelty), while another group would have no such experience (no combinatorial novelty). If imitation depends on the formation of vertical links between the sensory components of each of the actions in a sequence and their motor components, then one would expect that the probability of imitative behaviour would increase with decreasing combinatorial novelty. Unfortunately, there are no known experiments in which evidence of imitation has been sought in this manner.

6.2.2 What are the distinctive conditions favouring imitative and nonimitative social learning?

The two-object/two-action procedure could also be used to investigate the distinctive conditions favouring imitative and nonimitative social learning. To obtain some indication as to what these might be, it is profitable to turn, once again, to animal learning theory.

According to Mackintosh (1974), when animals are first exposed to either a natural and/or an experimental environment, their behaviour will be modified by the classical contingencies embedded in that situation. For example, the animal may approach and contact an object because it has learned, through a process of classical conditioning, that this part of the environment is associated with the availability of food. Then, as the animal begins to interact with the object, it may learn that food can be obtained more promptly and with less wasted effort by adopting a precise and efficient pattern of responding. It is at this point that behaviour is subject to the laws of instrumental conditioning.

That animals may acquire information about stimuli before responses, is strengthened by a study of avoidance learning in dogs. Wahlsten & Cole (1972) repeatedly exposed dogs to stimulus-shock pairings, and recorded the number of trials on which a paw flexion response occurred. One group of dogs was trained on an omission control schedule, such that shock could be avoided altogether if animals responded to the stimulus. The other group was trained on a standard classical conditioning schedule, such that shock was delivered independently of behaviour. At first, the two groups did not differ; both responded on 50% of trials with a brief paw flexion initiated immediately prior to the scheduled onset of shock. However, as training progressed, animals in the omission control group underwent a dramatic increase in the probability of responding. They also showed an increase in the duration of responding accompanied by a decrease in the latency of the flexion response.

These findings are of considerable relevance to the study of social learning. They suggest that with limited training, animals may engage, almost exclusively, in nonimitative social learning. They may learn about the stimulus with which demonstrators are interacting; its presence or location, dynamic properties, and/or value. Then, once the observers' familiarity with this stimulus increases, they may begin to engage in imitative social learning. They may learn about the demonstrators' responses; how to execute them and what are their consequences.

This prediction could be tested in a two-object/two-action procedure by examining the rate of response learning by observation as a function of previous exposure to stimulus properties, and vice versa. For example, one might expect that exposing naive animals to the objects with which demonstrators are subsequently observed to interact, would substantially increase the probability of response learning by observation. Alternatively, depriving animals of the opportunity to observe the behaviour of conspecifics, might be expected to increase the probability of stimulus learning by observation.

If this is correct, then it may lead to some interesting predictions concerning the incidence of imitative and nonimitative social learning in natural environments. It seems likely that when animals have considerable experience of one another (i.e. when they belong to the same colony), they will be more likely to engage in response learning by observation than stimulus learning by observation. When, on the other hand, animals have limited experience of one another (i.e. when they belong to neighbouring colonies), they may engage in stimulus learning by observation to the expense of response learning by observation.

6.2.3 Summary and conclusion

The methodological significance of the two-object/two-action procedure lies in its ability to provide the answer to two different, but related, questions. First, what are the psychological mechanisms of social learning? Second, what are the distinctive conditions favouring imitative and nonimitative social learning? The experiments reported in this thesis used both rats and starlings. Surprisingly, they indicated that, despite their widespread use in psychological laboratories, rats are not well-suited for this task. Starlings, on the other hand, appear to be more valuable.

Rats in the two-object/two-action procedure do not show robust effects of exposure to the location and direction of demonstrators' responses. They fail to provide an unambiguous demonstration of imitation, or response learning by observation and are very sensitive to the effects of odour cues deposited by conspecifics. Starlings, on the other hand, show strong effects of exposure to both the location and direction of demonstrators' responses, and neither of these effects can be accounted for by demonstrator-deposited odour cues. Finally, they appear to provide a reasonably strong demonstration of imitation and have the added advantage of being easy to obtain, relatively inexpensive, and adapt well to conditions in captivity.

References

Aisner, R. & Terkel, J. (1992). Ontogeny of pine 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.

Akins, C. K. & Zentall, T. R. (1998). Imitation in Japanese quail: The role of reinforcement of demonstrator responding. *Psychonomic Bulletin and Review*, 5, 694-697.

Baker, M. C., Belcher, C. S., Deutsch, L. C., Sherman, G. L., & Thompson, D. B. (1981). Foraging success in junco flocks and the effects of social hierarchy. *Animal Behaviour*, 29, 137-142.

Bandura, A. (1965). Influence of models' reinforcement contingencies on the acqusition of imitation responses. *Journal of Personality and Social Psychology*, 1, 589-595.

Bandura, A. (1986). Social Foundations of Thought and Action: A Social Cognitive Theory. Englewood Cliffs, NJ: Prentice Hall.

Bayer, E. (1929). Beitrage zur Zweikomponententheorie des Hungers. *Zeitschrift fuer Psychologie*, 112, 1-53.

Beauchamp, G. & Kacelnik, A. (1991). Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata. Animal Behaviour*, 41, 247-253.

Bolles, R. C., Holtz, R., Dunn, T., & Hill, W. (1980). Comparisons of stimulus learning and response learning in a punishment situation. *Learning and Motivation*, 11, 78-96.

Brown, C. R. (1988). Social foraging in cliff swallows: Local enhancement, risk sensitivity, competition and the avoidance of predators. *Animal Behaviour*, 36, 780-792.

Brown, P. L. & Jenkins, H. M. (1968). Auto-shaping the pigeon's key peck. *Journal of the Experimental Analysis of Behaviour*, 11, 1-8.

Bunch, G. B. & Zentall, T. R. (1980). Imitation of a passive avoidance response in the rat. *Bulletin of the Psychonomic Society*, 15, 73-75.

Cadieu, J. C., Cadieu, N., & Lauga, J. (1995). Local enhancement and seed choice in the juvenile canary, *Serinus canarius. Animal Behaviour*, 50, 793-800.

Chesler, P. (1969). Maternal influence in learning by observation in kittens. *Science*, 166, 901-903.

Church, R. M. (1957). Two procedures for the establishment of imitative behaviour. *Journal of Comparative and Physiological Psychology*, 50, 315-318.

Clayton, D. A. (1978). Socially facilitated behaviour. *Quarterly Review of Biology*, 53, 373-391.

Coleman, S. L. & Mellgren, R. L. (1997). Social enhancement and interference of food finding in zebra finches (*Taeniopygia guttata*). *Journal of Comparative Psychology*, 111, 242-250.

Cook, M., Mineka, S., Wolkenstein, B., & Laitsch, K. (1985). Observational conditioning of snake fear in unrelated rhesus monkeys. *Journal of Abnormal Psychology*, 94, 591-610.

Darby, C. L. & Riopelle, A. J. (1959). Observational learning in the rhesus monkey. *Journal of Comparative and Physiological Psychology*, 52, 94-98.

Davis, M. (1974). Sensitization of the rat startle response by noise. *Journal of Comparative and Physiological Psychology*, 87, 571-581.

Dawson, B. V. & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour*, 13, 470-474.

Del Russo, J. (1971). Observational learning in hooded rats. *Psychonomic Science*, 24, 37-38.

Del Russo, J. E. (1975). Observational learning of discriminative avoidance in hooded rats. *Animal Learning and Behaviour*, 3, 76-80.

Ekman, J. & Hake, M. (1988). Avian flocking reduces starvation risk: An experimental demonstration. *Behavioural Ecology and Sociobiology*, 22, 91-94.

Feare, C. J. (1984). The Starling. Oxford: Oxford University Press.

Fisher, J. & Hinde, R. A. (1949). Further observations on the opening of milk bottles by birds. *British Birds*, 42, 347-357.

Fleming, S. P., Smith, P. C., Seymour, N. R., & Bancroft, R. P. (1992). Ospreys use local enhancement and flock foraging to locate prey. *Auk*, 109, 649-654.

Galef, B. G. (1971). Social effects in the weaning of domestic rat pups. *Journal of Comparative and Physiological Society*, 75, 358-362.

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In T. R. Zentall and B. G. Galef (Eds), Social Learning: Psychological and Biological Perspectives, pp. 3-28, Hillsdale, NJ: Erlbaum.

Galef, B. G. & Beck, M. (1985). Aversive and attractive marking of toxic and safe foods by Norway rats. *Behavioural and Neural Biology*, 298-310.

Galef, B. G. & Clark, M. M. (1971). Social factors in the poison avoidance and feeding behaviour of wild and domesticated rat pups. *Journal of Comparative and Physiological Psychology*, 3, 341-357.

Galef, B. G. & Clark, M. M. (1972). Mother's milk and adult presence: Two factors determining initial dietary selection by weanling rats. *Journal of Comparative and Physiological Psychology*, 78, 220-225.

Galef, B. G. & Durlach, P. J. (1993). Absence of blocking, overshadowing and latent inhibition in social enhancement of food preferences. *Animal Learning and Behaviour*, 21, 214-220.

Galef, B. G. Manzig, L. A. & Field, R. M. (1986). Imitation learning in budgerigars: Dawson and Foss (1965) revisited. *Behavioural Processes*, 13, 191-202.

Galef, B. G. & Wigmore, S. W. (1983). Transfer of information concerning distant foods: A laboratory investigation of the 'information centre' hypothesis. *Animal Behaviour*, 31, 748-758.

Gardner, M. R. (1997). Imitation: The methodological adequacy of directional control tests. Unpublished doctoral thesis, University of London.

Gardner, E. L. & Engel, D. R. (1971). Imitational and social facilitatory aspects of observational learning in the laboratory rat. *Psychonomic Science*, 25, 5-6.

Gates, M. F. & Allee, W. C. (1933). Conditioned behaviour of isolated and grouped cockroaches on a simple maze. *Journal of Comparative Psychology*, 15, 331-358.

Groesbeck, R. W. & Duerfeldt, P. M. (1971). Some relevant variables in observational learning of the rat. *Psychonomic Science*, 22, 41-43.

Groves, P. M. & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological*

Review, 77, 419-450.

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 Reviews*, 69, 207-231.

Heyes, C. M. (1996). Genuine imitation? In C. M. Heyes and B. G. Galef (Eds), Social Learning In Animals: The Roots of Culture, pp. 371-389. New York: Academic Press.

Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology*, 42B, 59-71.

Heyes, C. M., Dawson, G. R. & Nokes, T. (1992). Imitation in rats: Initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology*, 45B, 229-240.

Heyes, C. M., Jaldow, E., & Dawson, G. R. (1993). Observational extinction: Observation of nonreinforced responding reduces resistance to extinction in rats. *Animal Learning and Behaviour*, 21, 221-225.

Heyes, C. M., Jaldow, E., & Dawson, G. R. (1994). Imitation in rats: Conditions of occurrence in a bidirectional control procedure. *Learning and Motivation*, 25, 276-287.

Heyes, C. M. & Ray, E. D. (In press). Transformational and associative theories of imitation.

Advances in the Study of Behaviour.

Heyes, C. M., Ray, E. D., Mitchell, C. J. & Nokes, T. (1999). Stimulus enhancement: Controls for Social Facilitation and Local Enhancement. *Learning and Motivation.*

Hinde, R. A. & Fisher, J. (1951). The opening of milk bottles by birds. *British Birds*, 44, 393-396.

Huang, I. N., Koski, C. A. & De Quardo, J. R. (1983). Observational learning of a bar-press by rats. *Journal of General Psychology*, 108, 103-111.

Jacoby, K. E. & Dawson, M. E. (1969). Observation and shaping learning: A comparison using Long Evans rats. *Psychonomic Science*, 16, 257-258.

John, E. R. Chesler, P. Bartlett, F. & Victor, I. (1968). Observation learning in cats. *Science*, 159, 1489-1491.

Kaiser, D. H., Zentall, T. R., & Galef, B. G. (1997). Can imitation in pigeons be explained by local enhancement together with trial-and-error learning? *Psychological Science*, 8, 459-460.

Knight, S. K. & Knight, R. L. (1983). Aspects of food finding by wintering bald eagles. *Auk*, 100, 477-484.

Kohn, B. (1976). Observation and discrimination learning in the rat: Effects of stimulus substitution. *Learning and Motivation*, 7, 303-312.

Krebs, J. R., MacRoberts, M. H., & Cullen, J. M. (1972). Flocking and feeding in the great tit *Parus major* - an experimental study. *Ibis*, 114, 507-530.

Laland, K. N. & Plotkin, H. C. (1990). Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning and Behaviour*, 18, 246-251.

Laland, K. N. & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169.

Leaton, R. N. (1976). Long-term retention of the habituation of lick suppression and startle response produced by a single auditory stimulus. *Journal of Experimental Psychology: Animal Behaviour Proccesses*, 2, 248-259.

Lefebvre, L., Templeton, J., Brown, K., & Koelle, M. (1997). Carib grackles imitate conspecific and Zenaida dove tutors. *Behaviour*, 134, 1003-1017.

Levine, J. M. & Zentall, T. R. (1974). Effect of a conspecific's presence on deprived rats' performance: Social facilitation versus distraction/imitation. *Animal Learning and Behaviour*, 2, 119-122.

Ludvigson, H. W. & Sytsma, D. (1967). The sweet smell of success: Apparent double alternation in the rat. *Psychonomic Science*, 9, 283-284.

McQuoid, L. M. & Galef, B. G. (1992). Social influences on feeding site selection by Burmese fowl (*Gallus gallus*). *Journal of Comparative Psychology*, 106, 137-141.

Mackintosh, N. J. (1974). The psychology of Animal Learning. London: Academic Press.

Mason, J. R. & Reidinger, R. F. (1982). Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *Auk*, 99, 548-554.

Meltzoff, A. N. (1985). The roots of social and cognitive development: Models of man's original nature. In T. M. Field and N. Fox (Eds), Social Perception in Infants, pp. 1-30. Norwood, NJ: Ablex.

Miller, N. E. & Dollard, J. (1941). Social Learning and Imitation. New Haven: Yale University Press.

Mitchell, C. J., Heyes, C. M., Gardner, M. R., & Dawson, G. R. (1999). Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour cues on the manipulandum. *The Quarterly Journal of Experimental Psychology*, 52B, 193-202.

Neuringer, A. & Neuringer, M. (1974). Learning by following a food source. *Science*, 184, 1005-1008.

Oldfield-Box, H. (1970). Comments on two preliminary studies of "observation" learning in the rat. *Journal of Genetic Psychology*, 116, 45-51.

Palameta, B. & Lefebvre, L. (1985). The social transmission of a food-finding technique in pigeons: What is learned? *Animal Behaviour*, 33, 892-896.

Petit, O. & Thierry, B. (1993). Use of stones in a captive group of Guinea baboons (*Papio papio*). *Folia Primatologica*, 61, 160-164.

Piaget, J. (1951). Play, Dreams, and Imitation in Children. New York: Norton.

Powell, R. W. (1968). Observational learning versus shaping: A replication. *Psychonomic Science*, 10, 263-264.

Powell, R. W., Saunders, D., & Thompson, W. (1968). Shaping, autoshaping and observational learning with rats. *Psychonomic Science*, 13, 167-168.

Prior, K. A. & Weatherhead, P. J. (1991). Turkey vultures foraging at experimental food patches: A test of information transfer at communual roosts. *Behavioural Ecology and Sociobiology*, 28, 385-390.

Ray, E. D. (1997). Social and associative learning. Unpublished doctoral thesis, University of London.

Rescorla, R. A. (1988). Behavioural studies of Pavlovian conditioning. *Annual Review of Neuroscience*, 11, 329-352.

Ryer, C. H. & Olla, B. L. (1992). Social mechanisms facilitating exploitation of a sptially variable ephemeral food patches in a pelagic marine fish. *Animal Behaviour*, 44, 69-74.

Ryer, C. H. & Olla, B. I. (1995). Influences of food distrinution on fish foraging behaviour. *Animal Behaviour*, 49, 411-418.

Rypstra, A. L. (1989). Foraging success of solitary and aggregated spiders: Insights into flock formation. *Animal Behaviour*, 37, 274-281.

Senar, J. C. & Metcalfe, N. B. (1988). Differential use of local enhancement for finding food by resident and transient siskins. *Animal Behaviour*, 36, 1549-1550.

Sherry, D. F. & Galef, B. G. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour*, 32, 937-938.

Sherry, D. F. & Galef, B. G. (1990). Social learning without imitation: More about milk bottle opening by birds. *Animal Behaviour*, 40, 987-989.

Spence, K. W. (1937). Experimental studies of learning and higher mental processes in infr-human primates. *Psychological Bulletin*, 34, 806-850.

Sullivan, K. A. (1984). The advantages of social foraging in downy woodpeckers. *Animal Behaviour*, 32, 16-22.

Taylor, R. D. & Ludvigson, H. W. (1980). Selective removal of reward and nonreward odours to assess their control of patterned responding in rats. *Bulletin of the Psychonmic Society*, 16, 101-104.

Thorpe, W. H. (1963). Learning and Instinct In Animals (2nd ed.). Cambridge, MA: Harvard University Press.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S. Parker and K. Gibson (Eds), "Language" and Intelligence In Monkeys and Apes: Comparative Developmental Perspectives, pp. 271-311. Cambridge: Cambridge University Press.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool use by young chimpanzees. *Human evolution*, 2, 175-183.

Turner, E. R. A. (1964). Social feeding in birds. *Behaviour*, 24, 1-47.

Wahlsten, D. L. & Cole, M. (1972). Classical and avoidance training of leg flexion in the dog. In A. H. Black and W. F. Prokasy (Eds), Classical Conditioning II: Current Research and Therapy. New York: Appleton Century Crofts.

Warden, C. J. & Jackson, T. A. (1935). Imitative behaviour in the rhesus monkey. *Journal of Genetic Psychology*, 46, 103-125.

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees. *Journal of Comparative Psychology*, 112, 270-281.

Whiten, A., Custance, D. M., Gomez, J. C., Texidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimapnzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 3-14.

Williams, D. R. & Williams, H. (1969). Automaintenance in the pigeon: Sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behaviour*, 12, 511-520.

Zajonc, R. B. (1965). Social facilitation. *Science*, 149, 269-274.

Zajonc, R. B. (1969). Imitation. In R. B. Zajonc (Ed.), Animal Social Psychology, pp. 62-64. New York: Wiley.

Zentall, T. R. (1988). Experimentally manipulated imitative behaviour in rats and pigeons. In T. R. Zentall and B. G. Galef (Eds), Social Learning: Psychological and Biological Perspectives, pp. 191-206. Hillsdale, NJ: Erlbaum.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In C. M. Heyes and B. G. Galef (Eds), Social Learning In Animals: The Roots of Culture, pp. 221-243, New York: Academic Press.

Zentall, T. R. & Hogan, D. E. (1976). Imitation and social facilitation in the pigeon. *Animal*

Learning and Behaviour, 4, 427-430.

Zentall, T. R. & Levine, J. M. (1972). Observational learning and social facilitation in the rat. *Science*, 178, 1220-1221.

Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, 7, 343-346.