

**Imitation and Social Learning in the
Budgerigar**
(Melopsittacus undulatus)

Charlotte Louise Elizabeth Richards
University College London

Thesis submitted for the degree of Doctor of Philosophy
September 2003.

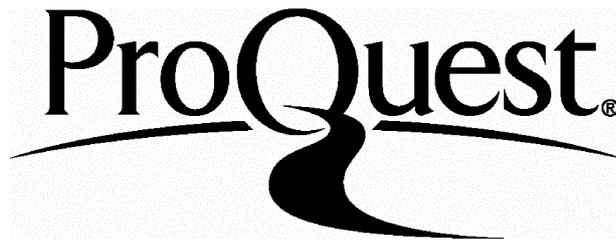
ProQuest Number: U644176

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest U644176

Published by ProQuest LLC(2016). Copyright of the Dissertation is held by the Author.

All rights reserved.

This work is protected against unauthorized copying under Title 17, United States Code.
Microform Edition © ProQuest LLC.

ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

Acknowledgements

First and foremost I would like to thank my supervisor Dr Cecilia Heyes without whom there would never have been a thesis. She has provided constant support and advice and I wish her the best of luck with future imitation work. I am also indebted to my parents, who accepted my desire to pursue a PhD, and were fully supportive throughout.

I would also like to thank my boyfriend, Chris Anker. I suspect I have not been the easiest person to live with for the last year, and without him my thesis would certainly be lacking in both commas and figures. Along with my boyfriend, I would like to thank my many friends who have forgiven me for my disappearance during my experiments and then later during my write up. I am looking forward to making it up to them.

Throughout my PhD, Roger Bunce provided technical assistance and helped greatly with both the design and construction of the apparatus used. Brian Bye made working in the animal laboratory a pleasure, while Allun Stewart was invaluable with his expert knowledge of bird health and husbandry.

Finally I would like to thank Christine Nicol and everyone I met during a six month visit to Bristol Veterinary College. The experience was extremely useful in broadening my knowledge of animal behaviour research as well as being thoroughly enjoyable.

The experiments reported in this thesis were supported by BBSRC research grant.

Abstract

Imitation is a form of social learning in which animals learn responses through conspecific observation. It is considered to be unique as in order to imitate, animals must somehow translate visual information about the body movements of others into matching motor outputs. The psychological mechanism of imitation is not currently known although both complex and simple mechanisms have been proposed. The experiments reported in this thesis sought to obtain evidence of imitative abilities in a species of bird, the budgerigar (*Melopsittacus undulatus*).

Eight experiments were run in total; two utilising a bidirectional control design, and six based on a two-action stopper paradigm. The pole bidirectional control procedures (Experiments 2.1 and 2.2) used a pole manipulandum. No evidence of social learning was obtained in these experiments, as bird responding was affected by cues external to the apparatus, suggesting that this paradigm was not ideal for investigating imitation.

Experiments 3.1- 4.3 used a two-action paradigm in which observers saw a virtual demonstrator remove a stopper from a food box using either its feet (group Foot) or its beak (group Beak). In Experiment 3.1, birds in group Beak made proportionally more beak removals on test than birds in group Foot. However, social facilitation plus stimulus enhancement were potential explanations. Experiments 3.2 and 3.3 addressed the problem social facilitation using a conditional discrimination paradigm but results were not convincing.

The final experiments (4.1- 4.3) introduced a delay between observation and testing in order to prevent social facilitation. Experiment 4.3 provided evidence of effector learning in the Beak, but not the Foot group. Imitation and higher order conditioning are both potential explanations for these results. The experiments with budgerigars therefore highlighted two additional factors, which require exclusion from imitation experiments. Although no conclusive evidence of imitation was obtained effector learning was seen using a virtual demonstrator and after a 24hour delay, suggesting that the two-action stopper paradigm has the potential to isolate imitative abilities in budgerigars.

List of Figures

- Figure 1: Diagram of the pole bidirectional control procedure used in Experiments 2.1 and 2.2 showing a) a left pushing demonstrator during observation, b) the position of OP observers on test, and c) the position of DP observers on test. 54
- Figure 2: Diagram of test apparatus used in Experiments 2.1 and 2.2, showing a) overhead view, and b) side view. 56
- Figure 3: Mean directional discrimination ratios ($X/X+Y$) and standard errors of the means for groups OP and DP on Tests 1, 2, and 3 of Experiment 2.1. 64
- Figure 4: Mean directional discrimination ratios ($X/X+Y$) and standard errors of the means for all responses made by birds in groups LOP, LDP, ROP and RDP in Experiment 2.2. 74
- Figure 5: Mean directional discrimination ratio ($X/X+Y$) and standard errors of the means for all responses made in replication 1, 2, 3, and 4 in Experiment 2.2. 75
- Figure 6: Mean directional discrimination ratio ($X/X+Y$) and standard errors of the means for replications 1, 2, 3, and 4, on Test 1 and Test 2 in Experiment 2.2. 76

Figure 7: Diagram of the basic apparatus used in Experiments 3.1-4.3, showing a) Side view, and b) Overhead view.	90
Figure 8: Mean effector discrimination ratio (beak/total) and standard errors of the means across the three tests administered for birds in groups Beak, Foot and Control in Experiment 3.1.	98
Figure 9: Mean number of beak and foot responses and standard errors of the means made across all three tests administered in groups Beak, Foot and Control in Experiment 3.1.	99
Figure 10: Total number of pecks made to the lid of the test box during observation (and standard errors of the means) by birds in groups Beak, Foot and Control in Experiment 3.1.	103
Figure 11: Mean peck discrimination ratio (pecks to stopper/total) and standard errors of the means during test trials for birds in groups Beak, Foot, and Control in Experiment 3.1.	104
Figure 12: Mean effector discrimination ratio (beak/total) and standard errors of the means for responses made to the left and right stoppers by birds in groups RBLF and LBRF in Experiment 3.2.	111

Figure 13: Mean correct discrimination ratio (correct/total) and standard errors of the means for responses made to the Black and White stoppers in Blocks 1 and 2, by birds in group Same and group Different in Experiment 3.3.	119
Figure 14: Mean effector discrimination ratio (beak/total) and standard errors of the means for responses to the Black and White stopper in Block 1 and 2, for birds in group Same and group Different in Experiment 3.3.	120
Figure 15: Mean effector discrimination ratio (beak/total) and standard errors of the means for groups Beak and Foot in Experiment 4.1.	136
Figure 16: Mean number of beak and foot responses and standard errors of the means made across all three tests administered in groups Beak and Foot in Experiment 4.1.	137
Figure 17: Mean number of responses and standard errors of the means made in all three tests administered by groups Beak, Foot, and Control in Experiment 4.2.	142
Figure 18: Mean effector discrimination ratio (beak/total) and standard errors of the means across the three tests administered for birds in groups Beak, Foot and Control in Experiment 4.2.	143

Figure 19: Mean number of responses and standard errors of the means made in all three tests administered by groups Beak, Foot, and Control in Experiment 4.3. 150

Figure 20: Mean effector discrimination ratio (beak/total) and standard errors of the means in each of Test 1, 2, and 3 for birds in groups Beak, Foot and Control in Experiment 3.3. 151

List of Tables

Table 1: Summary of the directional discrimination ratios expected from each group in Experiment 2.2 as a result of each possible observer strategy.	67
Table 2: Mean rate of responding (responses/minute) and standard errors of the means for demonstrators and observers in each group in Experiment 2.2.	72
Table 3: Mean rate of responding (responses/minute) and standard errors of the means for observers in each of the four replications.	73

Table of Contents

Chapter 1. Introduction: Imitative and Non-Imitative Social Learning in Animals	12
1.1 Categories	14
1.1.1 Social Influence	14
1.1.2 Social Learning: Non-Imitative	17
1.1.3 Social Learning: Imitative	20
1.2 Psychology Mechanisms for Imitation	21
1.2.1 Complex Mechanisms	21
1.2.2 Simpler Mechanisms	26
1.2.3 Summary and Conclusions of Mechanisms	29
1.3 Evidence of Imitation in Animals	31
1.3.1 Observational Evidence	31
1.3.2 Experimental Evidence	34
1.3.3 Summary and Conclusions	43
1.4 Two-Action Tests with Budgerigars	44
Chapter 2. Imitative Learning in the Budgerigar using the Bidirectional Control Procedure	46
Experiment 2.1	53
Experiment 2.2	66
2.3 Summary and Conclusions	78

Chapter 3. Imitative Learning in the Budgerigar using a Two-Action Stopper Paradigm, I	81
Experiment 3.1	87
Experiment 3.2	105
Experiment 3.3	114
3.4 Summary and Conclusions	121
Chapter 4. Imitative Learning in the Budgerigar using a Two-Action Stopper Paradigm, II	126
Experiment 4.1	129
Experiment 4.2	139
Experiment 4.3	147
4.4 Summary and Conclusions	154
Chapter 5. General Discussion: The Methodological and Substantive Implications of Imitation Experiments with Budgerigars	156
5.1 Summary of Experimental Results	157
5.1.1 The Bidirectional Control Procedure	158
5.1.2 The Two-Action Stopper Paradigm	159
5.2 Methodological Implications	160
5.2.1 Suitability of Budgerigars for Social Learning Work	161
5.2.2 Experimental Design	164
5.2.3 Experimental Apparatus	168
5.2.4 Summary and Conclusion of Methodological Implications	170
5.3 Substantive Implications	171

5.3.1	Effector Matching	171
5.3.2	Potential Explanation for Effector-Matching	174
5.3.3	Summary and Conclusions of Substantive Implications	176
5.4	Imitation in Primates	177
5.4.1	Marmoset Two-Action Experiment	177
5.4.2	Do-As-I-Do Experiments	179
5.4.3	Summary and Conclusions of Primate Imitation Evidence	180
	References	182

Chapter 1

Introduction:

Imitative and non-imitative social learning in animals.

Social learning refers to instances in which the behaviour of a naïve animal, the 'observer', is modified by observation of or interaction with another animal (typically a conspecific), the 'demonstrator', or its products (Heyes, 1994). Imitation is a unique form of social learning in which animals learn 'responses, actions or patterns of behaviour' (Heyes, 1993). In contrast, in non-imitative social learning the naïve animal learns about the 'presence, location, and/or value of stimuli, objects or events in their environment' (Heyes, 1993).

Imitation has long been regarded as a special kind of social learning, unique in both its psychological complexity and potential to support cultural transmission (e.g. Thorndike, 1898; Galef, 1988; Tomasello, 2000). The requirement that is unique to imitation, and therefore the distinctive explanatory challenge for theories of imitation, is a mechanism that can translate visual information about the body movements of others into matching motor output (Heyes, 2001). This is referred to as the correspondence problem (Nehaniv & Dautenhahn, 2001). The problem is greatest when actions are perceptually opaque, yielding dissimilar sensory inputs when observed and executed. For example, observation and execution of a facial gesture will result in very different sensory inputs. In contrast if an action involved a distal limb the sensory input, in terms of what is seen, during observation will be

similar to the visual input during execution. In these cases the action is said to be perceptually transparent.

Imitation of perceptually transparent actions could be achieved through a sensory matching process in which the observer generates various actions, compares the sensory feedback from these actions with a concurrently present or memorial sensory representation of the demonstrators actions, and selects the variant for which the discrepancy is minimal (Mowrer, 1960). When the actions are perceptually opaque it is not clear how the observer could derive the information necessary to produce a behavioural match. Imitation of perceptually opaque actions is therefore the greatest challenge of any hypothesis concerning the mechanisms of imitation.

This chapter is divided into four parts. In Part 1 various categories of social effects and social learning are defined. Part 2 looks at the psychological mechanisms that have been proposed for imitative learning, covering both complex cognitive processes and simpler ones, and discusses how they can be investigated. Part 3 looks at the methodologies used to obtain evidence of imitation, and identifies both the strongest technique and the strongest evidence. Finally, Part 4 introduces two-action tests with the budgerigar, *Melopsittacus undulates*, with the aim of showing imitative abilities in this species, and developing a procedure that can be used to investigate the mechanism of imitation.

1.1. Categories

In order to investigate imitative learning in animals it is first necessary to isolate the process from a variety of types of social influence and non-imitative social learning which can also result in matching behaviour in animals. Social influence, also referred to as social enhancement, refers to instances in which the presence of another animal, or its products results in the observer producing matching behaviour either as a result of releasing established responses, or individual trial and error learning following exposure to the same stimuli (Whiten & Ham, 1992; Galef, 1988). Social learning, in contrast, occurs when the presence of another animal, or its products results in matching behaviour by directly influencing learning in the observer.

1.1.1. Social Influence

Presence effects

The mere presence of another animal may result in matching behaviour. Zajonc (1965; 1969) suggested that the simple presence of others 'energises 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.' This was termed 'social facilitation' but is placed under the heading 'presence effects' to prevent confusion with an alternative definition of social facilitation that will be discussed later.

Presence effects is a possible explanation for the results obtained in a study carried out by Cadieu, Cadieu & Lauga (1995). They found that juvenile canaries, *Serinus canaries*, fed in the presence of their father ate more seed than juvenile canaries fed in isolation. The presence of the father in this case may have 'energised' a feeding response in the offspring. It is also possible that the father reduced isolation-induced fear in the canaries which would otherwise have inhibited feeding (Clayton, 1978). Alternatively, the offspring may have been able to devote less time to vigilance, and more time to feeding in the presence of the adult. Sullivan (1984) investigated the effect of group number on feeding in woodpeckers and found that as the number of birds increased head lifting to scan for threats decreased and feeding rate increased.

Zajonc's social facilitation would therefore seem to refer to a heterogeneous collection of phenomena that is unlikely to 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.

Social Facilitation

Thorpe (1956) defined social facilitation as 'contagious behaviour' where 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 another. Examples 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 'contagion' is often used synonymously with social facilitation (Whiten & Ham, 1992; Galef, 1988; Zentall, 2001).

There has been little theorising about the mechanism of social facilitation. It tends to be assumed, not only that the behaviour pattern is instinctive, but also that the potential for its release by observation of the same pattern is also innate.

Local Enhancement

Thorpe (1963) defined local enhancement as, 'apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment'. It has been argued that to enable local enhancement to be distinguished from stimulus enhancement, a form of social learning, it should be reserved for instances in which the demonstrator or signs of the demonstrator's activity are still present (Heyes, 1994; Galef, 1988). This would mean that local enhancement was not a type of social learning but instead an example of a social influence.

One possible example of local enhancement comes from the feeding behaviour of black rats, *Rattus rattus*. In Israel these rats feed on the seeds of Jerusalem pine cones which they open using a complex spiralling technique. Aisner & Terkel (1992) found that naïve rats were unable to open pine cones even after an extensive period of trial-and-error learning. In contrast naïve 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. The presence of a demonstrator was not necessary in this example, just the results of their activity.

1.1.2. Social learning: non-imitative

Stimulus enhancement

Stimulus enhancement was used by Spence (1937) to refer to ‘ 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’. In stimulus enhancement the activity of the demonstrator draws the attention of the observer to a particular object, or part of an object (Zentall, 2001). Stimulus enhancement differs from local enhancement in that it is less specific. Observers attention is not just attracted to the specific stimuli but can be attracted to the entire class of objects sharing stimulus characteristics with an object a demonstrator manipulates, contacts, or marks (Galef, 1988; Heyes, 1994). For example Huffman (1996) carried out a longitudinal study on a population of Japanese macaques (*Macaca fuscata fuscata*), and observed that a behaviour he termed stone handling spread from one individual in 1979, to 49% of the population by 1984. The macaques did not all handle the same stone, suggesting that the original macaque drew their attention in general towards stones of a certain shape, and therefore that the behaviour spread through stimulus enhancement.

A further difference with local enhancement is that the effects of stimulus enhancement can persist when both the demonstrator and its traces are gone. For

example McQuoid & Galef (1992) allowed naïve Burmese red jungle fowl, *Gallus gallus*, to observe conspecifics 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 demonstrator.

Observational Conditioning

The term observational conditioning was first used by Cook, Mineka, Wolkenstein & Laitsch (1985). It is 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, *Macaca mulatta*, observed a conspecific behaving fearfully in the presence of real and toy snakes and non-fearfully in the presence of neutral objects. When subsequently presented with the same stimuli on test, the observer became agitated and tried to avoid the snake stimuli. If the behaviour of the demonstrators had exposed the observers to the snake – fear relationship then this would be an example of observational conditioning.

Heyes (1994) argued that the definition given above is too restrictive and that the term observational conditioning should refer to all instances where the behaviour of a demonstrator increases the likelihood that an observer will be exposed to a relationship between two stimuli, and not just those in which the demonstrator acts as the source of the second stimulus and /or the second stimulus is aversive.

Emulation

Tomasello (1990) used the term emulation to describe the results of social learning experiments carried out with chimpanzees, *Pan troglodytes*. Following Wood (1988) emulation was defined as reproducing the observed goal of an action. However, since its introduction emulation has been defined in many different ways. Custance, Whiten & Fredman (1999) and Byrne (1998) have identified four different meanings that have been used. These are: 1) goal enhancement, in which the observers tries to achieve the observed goal; 2) affordance learning, in which the observer learns about the affordances of an object; 3) object movement re-enactment, in which the observer learns how an object, or the various parts of the object move; and, 4) end state re-creation, in which the observer attempts to re-create the final state, or results.

Tomasello (1996) clarified what he meant by emulation, defining it as occurring when the learner 'observes and understands a change of state in the world produced by the manipulation of another', and this general definition will be adopted in this thesis. An example comes from an experiment run by Tomasello, Davis-Dasilva, Camak & Bard (1987). They allowed naïve chimpanzees to observe a trained demonstrator use a T bar to rake food into his cage. The performance of these observers on test was compared with chimpanzees that had observed an inactive demonstrator. Chimpanzees in both groups handled the T bar equally, but those in the experimental group were more successful in its use, although the demonstrator's actions were not matched. This suggested that the chimpanzees were learning something about how the T bar could be moved (emulation) but not about the body

movements of the demonstrator (imitation). Similar results were obtained in a further rake study (Nagell, Olguin & Tomasello, 1993b).

1.1.3. Social learning: imitative

There is no common consensus as to how imitation should be defined. Three main approaches to defining imitation are commonly used. The first is to use Thorndike's (1898) original definition, which states that imitation is learning to do an act from seeing it done (e.g. Whiten & Ham, 1992; Heyes, 1996). The second is to follow Thorpe (1963) and define imitation as, 'the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency' (e.g. Galef, 1988). Third, many authors define imitation in terms of the ascription of purposes or goals by the imitator to the actor (e.g., Tomasello, Kruger & Ratner, 1993a; Tomasello, 1996; Whiten, 1996).

If interested in the psychological mechanisms mediating imitation, the most useful definition is arguably that of Thorndike. Imitation is therefore learning to do an act from seeing it done. If the problem an animal faces is how to translate visual information about the body movements of others into matching motor output (Heyes, 2001), then it is not clear why novelty is an important criterion. Definitions ascribing goals or intentions are also unable to account for this problem (Heyes, 1998) and are difficult to test experimentally (Custance et al 1999).

It is important to note that imitation as defined above concerns copying of actions.

Vocal imitation, the copying of vocalisations, is beyond the scope of this thesis.

Although it is not clear that the two forms of imitation should be seen as distinct. Both involve an animal socially learning responses, actions or patterns of behaviour. The most important difference is that, given the perceptual transparency of vocalisations, vocal imitation does not pose the correspondence problem. The auditory inputs to an animal on hearing the vocalisations of another are very similar to the auditory inputs from production of the vocalisation by the listener. Therefore, sensory matching of outputs to the original input could account for matching vocalisations (see Janik & Slater, 2000 for a review).

1.2. Psychological mechanisms for imitation

Any mechanism proposing to account for how animals imitate should address the correspondence problem, how animals translate the sensory inputs during observation, to the sensory inputs during execution of the matching action.

Numerous mechanisms have been proposed and these can be broadly divided into two categories depending on how the animal obtained the information needed to imitate. Complex, or transformational, mechanisms claim at least some of the information comes from complex cognitive processing. While in simpler, typically associative, mechanisms the information is derived from experience.

1.2.1. Complex mechanisms

Three complex mechanisms will be considered: those postulated by Meltzoff & Moore (1977); Whiten (1996); and, Tomasello & Call (1997).

Meltzoff and Moore: Active Intermodal Mapping (AIM)

AIM was developed to account for infants' imitation of facial expressions but has been applied to imitation generally and offers a solution to the correspondence problem. It proposes that there is a dedicated, innate imitation mechanism in humans. Perceived and produced human acts are coded within a common 'supramodal' framework. This enables the imitator to compare the sensory information from motor behaviour to the representation of the visually perceived gesture and construct the match required. Imitation is considered to be a matching to target process i.e. it is goal directed.

The primary evidence in support of AIM is imitative abilities in human neonates. Meltzoff & Moore (1977) carried out an experiment with human infants between 12 and 21 days of age. In the first experiment a human demonstrator faced the infant and performed four gestures (lip protrusion, mouth opening, tongue protrusion, finger movement). The infants were filmed during the demonstration and videos were watched by naïve raters. On average they correctly identified what gesture the child had been watching from the responses it made. In a second experiment mouth opening or tongue protrusion were demonstrated. The frequency of tongue protrusions relative to mouth opening was higher when tongue protrusions were observed, and vice versa. It was argued that the young age of the subjects makes it unlikely that imitation could result from experience, making an innate mechanism more likely.

Although AIM is useful in that it attempts to solve the correspondence problem, Heyes (2001) argues that there is a poor fit between AIM and recent data on

imitation. Evidence is accumulating that neonatal facial imitation, the primary evidence in support of AIM, is limited to tongue protrusion and based on an innate releasing mechanism or a non-specific arousal process (Anisfeld, 1991; 1996; Jones, 1996). AIM is also incompatible with imitation in nonhuman animals, unless they too have an innate imitation mechanism. The goal directedness of AIM is also problematic as human adults have been shown to engage in unintentional imitation of facial expressions, gestures and mannerisms (Chartrand & Bargh, 1999; Wallbott, 1991), which is known as the 'chameleon effect'.

Whiten: Secondary representation

Whiten (1996) proposed that imitation was linked to theory of mind (the ability to recognise states of mind) and pretence (pretend play). He argued that all three cognitive abilities depended on secondary representation, the ability to mentally represent the mental representations of others. Imitation may be based on this ability in two ways. First, in order to imitate an animal may translate from the actor's perspective when performing the action, to its own perspective. Alternatively the goals of the actor may be recognised and replicated in the imitator. A specific account of how imitation occurs was not provided. It is assumed that the process of secondary representation could overcome the correspondence problem.

Whiten (1996) acknowledges that the empirical basis of this theory is tentative. The principal evidence put forward is the similarity in the distribution of theory of mind, pretence and imitation. These abilities are claimed to be present in humans and other apes, but absent in monkeys and non-primates. The requirement for secondary

representation means that this theory is incompatible with the imitative abilities in human neonates which are not sufficiently mentally developed. However, as indicated above, this evidence is questionable. Evidence of imitative abilities in non-apes is more problematic as representational abilities are typically thought to be absent. Whiten addresses this by distinguishing imitation, which has a secondary representational basis, from mimicry which does not.

Heyes (1998) argues that in order to imitate it would seem essential for the observing animal to represent what the demonstrator did but not what it thought or wanted. In order to mimic the correspondence problem still needs to be solved and this cannot be accounted for by Whiten's theory.

Tomasello: Intention reading

Tomasello & Call (1997) do not take the representational approach taken by Whiten (1996). They do, however, agree with Whiten in that they believe imitation involves an ability to perceive the goals or intentions of the actor. Without this understanding it is argued that the observer would be unable to know what aspect of the actor's behaviour was relevant. Tomasello and Call argue that only children above nine months, and human reared, enculturated, chimpanzees have the ability to read intentions and therefore imitate. Like Whiten, Tomasello and Call discounts response learning by observation in other animals as mere mimicry.

The correspondence problem is not addressed by this account and it is incompatible with the chameleon effect in human adults. Evidence put forward for the

involvement of intention reading in imitation can be questioned. For example Meltzoff (1995) presented 18 month old children with a full goal directed action on an object, or a partial demonstration in which the goal was never achieved. On test it was found that children would reproduce the goal regardless of the demonstration type, indicating that they had perceived what the demonstrator was intending to do even if he failed to achieve it. However it is possible that children were literally imitating what they saw. For example whether they saw a dumbbell pulled apart or someone trying to pull it apart, they would have seen pressure exerted on the ends of the dumbbell. If they imitated this on test they would pull the dumbbell apart regardless of whether they had seen the full demonstration.

In a second experiment Carpenter, Akhtar & Tomasello (1998) allowed children, aged 14 to 18 months, to observe adults make actions on objects. One action was marked vocally as intentional ('there!') and one action was marked vocally as accidental ('woops!'). On test children imitated twice as many intentional actions as accidental ones, suggesting a preference for reproducing intentional actions. However, children may have learned how to imitate all the actions observed but may have only reproduced those followed by 'there' due to previously learning that 'woops' was unlikely to be associated with a pleasant outcome.

Other evidence for the involvement of intention reading in imitation comes from enculturated chimpanzees. There is evidence that these chimpanzees perform better than mother-reared chimpanzees in imitation experiments (e.g. Tomasello et al 1993b). Little research has been done investigating the difference between the perspective taking skills of enculturated and non-enculturated chimpanzees, but

Tomasello et al (1993a) argue that enculturated chimpanzees do show more sophisticated skills of perspective taking based on personal observations. However enculturated capuchins, *Cebus apella*, have also been shown to out-perform mother reared capuchins in an imitation task (Fredman & Whiten, 2002), suggesting that rearing by humans gives animals an advantage, other than an ability to read intentions. For example they may have been less timid on test and therefore more likely to respond.

1.2.2. Simpler mechanisms

Two simpler mechanisms for imitation are outlined: those postulated by Heyes & Ray (2000); and, Byrne (2003). Both of these accounts of imitation require that the observers have experience viewing and performing the action to be imitated. Heyes & Ray's Associative Sequence Learning (ASL) relies on associative learning, while Byrne's response facilitation and behaviour parsing hypotheses rely on neural priming and on statistical regularities in observed behaviour, respectively.

Heyes & Ray: Associative sequence learning(ASL)

The associative sequence learning hypothesis was proposed by Heyes & Ray (2000) and, although still in a rudimentary form, does provide a testable associative learning account of imitation. It was developed specifically to tackle the correspondence problem, and therefore concentrates on how an animal can use sensory inputs from observation of an action to produce the matching action even when the action is perceptually opaque.

ASL assumes that every action is actually comprised of a sequence of action units. The extent to which an observer can imitate a novel sequence of action units is determined by two sets of associative processes, which result in 'horizontal' and 'vertical' links. Through the horizontal processes associations are formed which link the sensory representations of the action units in a sequence, allowing the observer to learn what the action sequence looks like.

Vertical processes operate before the novel sequence is observed and result in a sensory representation of each action component becoming associated with a motor representation of the same component. Direct vertical associations are formed when an action unit is contiguously observed and executed. Indirect links can also be formed when a second stimulus is consistently paired on some occasions with sensory input from observation of the action unit, and on other occasions with the performance of that unit. To the extent that such vertical links have been formed, exposure to the novel action sequence, or recollections of that sequence mediated by the horizontal processes, will activate motor representations in the order appropriate for sequence reproduction.

When ASL theory was developed the aim was to provide a theory consistent with what is already known about imitation and one that was sufficiently well specified that it could generate testable predications. As no complex cognitive ability is required it can account for imitative abilities in all animals that are capable of learning a stimulus sequence and which have had contiguous experience of observation and execution of components of the action sequence. Unlike the elaborate mechanisms it is therefore consistent with imitation in non-primate species.

ASL is also consistent with the chameleon effect because it does not suggest that imitation is mediated by an intrinsically goal directed process.

Byrne: Response facilitation and behaviour parsing

Byrne introduced response facilitation to explain the copying of all non-novel simple action patterns. Response facilitation occurs when a pre-existing response is facilitated by seeing it done, causing a higher probability of the response occurring subsequently. It is argued that observation of a behaviour, already in an animal's repertoire, primes the neural correlates of the action pattern. No explanation is given for how this priming occurs, and any behavioural matching resulting is not thought to be an example of imitation, although the animal would be solving the correspondence problem.

Imitation itself is divided into two categories, action- and program-level imitation (Byrne & Russon, 1998). In action-level imitation sequential acts are copied. ASL is invoked to account for this. In contrast, in program-level imitation complex hierarchically organised behaviours are imitated. This is explained using a purely mechanistic model called behaviour parsing. This was developed to account for the complex food processing seen in great apes, for example the nettle processing of mountain gorillas (*Gorilla beringei*) in Rwanda. Byrne argues that this elaborate food preparation may involve imitation because the overall behaviour is highly standardised within a population, with all gorillas adopting the same behaviour, despite the fact that other techniques could be employed just as successfully.

The behaviour parsing model does not require an understanding of intentions or causal logic. The observer needs to be capable of segmenting behaviour into a vocabulary of elements. The behaviour parsing model, operating on strings of these elements, is hypothesised to extract the statistical regularities that specifically correlate with organisational structure. Put more simply, during observation over an extended period of time, a pattern of elements could be detected allowing the observer to learn about the structure of the behaviour. It is important that each element of action is already in the repertoire. Statistical regularities then separate the minimal set of essential actions and their order, which are required for success. Even the hierarchical organisation can be deduced.

Behaviour parsing is an interesting theory but does not concern the central problem of imitation which is the correspondence problem. The distinction between program level and action level imitation is also not seen as a useful distinction by many as there are problems in separating the two (Whiten & Custance, 1996). Program level imitation is defined by Byrne (1994) as copying only the logical structure of a task, but, all imitation is likely to be inexact to a certain degree. The distinction between response facilitated actions and imitated actions is also not clear. If animals are solving the correspondence problem then arguably they are imitating.

1.2.3. Summary and Conclusions of Mechanisms

Five imitation mechanisms have been outlined. Meltzoff and Moore's AIM theory specifically addresses the correspondence problem proposing an innate goal directed mechanism in humans. Whiten links the ability to imitate with an ability to form

secondary representations, and in a similar account, Tomasello argues that imitation is goal directed involving reading intentions in the demonstrator. Neither Whiten nor Tomasello solve the correspondence problem. Heyes and Ray's ASL theory is an example of an associative account of imitation and claims that the ability to imitate depends on contiguous experience of observing and executing actions. Finally Byrne proposes response facilitation to account for copying simple non-novel actions and ASL for the imitation of more complex novel sequences of actions.

Only AIM and ASL specifically address the correspondence problem, explaining in some detail how visual information about the body movements of others is translated into matching motor output. AIM, however, cannot account for imitation in non-human animals, and neonatal imitation, the primary evidence supporting AIM, has been questioned. ASL theory is consistent with current evidence of imitation (Heyes, 2001). It has yet to be specifically investigated but makes testable predictions.

Imitation will be possible to the extent that the observer; 1) is capable of stimulus sequence learning, and 2) has contiguous experience of observation and execution of components of the action sequence. Training experiments in which observers are given varying degrees of experience of seeing-and-doing action components before an imitation test are likely to be the most effective means of testing ASL theory and these would be easiest to carry out with an animal species in which experience prior to testing can be known and manipulated.

1.3. Evidence of imitation in animals

The presence of imitative abilities in a range of species, not just apes, would suggest that the mechanism of imitation is more likely to have a simple associative basis than to be mediated by more complex processes. Evidence from observations of both wild and captive animals, along with evidence from purposefully designed experiments, has been used to argue that imitative abilities are present in a range of species.

1.3.1. Observational evidence

It has been argued that interpopulation differences in behaviour, the spread of behaviours within a population, and the appearance of novel behaviour can all indicate imitative abilities in a species (Whiten, 2000).

Interpopulation differences have been studied extensively in chimpanzees and primarily concern different tool use behaviours. A difference in behaviour between two groups is assumed to result from social learning only when no genetic or ecological differences exist (Boesch & Tomasello, 1998). Two population specific behaviours which arguably cannot be attributed to ecological or genetic differences are ant dipping and nut cracking.

Ant dipping behaviour in chimpanzees has been observed in four populations; Bossou, Tai, Assirik and Gombe (Boesch & Tomasello, 1998). Two different techniques of dipping have been observed. At Tai chimpanzees use sticks 30cm long which they hold with one hand and dip among soldier ant (*Dorylus nigricans*). When ants have swarmed about 10cm up the tool, they withdraw it, twist the hand holding

it and sweep off the ants with the lips. Gombe chimpanzees in contrast use a stick on average 66cm long. This is dipped in the ants and they are allowed to reach halfway up the stick before it is withdrawn. The stick is drawn through the closed fingers of the free hand resulting in a ball of insects which are then transferred to the mouth. This latter technique is the most efficient but is not used by chimps at Tai, where it is suggested their less efficient method is maintained by social learning.

Nut cracking behaviour has been observed in a population of chimpanzees in Côte d'Ivoire. This population is separated from one which has not learnt to crack nuts by a river (Boesch, Marchesi, Marchesi, Fruth & Joulian, 1994). No obvious ecological differences exist between the two populations so it is argued that the river has prevented the social transmission of the behaviour. Although imitation is the explanation invoked by some researchers, further study has suggested that nut cracking behaviour is learned through local enhancement and trial and error learning. Sumita, Kitahara-Frisch & Norikoshi (1985) observed that in the population they studied there were many idiosyncrasies in the nut cracking technique used, which would not be apparent if imitation was involved.

Although interesting, interpopulation differences in behaviour cannot provide reliable information on how the behaviour is transmitted, and therefore whether imitation is involved. Longitudinal studies are preferable in some respects because they can provide information about the development and spread of novel behaviours through a population. For example one longitudinal study focussed on the spread of potato washing in the Koshimo troop of Japanese macaques. The behaviour was first observed in 1953 when an 18 month old female (Imo) washed a sweet potato in a

stream prior to eating it. Washing was later done in the ocean and it spread through the troop so that within three years around 40% of the troop were exhibiting this behaviour (Itani & Nishimura, 1973).

Imitation was initially proposed as an explanation for the spread of the potato washing behaviour but further work has provided evidence that imitation it is not necessary. When the rate of transmission was studied it was found to be relatively slow, while imitation would be expected to provide a rapid rate (Galef, 1990). Second, food washing behaviour appeared in other troops, suggesting it is easily learned without social learning (Kawai, 1965). The role of individual learning was confirmed by Visalberghi & Fragaszy (1990). They provided other species of captive monkeys with sandy food and a water bowl and found that they rapidly learnt washing behaviour. Evidence of imitation from longitudinal studies is therefore questionable as despite extensive observation it is not possible to know, without further investigation, exactly how the behaviour is transmitted.

Evidence of imitative abilities in animals also comes from anecdotal reports of 'incongruent' behaviours, i.e. ones not expected within a species. The most thorough evidence comes from Russon & Galdikas (1993, 1995) who carried out an observational study on rehabilitated free-ranging orangutans (*Pongo pygmaeus*) at Camp Leakey. Three-hundred and fifty-four incidents of matching behaviour were recorded. Fifty-four were believed to be examples of imitation, as they were novel complex behaviours. For example orangutans were observed weeding, painting and fire making after observing humans perform these actions.

There are many anecdotal reports of imitation in parrots. Parrots are often claimed to be great mimics (Moore, 1992). For example, Thorpe (1963) described an African grey parrot (*Psittacus erithacus*) which seemed to imitate the action of a man taking off and putting on his coat. Similarly galahs (*Cacatua roseicapilla*) have been reported to acquire the flight styles of congeneric foster parents (Rowley & Chapman, 1986). There are also anecdotal reports of imitative abilities in dolphins. For example a captive dolphin (*Tursiops aduncus*) cleaned the window in its pool using similar strokes to that used regularly by a diver (Taylor & Saayman, 1973).

However appealing, anecdotes cannot provide conclusive evidence of imitation. As with interpopulation differences, and even longitudinal studies, it is not possible to know how the behaviour is transmitted (Tomasello, 1990; Whiten & Ham, 1992). Various forms of non-imitative social learning and social influence can all result in matching behaviour therefore it can be argued that in all cases of observational evidence the behaviour could be explained by some means other than imitation (Heyes, 1998).

1.3.2. Experimental evidence

Experimentation is a much more powerful tool in the isolation of imitation than observation (e.g. Whiten, 2000; Tomasello & Call, 1997; Visalberghi & Fragaszey, 1990). Experiments provide a more controlled way to investigate imitative abilities and from early experiments through to modern two-action tests they have become increasingly more rigorous and sophisticated in order to exclude social influence and non-imitative social learning.

Early experiments

Thorndike (1911) provided an experimental design to investigate imitation known as the non-exposed control procedure. In this type of procedure the rate at which two groups acquire a task, such as lever pressing, is compared. Animals in one group are allowed to observe a trained demonstrator perform the task prior to testing. The other, 'non-exposed', group is tested without first observing a demonstrator. Typically, the task is acquired more rapidly by observers of demonstrator action than by control animals (e.g. Oldfield-Box, 1970; Gardner & Engel, 1971), and this was taken as evidence of imitation. However social influence in the form of local enhancement could also account for the group difference. When the demonstrator contacted the manipulandum he may have drawn the attention of the observer to it. On test the observer may have been more likely to go to the lever and contact it, resulting in more rapid response learning than animals in the non-exposed group, without the action of the demonstrator being imitated.

Warden & Jackson (1935) developed the duplicate cage procedure to overcome the problem of local enhancement. It is based on a similar design to the non-exposed procedure except that observers are given their own manipulandum in a separate cage. Local enhancement would draw the attention of the observers to the demonstrators manipulandum, not their own. However stimulus enhancement of the manipulandum could result in the observer's manipulandum, as well as the demonstrator's, being an attractive stimulus, again resulting in more rapid learning.

The two-action design

The bulk of early experiments did not include the procedures necessary to separate imitation from simpler forms of learning (Whiten, 2000; Tomasello & Call, 1997; Visalberghi & Fragaszy, 1990). An advance in experimental design allowing better elucidation of imitative abilities resulted from an experiment carried out by Dawson & Foss (1965) with budgerigars. On test, the birds in this experiment had to remove a piece of card from the top of a food bowl in order to feed. Observers were allowed to watch trained demonstrators remove the card, either by edging it off with their beak, lifting it off with their beak or dislodging the card with their feet. On all eight test trials administered observers used the same technique as their demonstrator. All demonstrators contacted the lid, and therefore stimulus enhancement cannot explain this result.

The advantage of this design is that performance, in terms of removal technique, of birds observing one action were compared with performance of birds seeing another action. As all observers saw a demonstrator contact the card, stimulus enhancement, along with mere presence effects, were equivalent for each group. If, as Dawson and Foss (1965) found, birds used the technique they had observed when they were tested the only explanation could be imitation. This design adopted became known as the two-action procedure. In the field of human research a similar design was developed by Meltzoff & Moore (1977), which they referred to as the cross-target procedure.

The two-action procedure has since been adapted to investigate imitative abilities in a variety of species. For example a series of two-action tests based on an “artificial fruit” have been carried out with primates. Whiten, Custance, Gomez, Teixidor & Bard (1996) carried out the first experiment with chimpanzees and children aged two to four years of age. The artificial fruit consisted of a clear box containing a reward. Access was gained by removing two latches. The bolt latch consisted of two rods which passed through a brass ring on the lid and one on the box. These could be poked out, or twisted out. The barrel latch consisted of a pin and a handle, the lip of which prevented the lid from being raised. The pin fixed the handle in place and had to be removed first. It could be turned or spun out, before the handle could be either turned or pulled out. Observers were divided into two groups, and only observed one of the alternative techniques on each of the three components. On test, children reliably copied the bolt technique and the handle technique but less fidelity was shown with the pin. For the chimpanzees, independent observers were able to determine what was observed for the bolt latch and subjects showed a greater proportion of twists if they had observed twisting. Human children therefore outperformed chimpanzees in the artificial fruit task, but the bolt latch provided some evidence of imitative abilities in the chimpanzees.

In a similar experiment Custance et al (1999) obtained similar results with capuchin monkeys, *Cebus apella*. Stoinski, Wrate, Ure & Whiten (2001) found that captive western lowland gorillas (*Gorilla gorilla gorilla*) would copy the pin removal technique and the direction of bolt removal but not the action used. These artificial fruit experiments therefore go some way to provide evidence of imitative abilities in various primates. However, although stimulus enhancement and social effects are

excluded, it is possible that emulation as opposed to imitation was occurring. The movement of the latches depended on the removal technique used. If chimpanzees could learn how the latch was moving through emulation, in trying to achieve this movement they may have matched the original actions used. This may be unlikely, at least for copying involving the bolt latch, because the demonstrator's hand obscured the latch from view (Custance, 1998), however further experimentation is needed before the emulation explanation can be rejected.

A two-action experiment with marmosets, *Callithrix jacchus*, provides more conclusive evidence of imitative abilities. Voelkl & Huber (2000) allowed observers to watch a demonstrator remove the lid of a film canister to obtain a food reward using either its mouth or its hand. On test, observers that had seen the hand technique only used their hands, while observers of the mouth-opening technique used their mouths as well. One possible explanation for this was that mouth-opening demonstrators left scent deposits on the canisters which made their observers more likely to use their mouths. The role of scent was tested by giving a non-exposed control group mouth-opened canisters. Marmosets in this group preferentially used their hands, suggesting that scent cues had no effect on removal technique used. As the canister lids moved in the same way following hand and mouth removals, emulation cannot explain the results, which suggests that imitation was occurring.

A logical extension of the two-action test are the do-as-I-do experiments which have been carried out with chimpanzees and orangutans. In a replication of Hayes and Hayes's (1952), Custance, Whiten & Bard (1995) carried out a do-as-I-do experiment using two human reared chimpanzees. The chimpanzees were trained to

imitate 15 gestures and were then tested on 48 novel gestures. Independent observers correctly identified a significant number of the chimpanzees imitations (13 responses for one animal and 17 for another). Do-as-I-do experiments have also been run with an enculturated orangutan, Chantek. Miles, Mitchell & Harper (1996) took data from training sessions with Chantek over a period of 2 years in which Do-as-I-do tests were run. Chantek was argued to have produced full imitations on 56.2% of responses. Call (2001) used Chantek in a more controlled do-as-I-do experiment based on Custance et al (1995). Chantek was asked to imitate 48 actions and 58.3% of the time he made a full reproduction. These experiments provide good evidence of imitative abilities in these species. As no objects were used it is not possible that non-imitative social learning could account for the matching behaviour.

Following Dawson & Foss (1965), two-action experiments have also been run with various species of bird. The original two-action test with budgerigars provided some evidence of imitative abilities in a species of bird. However, this was undermined by difficulty in replicating the effects. Galef, Manzig & Field (1986) attempted to replicate Dawson and Foss's experiment with budgerigars, but an initial attempt was unsuccessful. A second attempt did confirm the results of the earlier experiment but the effect was of brief duration (birds used the same appendage as their demonstrator to remove their cover only on the first two test trials) and marginal significance. Given the difficulty in obtaining the results the authors concluded the design was not ideal for investigating imitative abilities. In addition, the lid followed different trajectories depending on the action used to remove it, which meant emulation was not excluded.

Campbell, Heyes & Goldsmith (1999) ran a two-object/two-action test with European starlings, *Sturnus vulgaris*, to investigate simultaneously imitative and non-imitative social learning. Birds were allowed to observe a trained demonstrator remove a red or black stopper from a hole in the lid of a plastic box. These stoppers could either be removed by pulling up on a piece of string, or by pushing down on the stopper. On test, observer birds removed the same stopper in the same direction as their demonstrator and the effect persisted across all three test sessions administered. This experimental design was adapted for use with budgerigars, and both Heyes & Saggerson (2002) and Mottley & Heyes (in press) found that on test observers would remove the stopper in the same direction as they observed. These experiments do not, however, provide conclusive evidence of imitation however because demonstrators of up and down actions contacted different parts of the stopper and moved the stopper in different directions. Therefore, stimulus enhancement of parts of the stopper, or emulation of stopper movement could account for the results obtained.

Although two-action procedures have the potential to exclude non-imitative social learning, emulation appears to be particularly difficult to overcome. It was specifically addressed in a series of experiments with quail, *Coturnix japonica*, and pigeons, *Columbia livea* (Akins & Zentall, 1996; Zentall, Sutton & Sherburne, 1996). A treadle manipulandum was used which could be pecked or stepped on by birds to obtain a food reward. It was designed so that it moved in the same way for both responses, thereby preventing emulation. On test it was found that both pigeon and quail observers responded using the same action as they observed, i.e. birds which observed a pecking demonstrator made proportionally more pecking

responses on test than birds which had observed a stepping demonstrator. This was taken as evidence that quail and pigeons were capable of imitation. However, while these experiments provide good evidence that observation of pecking promotes pecking, closer examination of the data suggests evidence for a similar effect of stepping is not strong. As pecking forms part of a bird's innate behavioural repertoire it is possible that the sight of a pecking demonstrator released pecking in the observers through social facilitation. This, as opposed to imitation, could explain the elevated pecking on test shown by observers of pecking demonstrators.

In a similar approach to the do-as-I-do studies with primates Moore (1992) studied imitation in a grey parrot, *Psittacus erithacus*. Over a five year period, the bird's room was entered for 3-10 minutes several times daily, during which time the experimenter performed repeatedly a small number of actions, each of which was accompanied by a word or phrase. The parrot's behaviour was observed via a video camera linked to a monitor. The monitor was left on for approximately 60 hours a week but only two sampling sessions were done in this time, and these were initiated by vocalisations of the parrot. The bird was found to copy movement and vocalisations. For example it would say 'Ciao' and wave using its feet. Responses imitated included at least 14 distinct reactions of 6 different parts of the body. Although these results suggest the parrot was capable of imitation this conclusion is undermined by the informal sampling method used. It is not possible to know the base rate of either vocalisations or bird movements and so their co-occurrence during sampling may have resulted from chance. This experiment therefore needs replication with a more rigorous sampling method before it can be concluded that the parrot was carrying out imitation.

The bidirectional control procedure is a variation of the two-action test. In this design an observer faces a demonstrator and watches as he moves a manipulandum to his left or his right. On test the direction of observer responding is examined. Heyes & Dawson (1990) carried out a bi-directional control procedure using rats, *Rattus norvegicus*. Naive rats observed a demonstrator push a joystick to either its left or its right. On test observers pushed the joystick in the same direction, relative to their own bodies, as had their demonstrators. It was possible that observers were carrying out emulation, learning the direction to move the joystick with respect to cues inside the test cage. However the same directional matching was obtained when the joystick was moved between observation and testing. Emulation cannot account for this, as the location of cues on test following joystick movement was different to their location during observation (Heyes, Dawson & Nokes, 1992). Unfortunately there is evidence suggesting that observers may have been using scent cues deposited by the demonstrators (Mitchell, Heyes, Gardner & Dawson, 1999).

The bidirectional control procedure has been adapted for use with quail. Akins, Klein & Zentall (2002) allowed observers to watch trained demonstrators slide a screen to the left or the right to obtain a food reward. On test observers made proportionally more slides in the direction they had observed the screen slide with respect to the demonstrators body. Emulation was not however excluded as the position of cues which could be used to code movement remained constant between observation and test sessions. A control group, who observed the screen moved automatically, did fail to learn direction of sliding, which suggested that they were unable to learn the direction of movement through emulation alone. However the control group was not

exposed to a bird interacting with the screen and therefore lack of learning in this group may result from the absence of stimulus enhancement.

1.3.3. Summary and conclusions regarding evidence

The development of the two-action procedure has enabled researchers to concentrate research on imitative abilities in a variety of species. Observational data, although interesting, cannot provide conclusive information regarding how behaviour is transmitted and the majority of examples could be explained by non-imitative social learning. However, given the difficulty in isolating imitation even in two-action procedures, it is clear that only very carefully designed experiments can be used to isolate imitation. Only when imitation has been successfully isolated can the mechanisms behind it be investigated.

There is much controversy over the results of two-action experiments with different reviews interpreting results in different ways (Caldwell & Whiten, 2002). If emulation is considered to be a serious alternative to imitation in experiments in which manipulandum movement is confounded with demonstrator action, then evidence for imitation in primates currently comes from do-as-I-do experiments with chimpanzees and orangutans (Custance et al 1995; Miles et al 1996; Call, 2001) and the two-action experiment with marmosets (Voelkl & Huber, 2000). Most experiments with birds can be explained by emulation (Dawson & Foss, 1965, budgerigars; Campbell et al, 1999, starlings; Heyes & Saggerson, 2002, budgerigars). While the treadle experiments with pigeons and quail may be explained by social facilitation, a form of social influence (Akins & Zentall, 1996;

Zentall et al, 1996). An indication of bird imitative abilities comes from the do-as-I-do style experiment carried out with an African grey parrot (Moore, 1992).

1.4. Two-action tests with budgerigars

Two-action experiments have indicated that birds are capable of imitation but the evidence is not conclusive. The experiments reported in this thesis are a series of two-action tests designed to obtain more conclusive evidence of imitative abilities in birds. If birds are capable of solving the correspondence problem and translating visual inputs during observation into motor outputs during execution then it would suggest that the mechanism of imitation is relatively simple. Birds are unlikely to be capable of the complex cognitive processing that transformational theories postulate. A two-action test providing evidence of imitation in birds would also provide a paradigm which could be used to test the predictions of ASL theory against those of alternative theories. For example, manipulating past experience would be easier in birds than primates, because with primates the training phase would have to be long and/or intensive enough to prevent masking of its effect by prior experience of a similar kind.

Budgerigars were chosen as a model species for a variety of reasons. First as outlined in section 1.3, two-action tests with this species have indicated the potential for imitation (Dawson & Foss, 1965; Galef et al 1986; Heyes & Saggerson, 2002; Mottley & Heyes, in press). Second budgerigars are a social species, in the wild they live in large flocks in central Australia (Masure & Allee, 1934; Wyndham, 1980). There is some evidence that social species will be more likely to learn socially than

asocial species (e.g. Templeton, Kamil, & Balda, 1999). Third they are widely available from commercial suppliers and can be easily bred in captivity. Four there is a substantial literature relating to budgerigar neurobiology (e.g. Jarvis & Mello, 2000), which would be important for investigations into the neural basis of imitation. Fifth budgerigars could be used in the future to investigate the link between vocal and motor imitation as they acquire their calls through vocal imitation (Farabaugh, Linsenbold, & Dooling, 1994; Hile, Plummer, & Streidter, 2000; Hile & Streidter, 2001).

The two-action procedure forms the basis of the experiments reported in this thesis. In Chapter 2, a bidirectional control procedure was used with budgerigars in an attempt to obtain evidence of imitative abilities in this species. Chapters 3 and 4 report a series of two-action experiments in which the alternative actions were removing a stopper from a test box using either the feet or the beak. Finally Chapter 5 discusses the significance of the results reported in Chapters 2-4.

Chapter 2

Imitative learning in the budgerigar using the Bidirectional control procedure.

The experiments reported in this chapter attempted to obtain evidence of imitative abilities in an avian species, the budgerigar, using a novel bidirectional control procedure. In this procedure a naïve observer faces a demonstrator as the demonstrator moves a manipulandum in one of two directions with respect to his body. On test the direction of observers' responses, as opposed to the topography of the action are examined. Evidence of imitation would be the observer responding in the same direction as the demonstrator with respect to the actor's body, or with respect to their own body.

Because direction of responding is the dependent variable, the bidirectional control procedure investigates imitation in a slightly different way than the two-action test. Matching the direction in which an action is performed makes similar demands as behaviour matching at the level of either appendages or muscles (Heyes, 1996). In both cases, animals need to solve the correspondence problem i.e. to match what they see a demonstrator doing during observation with what they themselves do on test. The directional nature of actions in bidirectional control procedures also enables this test to investigate how demonstrator actions are encoded by the observer, in particular whether they are coded relative to the actor or relative to the observer.

Like other two-action tests, the bidirectional procedure controls for presence effects and non-imitative forms of social learning. Demonstrators of variant actions contact

the manipulandum in the same place therefore there can be no group difference due to stimulus enhancement. An advantage of the bidirectional control procedure, relative to other two-action tests, is that it focuses on one action which is performed in two directions. There is generally an equal likelihood of occurrence of the two directions at baseline (Boysen & Himes, 1999) resulting in response symmetry typically not present when the two responses require manipulation with different parts of the body (Akins et al, 2002).

The bidirectional control procedure was developed in experiments using rats. In an initial experiment naïve observer rats faced a trained demonstrator and watched as it pushed an overhead joystick 50 times to either its left or its right in order to obtain a food reward. The observers were then allowed access to the joystick in the demonstration compartment and allowed to make 50 responses. They were rewarded for all joystick movements but showed a reliable tendency to push the joystick in the same direction as their demonstrators. Observers of left pushing animals pushed left, while observers of right pushing demonstrators pushed right (Heyes & Dawson, 1990).

The bidirectional control procedure has also been used to investigate imitative abilities in Japanese quail. Akins et al (2002) constructed a metal screen which could be moved to the left or right to allow access to a feeder located below. Observers watched a trained demonstrator slide the screen for a food reward, or the screen move automatically and a bird eat the resulting reward. Forty-eight screen slides were observed after which the observers were placed in the demonstration compartment and allowed access to the screen for a period of 20 minutes. On test,

eight out of the ten birds, which observed a demonstrator moved the screen in the same direction as the actor had with respect to its body. When compared with birds which had seen the screen move automatically, the ghost control, the proportion of responses made in the same direction, with respect to the apparatus, was greater.

The results from the rat and quail experiments were interpreted as evidence of imitation, however, but the results can be explained by non-imitative social learning. In both experiments the left and right pushing demonstrators moved the manipulandum towards opposite side walls of the test cage. It is therefore possible that observers acquired information about the movement of the joystick with respect to cues within the cage, which would be an example of emulation (Tomasello, 1996). Alternatively, the observers may have learned the relationship between the movement of the joystick in space and the delivery of food, which would be an example of observational conditioning.

The role of emulation and observational conditioning in the rat bidirectional control experiment was addressed in a specially designed transfer experiment (Heyes et al, 1992). For half the observers, the procedure was the same as in the experiment outlined above. For the other half, the joystick was moved to the centre of a side wall prior to testing. This altered the position of cues, which observers could have been using to code joystick movement, with respect to the joystick. On test, observers showed a bias towards responding in the same direction relative to the actor's body as their demonstrator, irrespective of joystick position. Given that spatial cues were not in the same position for both groups this result cannot be explained by either emulation or observational conditioning.

In the quail experiment (Akins et al, 2002) emulation was addressed by the control group, which observed the screen move automatically. On test, observers in this group did not show the same directional bias as birds in the experimental groups, either when first responses were examined, or when the overall proportion of responses in each direction were examined. This was taken as evidence that the quail were not capable of learning through emulation and, that as a consequence, birds which observed the demonstrator move the screen were learning direction through imitation. However, in the control group there was no stimulus enhancement of the screen by a conspecific. Therefore the attention of observers in this group may not have been drawn to the screen, which would make them less likely to learn by emulation about its movement.

The transfer test administered to the rats provides a much stronger technique of investigating emulation in bidirectional control procedures than using ghost control groups which do not allow for stimulus enhancement of the manipulandum. However, despite the sophistication of the transfer test, the evidence for imitation in rats is questionable. Further experiments revealed that, when the joystick was rotated 180° in its fixture between observation and testing, observers would push the joystick in the opposite direction to that which had been observed (Mitchell et al, 1999). This suggested that observers were responding to scent cues deposited by the demonstrator rats, rather than learning through imitation.

The reliance that rats naturally place on the use of olfactory cues made them unsatisfactory animals for research on imitation. Avian species in comparison are

highly visual and believed to be less reliant on olfactory cues, making them more suitable subjects (Mitchell et al, 1999). The experiment carried out by Akins et al (2002) indicated that birds are amenable to bidirectional control procedures. However, this study of quail unfortunately did not successfully exclude emulation and observational conditioning as potential explanations for the results obtained. The two experiments reported in this chapter use a species of bird, the budgerigar, in a bidirectional control procedure specifically designed to address the problems of emulation and observational conditioning. It was hoped that by improving the design of the bidirectional control procedure more conclusive evidence of imitative learning in birds could be obtained.

The bidirectional control procedure used in the present experiments was based on a pole manipulandum. This consisted of a length of cane suspended horizontally across a test cage. During observation a demonstrator stood behind this pole, faced by the observer bird, and pushed the pole to the left or right with respect to his body for a centrally delivered food reward. To make emulation more difficult for the observers the ends of the pole manipulandum were screened using card. This ensured that the appearance of the pole was fairly constant before, during, and after manipulation. The screen also prevented birds from seeing anything outside the test cage and therefore helped prevent the use of room cues (i.e. stimuli in the environment external to the test cage which the birds could use to code direction of movement). Cage cues (stimuli in the environment internal to the cage) were controlled to some degree by keeping the test cage symmetrical.

In addition to attempting to prevent the use of cage and room cues, the experiment was designed to detect their use if it occurred. Observers were tested in two groups. One group remained in the observation position and the pole was moved to their compartment (group OP), birds in the other group were moved to the demonstration position (group DP). Between observation and test the position of cage and room cues remained constant for birds in group OP, and was reversed for birds in group DP. By examining direction of pole pushing with respect to the cage side the demonstrator pushed towards it would be possible to determine if birds were using either cage, or room cues. A further within subjects test for room cues was used. The test cage was rotated 180° between test sessions, reversing the position of room cues across tests. Use of room cues could therefore be detected in a reversal of pole pushing direction across tests.

The bidirectional design adopted also sought to determine the type of imitation, if any, which occurred on test. Previous work with rats and quail sought evidence of transpositional imitation, which is when the observer responds in the same direction relative to the actor's body as the demonstrator. For example, if the demonstrator moved the manipulandum to his left, the observer would also move it to the left of his, the observer's, midline. However, in situations where an observer and a demonstrator are facing one another during observation and testing, another kind of demonstrator-consistent directional bias may be observed. The observer may direct its responses to the same place as those of the demonstrator. This would indicate that the observer had coded the demonstrator's responses relative to cage cues, or relative to the observer's body. In the latter case it would be described as 'mirror imitation'.

Based on the results of human studies it can be argued that mirror imitation may be more likely than transpositional imitation in rats and birds. For example Wapner & Cirillo (1968) carried out an experiment with children aged 8 to 18 years. The children faced and imitated a person who would touch a body part, or object, on his left or right side, with his left or right hand. When asked to copy, results from younger children indicated that they were coding the movements with respect to their own body, carrying out mirror imitation. When the demonstrator touched an object on his left, the child would touch an object on his own right side. In contrast, older children responded in the same direction, relative to the actor's body, as the demonstrator, carrying out transpositional imitation. If a demonstrator touched an object to his left, the children would touch an object to their left. In a similar experiment Bekkering, Wohlshlager & Gattis (2000) instructed 4 to 6 year olds to imitate and observed that they all carried out mirror imitation.

The evidence from these experiments indicates that, at least humans, mirror imitation abilities develop before transpositional abilities suggesting that mirror imitation is less cognitively demanding. In mirror imitation direction of movement is coded with respect to the observer's own body. An ability to carry out transpositional imitation would mean that, at minimum, the observers use the demonstrator's body, perhaps its vertical body axis, as a point of reference defining direction of manipulandum movement and then identifying their own body as being at that reference point on test (Heyes, 1996). Given this potential complexity one would expect species such as budgerigars to carry out mirror, rather than transpositional imitation.

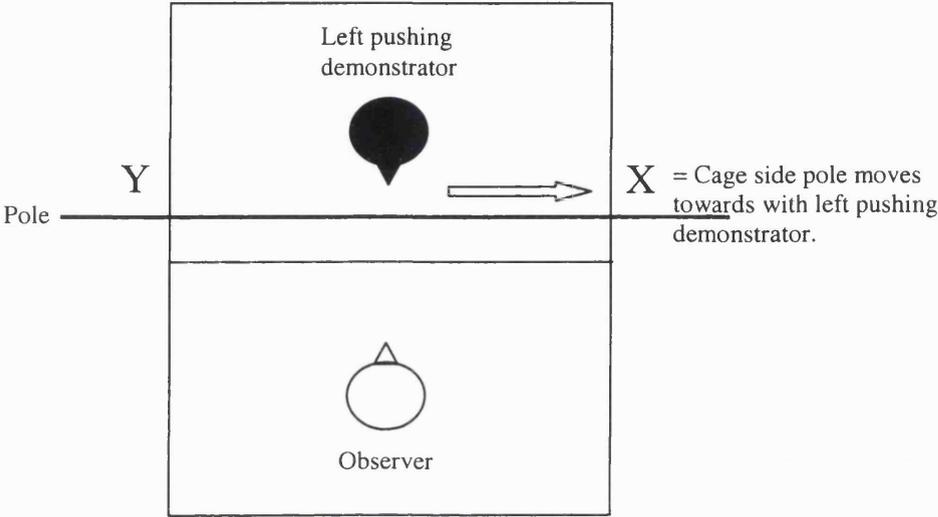
The OP and DP test conditions allowed mirror and transpositional imitation to be isolated in addition to the use of cage and room cues. Direction of observer pole pushing was coded with respect to the cage sides. The side towards which the left pushing demonstrator pushed the manipulandum was coded as X while the side towards which a right pushing demonstrator pushed the manipulandum was coded as Y (see Figure 1). Taking the observers of a left pushing demonstrator as an example, if the observers were learning to push towards a room or cage cue they would all push towards X. If the observers were mirroring their demonstrators, those in the OP condition would push towards X, but birds in the DP condition would be pushing away from X, towards Y. If, on the other hand, observers engaged in transpositional imitation, those in the DP condition would push towards X while those in the OP condition would be pushing towards Y.

Experiment 2.1

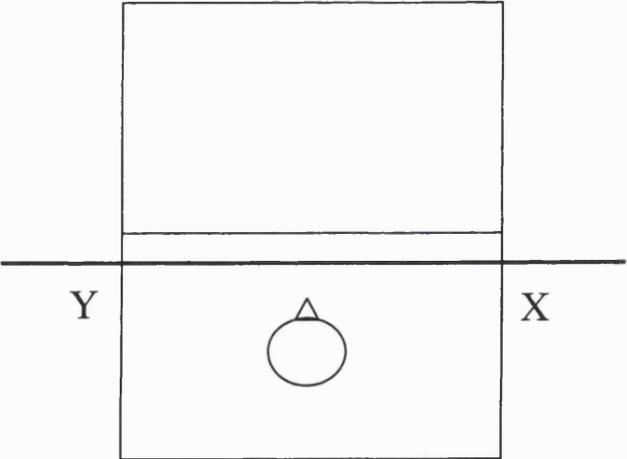
Experiment 2.1 was a small pilot study designed to assess the feasibility of using the bidirectional control procedure with budgerigars. The direction of demonstrator responding was not counterbalanced. All observers faced a demonstrator as the demonstrator pushed the pole to his left. As described above, half of the observers were subsequently moved to the demonstrator's position for testing (Group DP). The other half remained in the observation position and the pole was moved to their compartment (Group OP).

Figure 1: Diagram of the pole bidirectional control procedure used in Experiments 2.1 and 2.2 showing a) a left pushing demonstrator during observation, b) the position of OP observers on test, and c) the position of DP observers on test.

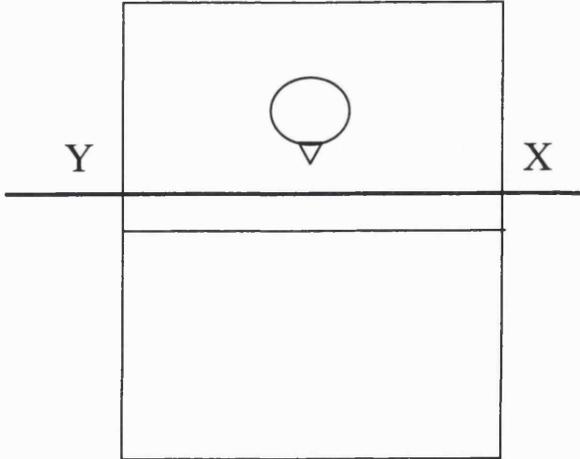
a)



b)



c)



Methods

Subjects

Ten budgerigars were obtained from a commercial supplier. Birds were naïve to experimental procedures and were allowed to habituate to their new environment for a period of at least one week prior to the onset of training. Two of the birds, both male, were trained as demonstrators. The remaining eight (four of each sex) were observers and were randomly assigned to the OP and DP groups (OP, N=4; DP, N=4). Each demonstrator was used for two OP birds and two DP birds.

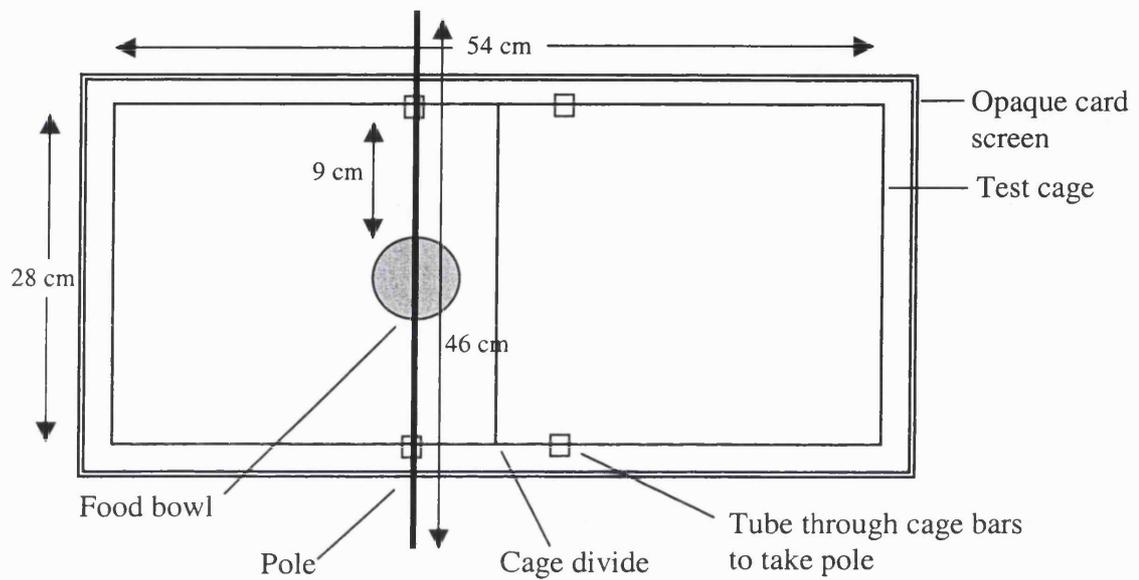
The birds were housed in cages within an aviary under natural light conditions (9:15, light:dark). The demonstrators were housed along with eight non-experimental birds, while the observers were housed in two pairs and one group of four in standard pet bird cages. The birds were all housed within close auditory, but not visual, range of one another. Throughout the experiment birds were on a restricted feeding schedule. They were fed 3-6gms millet/bird/day after the completion of training/testing and were weighed daily. Their weight was not allowed to fall below 90% free feeding weight. At the onset of scheduled feeding the birds' mean weight was 45.0gms (SEM=2.05). Water, grit and cuttlefish were freely available in the home cage.

Apparatus

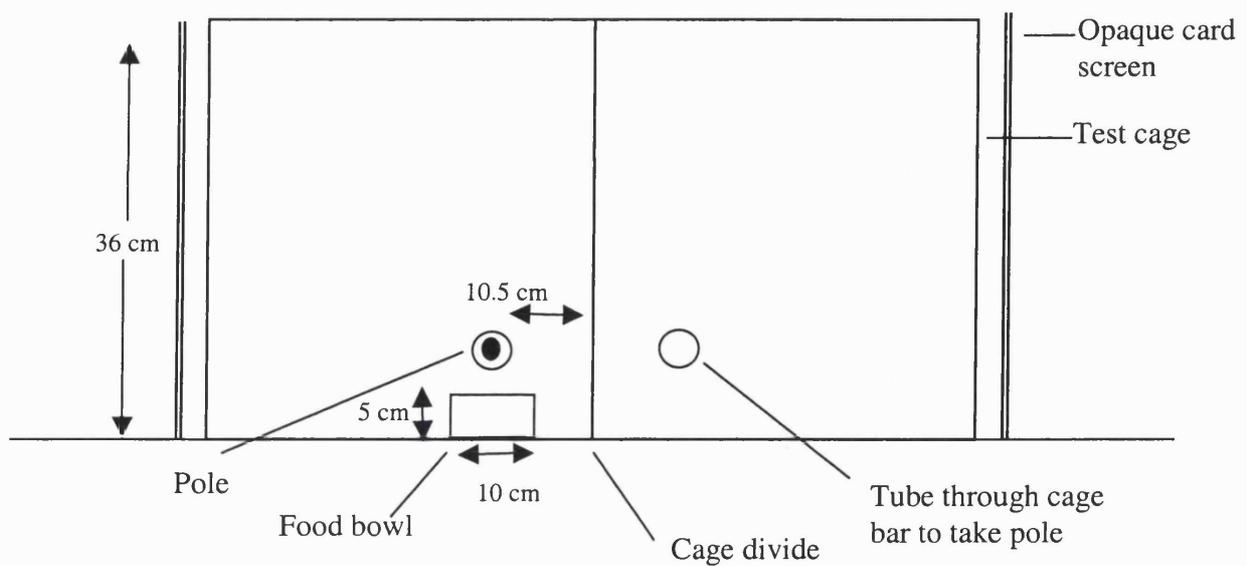
Training and testing was carried out in a test cage 54cm long x 28cm wide and 36cm high (see Figure 2). Entry to this cage was provided by four doors (8cm x 8cm), one at each end and two along one side. The side with doors, the 'access wall', was also

Figure 2: Diagram of test apparatus used in Experiments 2.1 and 2.2, showing a) overhead view, and b) side view.

a)



b)



distinguishable from the opposite side by the presence of four brown plastic hatches (6.5cm x 6.5cm) designed for food trays. The cage was divided into two equal parts by a wire grill, forming a demonstration compartment and an observation compartment. The grill consisted of vertical bars 1cm apart, which were identical to the bars of the main cage. The demonstration compartment was located such that the access wall was on the left of the demonstrator's body when the bird was facing the grill.

The manipulandum, a pole, consisted of a length of green garden cane (length 46cm; diameter 0.4cm, weight 4gm). It was suspended across the cage at a height of 8cm from the floor and 10.5cm from the central cage divide, by two tubes of diameter 1cm which were placed through the cage bars. These tubes were present in both the demonstration and the observation compartments, allowing the pole to be suspended in either compartment. The tubes also ensured that the pole could move freely in a horizontal plane to the left and the right.

The entire apparatus was surrounded by a screen of opaque buff card located approximately 5cm from the cage sides. The screen prevented the birds from seeing anything external to the cage, which could provide directional cues to them during the experiment. The pole was slotted through the screen, which ensured that the ends of the pole were not visible to the observers. The floor of the cage also consisted of buff card.

During testing the birds were rewarded for pole pushing responses with approximately four to five millet seeds which were delivered manually to a circular

food bowl (diameter 10cm, height 5cm) placed under the centre of the pole, 9cm from each side wall and 5.5cm from the central cage divide. The seeds were transferred to this bowl via a clear 1cm diameter plastic tube, which went straight down from the cage ceiling to 10cm above the bowl. As with the manipulandum, both the bowl and tube could be located in either the demonstration or observation compartment. The experimenter responsible for delivering reward was positioned behind the compartment containing the pole. This meant she was located behind the demonstration compartment during observation. She was also in this position during testing of the DP group, but was behind the observation compartment during testing of the OP group.

The entire experiment was recorded using a Hi8 Sony Camcorder. This was positioned at the end of the cage opposite the experimenter and was angled to focus on the pole through the cage ceiling. Sessions were timed with a stopwatch.

Procedure

Each session, with the exception of magazine training, began when the pole was inserted into the test cage and ended when the pole and food bowl were removed. Observation sessions ended when the demonstrator had made 30 responses or a period of 15 minutes had elapsed, whichever occurred first. Testing and magazine training sessions were of 15 minutes duration.

Demonstrator training

Initially the demonstrators were habituated to the test cage. This was achieved by positioning the open test cage alongside the demonstrators' home cage for two hours on each of two days. Birds were encouraged to enter through the availability of millet in the test cage. Once the demonstrators would readily enter the test cage of their own accord they were given two sessions of magazine training in the demonstration compartment. In these sessions the birds were trained for a period of 15 minutes, during which time food was delivered to the food bowl, through the plastic tube, at random intervals approximating to a RT 60sec schedule.

Following these sessions the demonstrators progressed to pole training.

Demonstrators were initially rewarded for any contact made with the pole and then their behaviour was shaped by successive approximation. Gradually they were required to touch the pole, move the pole, move the pole in one direction only, and finally to move it in one direction only by at least 5cm. Training continued until both demonstrators were capable of completing four sessions in which they made at least 30 reinforced slides within a 15 minute period. Both birds were trained to move the pole to their left only. Approximately 40 sessions, with two or three sessions administered each day, were required to reach this level of performance.

During the last two sessions of demonstrator training a "dummy observer" occupied the observation compartment. It was intended that the presence of this unfamiliar budgerigar would accustom demonstrators to being observed when pushing the pole.

Observer training and testing

The observers were habituated to the test cage in the same way as the demonstrators. This was followed by two magazine training sessions. These were identical to those given to the demonstrators, except that one was given in the observation compartment and one was given in the demonstration compartment.

After magazine training the observers were given six observation sessions on consecutive days. In these sessions the observers were placed in the observation compartment while their demonstrator made 30 rewarded pole slides of at least 5cm to his left. During the sessions only correct responses were rewarded and the pole was repositioned by the experimenter immediately after each response. At the end of the session the demonstrator was removed first followed by the observer. In order to reduce the possibility that the birds used room cues, and to make this apparent if they did, the cage was rotated 180° at the start of every day. This ensured that the demonstrator never pushed the pole towards the same room cues on consecutive days.

Immediately after the fourth, fifth and sixth observation sessions each observer was given a test session. The demonstrator was removed followed by the observer, who was isolated in a housing cage while the cage was prepared for the test session. For DP birds, demonstrator cues, such as seed husks, were removed from the demonstration compartment. For OP birds, the camera was moved to the opposite end of the cage so that it focussed on the observation compartment, and the reward apparatus was moved from the demonstration compartment to the observation compartment. The observer bird was then returned to the test cage, being placed in

the observation compartment (group OP) or the demonstration compartment (group DP). The pole was then added to the compartment in which the bird was positioned, and the bird was allowed access to the pole for 15 minutes. During this time the experimenter rewarded the observer whenever its behaviour led to a detectable lateral movement of the pole, regardless of direction. Following movement, the pole was immediately returned to its starting position by the experimenter.

Videotapes of the observers' behaviour during test trials were scored to provide the data for analysis. Whenever an observer pushed the pole the direction of pole movement with respect to cage side (X or Y) was recorded. Accuracy, in all experiments, was checked by comparing the performance of two independent raters across randomly selected test trials. The raters were in agreement regarding the cage side to which the pole was pushed in 92.3 % of a randomly selected 30% of test trials.

Results

Demonstrators' Behaviour

Each demonstrator employed a distinct response topography when pushing the pole. One demonstrator stood on the rim of the food bowl or on the floor and took the pole in its beak. It then moved its entire body to the left, holding on to the pole with its beak. This movement could start from side Y of the cage or from the centre. In contrast the second demonstrator stood on the rim of the bowl on side X. To move the pole it placed its left foot and its beak on the pole and used these appendages to

move the pole. The bird's right foot and torso did not leave their starting position. Both birds released the pole once it had been moved. The delivered rewards were then consumed before the birds positioned themselves to move the pole again.

Demonstrators showed perfect discrimination when being observed by their observers, i.e. they always moved the pole towards side X and never towards side Y. All pole movements also involved the pole moving 5cm, and usually more. The mean rate of responding (responses/minute) was higher for one demonstrator (mean=2.08, SEM=0.67) than for the other (mean=1.47, SEM=0.25). As each demonstrator was assigned both OP and DP observers, rate of responding was not expected to be different between the two groups. This was confirmed with a one-way ANOVA in which rate was the dependent variable and group was the independent variable. The effect of group was not significant ($F < 1$).

Observers' Behaviour

For the majority of each observation period all observers orientated towards the demonstrator. They remained close to the partition throughout each session, and each observer at some point actively attempted to gain access to the demonstration compartment through the partition.

On test all observers contacted the pole in a way that resulted in lateral movement. The total number of responses made by birds in each group across all three tests was similar (OP, mean=90.75, SEM=8.73, N=4; DP, mean=72.25, SEM=24.49, N=4). A one-way ANOVA with total number of responses as the dependent variable and

group as the independent variable confirmed that there was no significant difference between the groups ($F < 1$).

Observers used a variety of techniques to move the pole, including using their beak, feet and/or frontal plane of their bodies. The small N in this experiment and the variety of responses made by the observers meant that it was not possible to examine statistically whether observers used the same response topography as their demonstrator. Informal analysis suggested that this was not the case. Pole pushing technique appeared to develop over the test sessions, becoming more stereotyped, independent of the direction and topography of the demonstrator's responses.

Directional bias in the observers' pole pushing responses was assessed by means of a directional discrimination ratio. This was calculated for each test session by dividing the number of times the bird moved the pole to side X, the side of the cage to which the demonstrator had pushed the pole, by the total number of responses made in the session (i.e. $X/X+Y$).

If observers had learned which side of the cage to slide the pole towards they would be expected to slide to X irrespective of group (see Figure 1). This would result in all observers having a high $X/X+Y$ ratio on all days. If the observers had engaged in transpositional imitation, they would all slide the pole to their left, i.e., DP birds would slide to X and OP birds would slide to Y. This would result in DP birds having a high $X/X+Y$ ratio and OP birds having a low one. If on the other hand the observers were engaged in mirror imitation, they would all slide the pole to their right as this is the direction the pole moved with respect to their own bodies. OP

observers would therefore slide to X and DP observers would slide to Y. This would result in OP birds having a high ratio and OP birds having a low one.

Figure 3 shows the mean directional discrimination ratios for each group on each of the three test days. It can be seen that on all days birds in the DP condition had a higher X/X+Y ratio than birds in the OP condition. This difference was confirmed with a mixed model ANOVA in which the directional discrimination ratio on each test day was the within subjects variable and group was the between subjects variable. The effect of group was significant ($F(1,6)=11.634$, $p=0.014$). No other main effects or interactions were significant ($F<1$ in all cases).

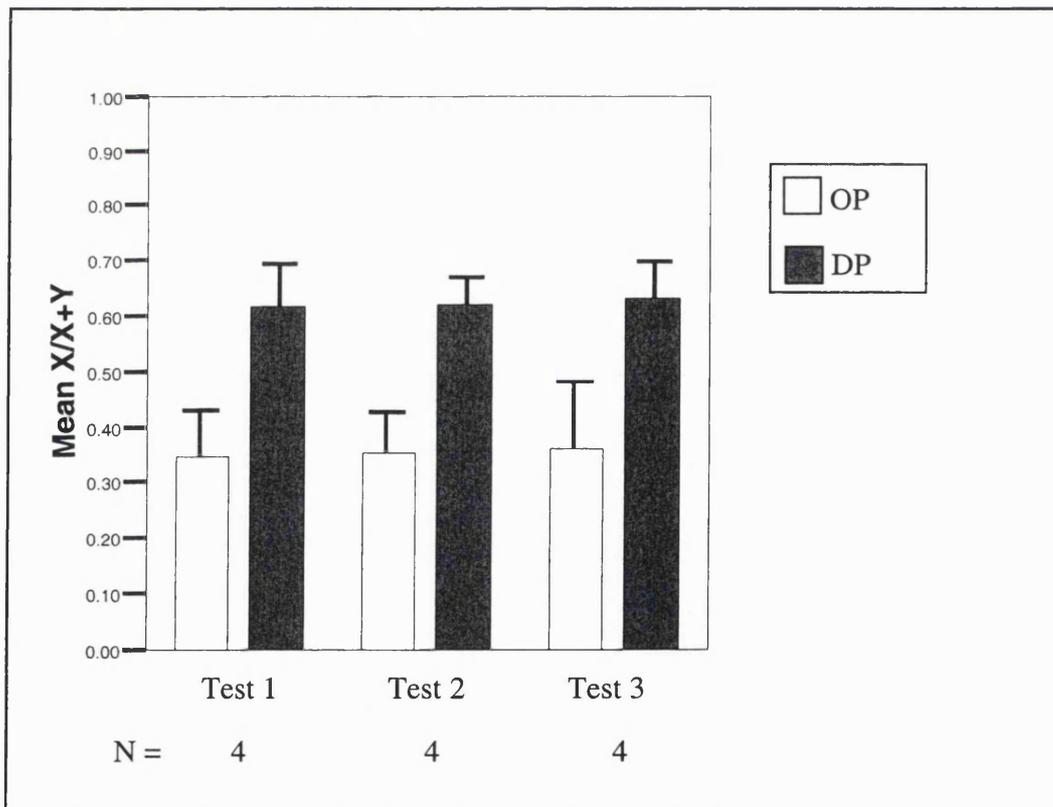


Figure 3: Mean directional discrimination ratios (X/X+Y) and standard errors of the means for groups OP and DP on Tests 1, 2, and 3 of Experiment 2.1.

Discussion

The results showed that DP birds pushed the pole proportionally more towards X than did OP birds. Interpreted within the logic used to design the experiment, this suggests that the observers were engaging in transpositional imitation. They were coding the direction of pole movement, during observation, with respect to the demonstrator's body as opposed to their own. As the demonstrator pushed the pole to his left during observation, the observers pushed the pole to their left when tested.

This result is similar to that obtained in both the rat and the quail bidirectional control procedures (Heyes & Dawson, 1990; Akins et al., 2002). In both these studies the observer responded in the same direction as the demonstrator, relative to the actor's body. However, the results of the rat bidirectional control procedure have since been undermined by evidence that they were influenced by scent cues (Mitchell et al, 1999), and the quail study did not adequately control for emulation or observational conditioning.

Evidence of transpositional imitation from the rat and quail procedures is therefore not conclusive. Given this, and the fact that mirror imitation was considered to be more likely in budgerigars than transpositional imitation, the results of Experiment 2.1 should be questioned. One flaw in the experiment's design was the absence of counterbalancing groups, which observed right pushing demonstrators. It is possible, especially given the lateralisation of vision and perhaps even foot use in birds (Hart, Partridge & Cuthill, 2000; Rogers & Workman, 1993), that left pushing was the most likely response in the birds even before a left pushing demonstrator was observed.

Apparatus asymmetries may also have affected the results. The most obvious asymmetry concerns the reward procedure. All birds were rewarded by an experimenter who stood directly behind the compartment the bird was responding in. Rewards were delivered to a tube, which in turn delivered the food to a bowl, using the experimenter's right arm. It is possible that in order to avoid the arm, which appeared above the screen to reward the birds, the observers kept to the left of the cage, making left pole movements more likely.

Experiment 2.2

The purpose of Experiment 2.2 was to establish whether the results of Experiment 2.1 were due to transpositional imitation, or to an observation independent bias towards left responding. In Experiment 2.2 left and right pushing demonstrators were used to control for any lateralisation in the birds and any asymmetries in the apparatus. The asymmetry in the reward mechanism was also removed by using a mechanised device. This device could be remotely activated by the experimenter allowing them to be positioned at a distance of 1m from the test cage. Once activated the device allowed birds access to food through a centrally positioned hole in the test cage floor.

The incorporation of left and right pushing demonstrators resulted in four groups of observers: 1) observed left pushing, tested in observation compartment (LOP); 2) observed left pushing, tested in demonstration compartment (LDP); 3) observed right pushing, tested in observation compartment (ROP); 4) observed right pushing, tested

in demonstration compartment (RDP). As in Experiment 2.1, the left pushing demonstrators were coded as pushing towards side X of the test cage, while the right pushing demonstrators were coded as pushing towards side Y.

If observers had learned which side of the cage to push the pole towards, birds in groups LOP and LDP would be expected to make proportionally more X responses (i.e. to have a higher directional discrimination ratio) than ROP and RDP birds. If birds were engaged in mirror imitation, observers in RDP and LOP would be expected to make proportionally more X responses than LDP and ROP birds. If birds were engaged in transpositional imitation, as suggested by Experiment 2.1, then birds in LDP and ROP would be expected to make proportionally more X responses than LOP and RDP birds. Finally, if there was an overall left pushing bias due to an asymmetry in the birds' vision or foot use, or one in the apparatus, then LDP and RDP birds would be expected to make proportionally more X responses than LOP and ROP birds. These four possible results are presented in Table 1.

		X/X+Y ratio expected depending on observer strategy			
Group	Side demonstrator pushed towards	Cage Cues	Left pushing bias	Mirror Imitation	Transpositional Imitation
LOP	X	HIGH	LOW	HIGH	LOW
LDP	X	HIGH	HIGH	LOW	HIGH
ROP	Y	LOW	LOW	LOW	HIGH
RDP	Y	LOW	HIGH	HIGH	LOW

Table 1: Summary of the directional discrimination ratios expected from each group in Experiment 2.2 as a result of each possible observer strategy.

Method

The method differed from that of Experiment 2.1 in the following respects:

Subjects

Thirty-six juvenile budgerigars of indeterminable sex were obtained from a commercial supplier. All birds were allowed a period of at least two weeks to habituate to the laboratory before the onset of training. Four of the birds were assigned the role of demonstrator. The remaining 32 birds were observers. The experiment was run in four replications each consisting of eight observer birds. Birds were randomly assigned to one of the four groups (LOP, N=8; LDP, N=8; ROP, N=8; RDP, N=8). At the beginning of scheduled feeding mean body weight was 39.69gms (SEM=0.96).

In each replication observers were housed with demonstrators for a period of at least one week before the first observation day in case familiarity with the demonstrator bird facilitated learning. Birds in the first three replications were housed in standard laboratory cages (100cm x 50cm x 50cm) from their arrival in the laboratory. Birds in the fourth replication were initially housed within a small freestanding aviary (2m x 1m x 2m high) but were moved to standard cages prior to observation. Five or six birds were housed in each cage.

Apparatus

The cage floor was modified to provide a more efficient reward system. In Experiment 2.2 the floor of the cage consisted of sheet metal. At its centre was a hole

(5cm diameter) from which birds could feed for 10 seconds when they earned a reward. Food was delivered to the hole by means of a cup which was raised electronically, by a motorised lever, when the experimenter pressed a remote button. By moving the top of the cage relative to the base the feeding hole could be placed in either the demonstration or observation compartments. In both compartments the centre of the hole was positioned 10.5cm from the partition grill, directly underneath the pole if it was present. During the experiment the cage floor was covered with a sand sheet (same dimensions as cage), with a hole cut in its centre (same dimensions as reward hole).

The feeding mechanism ensured that the experimenter could reward the birds from a distance. The mechanism itself was completely symmetrical and was therefore unlikely to promote any side bias in the observers.

Pole position in replication 1 was unchanged from Experiment 2.1. In the remaining replications the pole was elevated 15cm above the feeder. A perch (1cm diameter, 28cm long) was placed in each compartment 15cm from the divide and 11.5cm above the floor. This allowed easy access to the pole when it was present. The introduction of the raised pole and the perch was to make lateral pole movements by the observers less likely to result from accidental observer movements, for example perching on the pole, or climbing over it.

Procedure

Demonstrator training

Demonstrators were trained by successive approximation until they were capable of achieving 20 pole slides within a five minute session twice a day. This required approximately 35 sessions of training.

Observer training and testing

Birds were always trained and tested in the same order and this was random with respect to group assignment. Observers in the first three replications were given four magazine training sessions, while those in replication 4 were allowed up to 18. This was necessary as the birds in replication 4 were initially aviary housed and were therefore more difficult to catch and handle, and hence were slower to habituate to the test cage.

Demonstrators were allowed to make 20 responses in each observation session, and sessions ended when these responses had been achieved or when 15 minutes had elapsed. On test, observer birds were rewarded only when they were facing the pole at the time when their behaviour caused the pole to move laterally. This constraint was introduced to prevent observers from being rewarded for general activity on, and around the pole. On test observers were rewarded by an experimenter who was aware of this criterion but blind to group assignment. Testing continued until birds had made 40 responses or until five test sessions were administered.

Independent raters were in agreement regarding the cage side to which the pole was pushed towards in 89.1% of a randomly selected 30% of test trials.

Results

Demonstrator's behaviour

Each demonstrator employed a distinct but constant response topography in order to move the pole. One of the right pushing birds moved the pole by grasping it slightly to the left of the centre using his beak. He then moved to his right in one constant movement taking the pole with him. The other right pushing bird started in the same position and also contacted the pole with his beak. This bird however did not move instead remaining stationary and moving the pole to his right in one movement. One of the left pushing birds contacted the pole slightly to the left of centre with both the beak and the left foot, and used several distinct contacts to move the pole left. The other left pushing bird contacted the pole to the right of centre and made several contacts with the beak to move the pole left.

Demonstrators showed perfect discrimination when being observed and rarely made fewer than 20 responses. The mean rate of responding (responses/minute) for each group can be seen in Table 2 and was relatively constant. A one-way ANOVA with rate as the dependent variable and group and replication as the independent variables confirmed that the groups were not exposed to different rates of demonstrator responding. Neither the main effects nor the interaction were significant ($F < 1$ all cases).

Bird	Group	Mean	SEM	N
Demonstrator	LOP	4.37	0.37	6
	LDP	4.84	0.45	8
	ROP	4.10	0.45	8
	RDP	4.15	0.32	8
Observer	LOP	1.15	0.47	6
	LDP	1.65	0.60	8
	ROP	1.42	0.51	8
	RDP	1.42	0.37	8

Table 2: Mean rate of responding (responses/minute) and standard errors of the means for demonstrators and observers in each group in Experiment 2.2.

Observers' behaviour

As in Experiment 2.1, observers showed keen interest in the demonstration compartment during observation sessions.

Of the initial 32 observers, data were obtained from 30 birds. One LOP bird died during testing and one LOP bird failed to make any responses in any of the five tests administered. N values for each group were therefore; LOP=6; LDP=8; ROP=8; RDP=8. Response rates (responses/minute), shown in Table 2, varied little between groups. This was confirmed with a one-way ANOVA in which rate of responding was the dependent variable and group and replication were independent variables. Neither the effect of group nor the group x replication interaction were significant ($F < 1$, all cases) indicating that response rate did not vary across groups. However, the main effect of replication was significant ($F(3,14)=11.16$, $p=0.001$). Table 3 shows the response rates of birds in each replication. It can be seen that birds in

replication 1 responded at a higher rate than birds in the other replications, especially replication 4. This can be attributed to the low pole height in replication 1 which resulted in elevated rates of contact, and therefore responding, as the birds moved round the cage. This was addressed in later replications by raising the pole height which resulted in fewer contacts. The low response rates of birds in the last replication may have been related to the fact that their initial aviary housing made them slower to habituate to the test cage and procedure. They were more timid than birds in other replications which is likely to have reduced their response rates.

Replication	Mean	SEM	N
1	2.95	0.51	7
2	1.83	0.42	7
3	0.74	0.17	8
4	0.43	0.12	8

Table 3: Mean rate of responding (responses/minute) and standard errors of the means for observers in each of the four replications in Experiment 2.2.

Observers employed a variety of techniques to move the pole. They used their beaks, feet, both beak and feet and the frontal plane of their bodies. Responses did appear to become more stereotyped over sessions and informal analysis suggested that there was no link between technique used by the demonstrator and that used by the observers

Directional bias in the observers was examined by calculating the discrimination ratio, $X/X+Y$, for all responses made on test. Given that only 22 out of the 32 birds made 40 responses, and that the number of tests administered ranged from one to five, analysis of discrimination ratios for each test would have necessitated exclusion

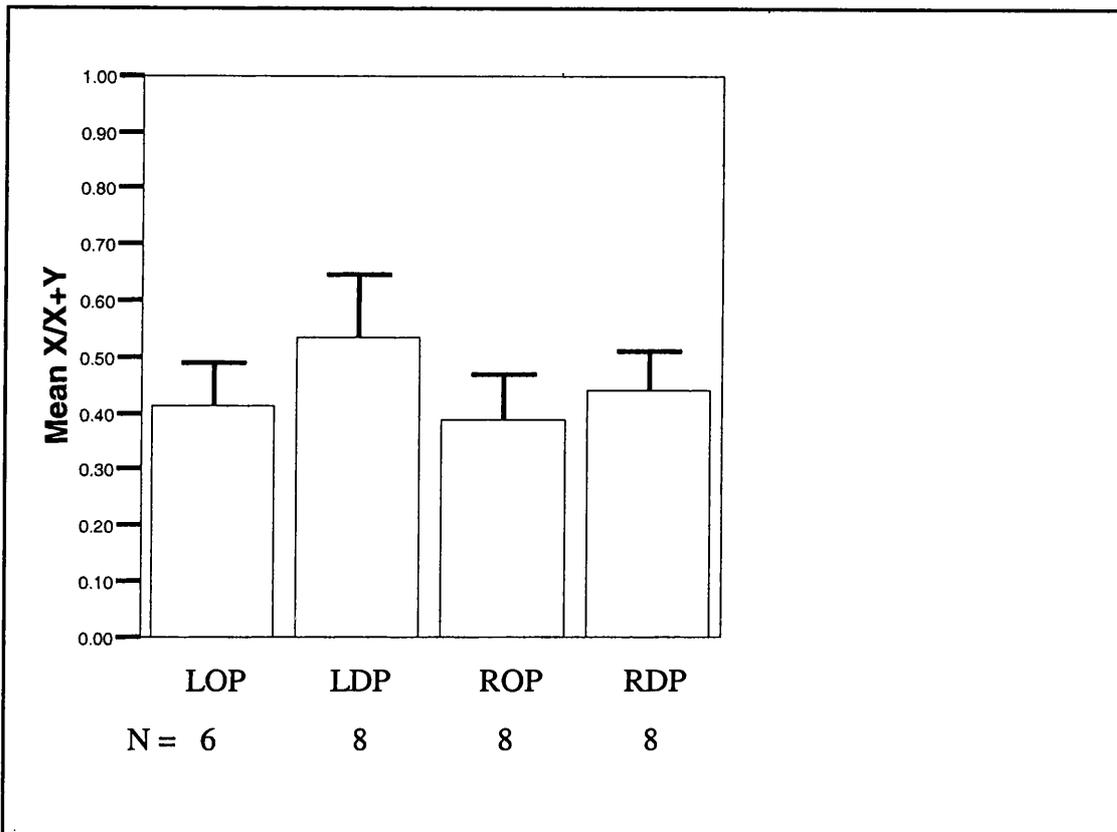


Figure 4: Mean directional discrimination ratios ($X/X+Y$) and standard errors of the means for all responses made by birds in groups LOP, LDP, ROP and RDP in Experiment 2.2.

of data from many birds. Figure 4 shows the directional discrimination ratio across all responses for birds in each of the four groups. It is apparent that birds in no group showed a directional bias; the mean ratio for each group is close to 0.5, indicating that the birds were pushing the pole to the left and to the right with equal frequency. The lack of a group difference was confirmed with a one-way ANOVA in which the directional discrimination ratio was the dependent variable and group and replication were the independent variables. Neither group ($F < 1$) nor the group x replication interaction were significant ($F = 2.04$). However, the ANOVA did reveal a significant

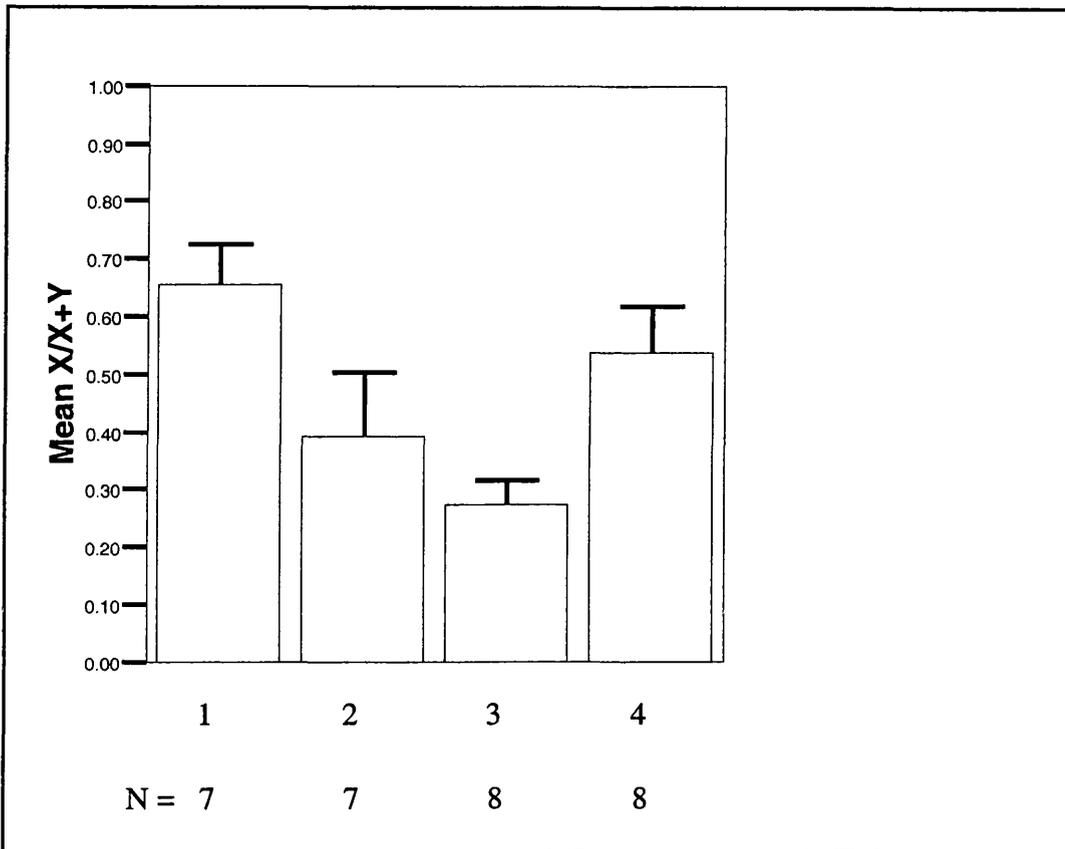


Figure 5: Mean directional discrimination ratio ($X/(X+Y)$) and standard errors of the means for all responses made in replication 1, 2, 3, and 4 in Experiment 2.2.

effect of replication ($F(3, 14)=6.20, p=0.007$). Figure 5 shows the mean discrimination ratio for birds in each of the four replications, and suggests that birds in replications 1 and 4 had a higher mean directional discrimination ratio than birds in replications 2 and 3. Birds in replications 1 and 4 pushed the pole proportionally more towards X, while birds in replications 2 and 3 pushed the pole proportionally more towards Y. Tukeys post hoc test examining replication revealed that the difference was significant between replications 1 and 3 ($p=0.012$) and between 3 and 4 ($p=0.010$).

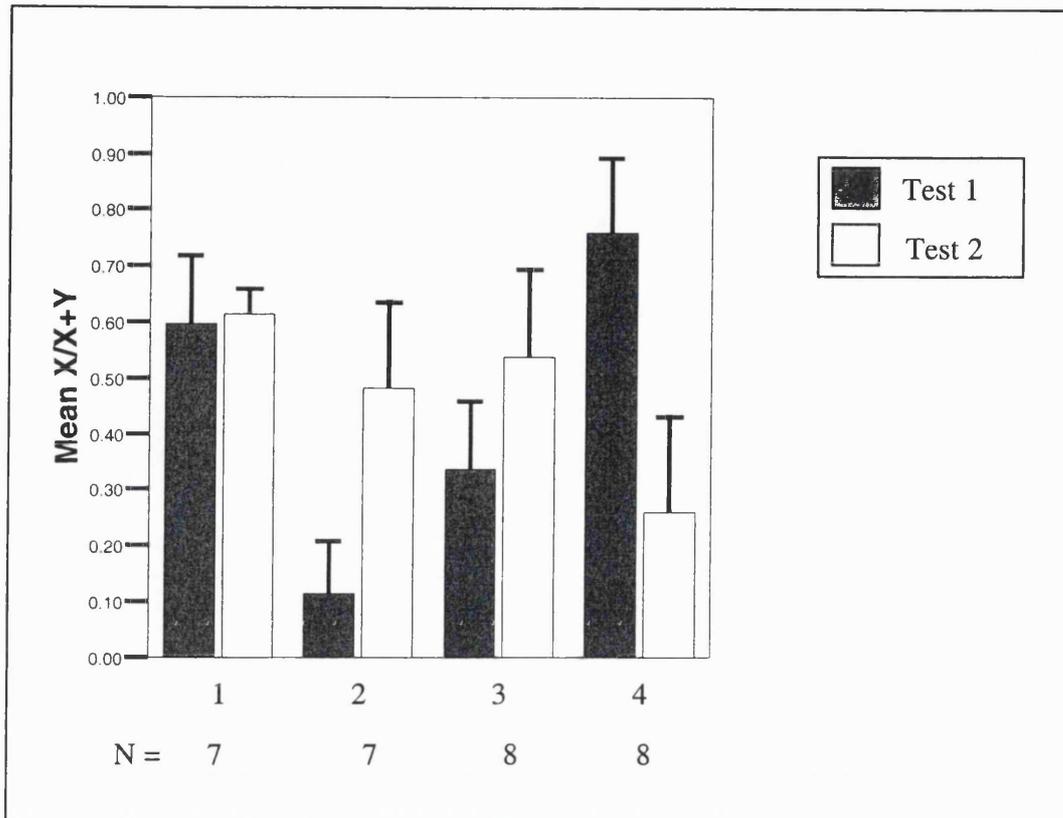


Figure 6: Mean directional discrimination ratio ($X/X+Y$) and standard errors of the means for replications 1, 2, 3, and 4, on Test 1 and Test 2 in Experiment 2.2.

The directional bias across all groups within a replication indicates that birds were not pushing with respect to the demonstrator's direction and were instead influenced by room or cage cues. If birds were pushing relative to a room cue this should be detected in a reversal in direction of pushing with respect to X from one test day to the next, as the test cage was rotated 180° between test sessions. To investigate this possibility the directional discrimination ratios from the first two tests in which a bird responded (all 30 birds received at least two tests) were examined. Figure 6 shows the mean directional discrimination ratio on the first and second tests for birds in each replication. In replications 2-4 it appears that the mean directional discrimination ratio reversed from test 1 to test 2. These data were subject to a mixed-model ANOVA, in which test was the within subjects factor and replication

was the between subjects factor. Neither the main effect of test nor replication were significant ($F < 1$ in both cases). However, the test by replication interaction was significant ($F(3,25)=5.13, p=0.007$) supporting the idea that within each replication direction of pole sliding with respect to the cage sides was reversing from test 1 to test 2, and thereby providing some evidence that birds were relying on room cues.

Discussion

The results of Experiment 2.2 suggest that observers did not learn direction of pole pushing from their demonstrator, either as a result of imitation, emulation or observational conditioning. There was no group difference in the side of the cage towards which the pole was pushed, despite the two distinct test positions and the two directions observed across the four groups. Instead there appeared to be a consistent side bias within each replication. In the first and last replications all birds pushed towards side X, while in the second and third replications all birds pushed towards side Y.

This result indicated that observers were simply pushing the pole with respect to a cage or room cue, irrespective of the direction of the demonstrator's responses.

When cage side pushed towards was compared on tests 1 and 2, it appeared that the ~~side~~ ^{pushed towards} side was reversing, in accordance with the cage rotations between tests. As cage cues remained constant across tests this reversal indicates that birds were biased by room cues. Although it is not possible to know exactly when the bias developed it is likely that it occurred in test 1 when observers were first given experience of manipulating the pole. If cage orientation on test 1 is examined, X was located on the same side as

the experimenter and holding cages, for replications 2 and 3, and on the opposite side for replications 1 and 4. Birds were therefore either pushing away from the holding cages or, they were pushing away from the experimenter. It is not clear why birds would want to move away from their holding cage and birds they lived with, instead it is much more likely that they were moving away from the experimenter. Birds were only given a short period with which to habituate to human contact and even by the end of the experiment birds were still difficult to both approach and handle, suggesting that the experimenter may act as a negative stimulus for the birds. Given that the test cage was surrounded by opaque card it is likely that the birds were influenced by auditory cues as opposed to visual cues.

2.3. Summary and Conclusions

Two experiments were carried out using a bidirectional control procedure. The first, Experiment 2.1, was a pilot study to investigate the applicability of the experimental design to budgerigars. The second was a larger scale replication. The design used in both was developed to separate the learning of direction of pole movement due to coding with respect to cage or room cues (emulation or observational conditioning), from imitation (mirror or transpositional).

In the first experiment, observers saw only left pushing demonstrators. The results were encouraging. They suggested that the observers were carrying out transpositional imitation, learning the direction in which the pole was pushed with respect to the demonstrator's body. However the lack of a right counterbalancing

group undermined these results. It was possible that an asymmetry in the design, or in the birds themselves, was responsible.

The results of the second experiment, in which demonstrators pushed the pole either left or right, were disappointing. No significant group difference was obtained. Instead a replication effect was observed, with birds in two replications favouring one direction with respect to the cage side, and birds in the other two replications favouring the opposite side. This was most likely caused by the use of room cues, which could have been located in opposite positions at the time when the birds' directional bias was established.

The results from Experiment 2.2 undermine the conclusions of Experiment 2.1 and make it likely that the left bias seen in all birds, in Experiment 2.1, was due to room cues, as opposed to transpositional imitation. The most likely explanation is that the birds in Experiment 2.1 were influenced by the asymmetry in the reward mechanism. The experimenter's arm was always positioned to the right of the demonstrators during observation and the right of the observers on test. Observers may have simply moved away from the arm resulting in more left responses. This explanation is suggested by the results of Experiment 2.2. Alternatively observers may have coded movement of the pole with respect to arm position, which would have been emulation learning.

The likely role of room and cage cues in Experiments 2.1 and 2.2 suggest that in these experiments they were more salient to the birds than the demonstrator's behaviour. As the bidirectional control procedure with quail (Akins et al, 2002)

failed to control adequately for emulation, it is possible that further investigations could reveal that these results can also be attributed to cage or room cues. It is interesting to note that a right bias in responding was observed in the results of the quail experiment and that this was explained in terms of cage asymmetries, the position of the cage door and a wire attached to the manipulandum, both of which may have been aversive to the birds.

Bidirectional control procedures were developed for birds following the finding that rats responding in these tasks could be influenced by scent cues on the manipulandum (Mitchell et al, 1999). It was thought that using a species less reliant on scent would increase reliance on the demonstrator's actions and make imitative learning more likely. The results of Experiment 2.2 suggest that this has not been the case and that birds, although unlikely to be relying on scent cues, were capable of taking advantage of other cues, most likely auditory, to develop directional biases. Given that Experiment 2.2 was carried out in a controlled manner, the results suggest that the bidirectional control procedure is not an ideal paradigm for the investigation of imitative learning.

Chapter 3

Imitative learning in the budgerigar using a two-action stopper paradigm, I.

The results presented in the previous chapter, in which a bidirectional control procedure was used to investigate imitation, suggest that budgerigars are a suitable species for use in research in this area. Although the results obtained were not conclusive of imitation in this species, the experiments showed that budgerigars are capable of adapting well to laboratory procedures. However, an alternative paradigm is required to investigate the social learning in this species.

A paradigm, which has shown potential in the investigation of imitative abilities in birds was initially developed by Campbell et al (1999) using starlings. Juvenile birds were allowed to observe a conspecific demonstrator using its beak to remove one of two distinctively coloured objects (i.e. a red or a black stopper) from a hole in the lid of a plastic box. Both stoppers could be removed by either pulling up on a piece of string inserted through their centre, or pushing down on them. When subsequently allowed access to the stoppers, observers were rewarded for both up and down responses. The results showed that on test observers ^{removed} the stopper in the same direction as their demonstrator. One possible explanation for this effect is that the observers were imitating the body movements of their demonstrators.

The design of the starling stopper experiment, however, meant that other explanations could account for the results obtained. First, demonstrators contacted different parts of the stopper; birds pulling the stopper up used a string while birds pushing the stopper down contacted the stopper directly. Stimulus enhancement is therefore a potential explanation of the results obtained. It is possible that birds attracted to and contacting the string are more likely to pull the stopper up, while birds attracted to and contacting the stopper itself are more likely to push it down. Second, pushing and pulling by demonstrators resulted in the stopper moving in different directions, and in the test apparatus looking different after the response had been made. It is therefore possible that the observers learned stopper removal through emulation, which is the process in which animals learn about the dynamic properties of an object as opposed to the action used (Tomasello, 1996). For example if a bird saw the stopper pushed down it could learn that the stopper moved down, as opposed to learning it had to push the stopper. Alternatively they could have learned a stopper movement-food relationship through observational conditioning. All three explanations can account for the matching behaviour observed.

Fawcett, Skinner & Goldsmith (2002) attempted to provide more conclusive evidence for imitation in a replication of the starling experiment by Campbell et al (1999). As well as the Push (stopper moves down) and Pull (stopper moves up) groups they introduced an 'Enhanced Ghost Control' in which a bird stood next to a stopper while it was moved up, or down, with wire. Fawcett et al argued that this control provided observers with all the information available to the Push and Pull observers except for information about demonstrator body movements. If the observers in this group learned to move the stopper in the same direction as they

observed then it would suggest that the birds were learning by emulation or observational conditioning. The results showed directional learning only in the experimental groups, i.e. in birds who saw a demonstrator remove the stopper, but not in birds who saw the ghost controls, suggesting that the experimental birds were learning by imitation. However the evidence presented suffered from a strong push bias and small sample size. In addition the ghost control groups did not experience stimulus enhancement of the stopper, which may have reduced their interest in it and as a consequence their learning about its movement via emulation.

Heyes & Saggerson (2002) advanced the use of the stopper paradigm with budgerigars. The stoppers were modified to ensure that all demonstrators contacted the stopper at the same location, so stimulus enhancement could be excluded as the cause of any observed response bias. This was achieved through the removal of the string and the addition of two wires crossing the centre of the stopper which could be used for both push and pull responses. On test it was found that observers reliably copied the direction of removal observed. The matching response result is again consistent with imitation, emulation and observational conditioning. However, Heyes and Saggerson's experiment established that the stopper paradigm is suitable for use with budgerigars.

Mottley & Heyes (in press) carried out one further experiment with this paradigm using budgerigars, introducing two important innovations. Instead of utilising live demonstrators as in the two previous experiments, 'virtual' demonstrators were used. They filmed the behaviour of trained demonstrators and played it back to observers on a thin film transistor (TFT) screen. The second innovation was the introduction of

a fixed trial procedure. In magazine training birds were given a series of one minute trials in which they were allowed to approach and feed from the stopper box. These trials were continued in testing with the purpose of retaining the observer's interest in the task. It was found that, on test, observers reliably copied the direction of stopper removal they had observed, both when testing and observation were simultaneous and when testing immediately followed observation.

The stopper two-action paradigm clearly has potential in the investigation of imitation, but it needs modification so that demonstrator action results in identical movement of the stopper whatever response the demonstrator is making. This will ensure that emulative learning, and observational conditioning, will have an equal effect on all experimental groups. Although the paradigm could be used with a ghost control it has been seen that results obtained using this technique are not always conclusive (Fawcett et al, 2002). It would be preferable to develop a procedure which excludes emulation as an explanation for results obtained, rather than relying on testing for its occurrence with an additional group.

The three experiments presented in this chapter sought evidence of imitation in budgerigars using a modified version of the stopper box paradigm. In these experiments, the stopper was designed only to move downwards into the box. Thus, instead of seeing the stopper removed in one of two different directions, the observers saw the stopper pushed downwards using one of two different actions. Demonstrators were trained to move the stopper by either pushing it down with their feet, or pushing it down using their beak. Observers were rewarded for all downward displacements of the stopper and responses were analysed in terms of whether the

beak or feet were used. If birds were capable of imitation they would be expected to respond using the same appendage as that used by their demonstrator.

This type of procedure was originally inspired by an experiment carried out by Dawson & Foss (1965) using budgerigars. In their experiment observers watched demonstrators remove lids from food bowls using one of three different actions. Emulation was a potential explanation for these results as the trajectory the lids followed varied depending on removal technique. The procedure has also been used in experiments with quail and pigeons, in which observers watched demonstrators step on or peck at a treadle for a food reward (Akins & Zentall, 1996; Zentall et al, 1996). The treadle was designed so that both pecking and stepping resulted in the treadle following the same trajectory, which meant that emulation was excluded. On test it was found that both quail and pigeons that had observed a pecking demonstrator, made proportionally more treadle pecks on test than observers of a stepping demonstrator. Unfortunately as pecking is a socially facilitated behaviour in birds, and there was little evidence of learning in the stepping observers, the results cannot be taken as conclusive evidence of imitation in these species.

In the first experiment presented in this chapter only one stopper was used and observers saw either beak or foot removal. In contrast, Experiments 3.2 and 3.3 were conditional discrimination experiments in which birds saw both beak and foot ~~stopper~~ removals but these were either in distinct locations (3.2) or to distinctly coloured stoppers (3.3). All three experiments adopted the fixed trial procedure which was first introduced by Mottley & Heyes (in press). Both observation and test sessions were broken up into one minute trials. In all three experiments ten observation and

ten test trials were alternated within one session. During observation trials access to the stopper box was prevented with a cover, while during test trials no demonstration was visible.

All three experiments also took advantage of the 'virtual' demonstrator technology developed by Mottley & Heyes (in press). Trained birds were filmed and the resulting clips were used as the stimuli in the experiments. This is an important advancement in experimental design as it ensures that the experimenter, as opposed to the demonstrator, is in control of what is observed. Timing of stimulus presentations can be regulated, identical stimuli can be presented repeatedly to the same or different subjects, interaction between demonstrator and observer is abolished and, importantly, it is possible to manipulate stimuli artificially (D'Eath, 1998; Morimura & Matsuzawa, 2001).

Despite the many advantages of using video technology, not all experiments utilising it have been successful (e.g. D'Eath & Dawkins, 1996). Some of the negative results obtained may have been due to the use of cathode ray tube (CRT) displays. For example, Ikebuchi & Okanoya (1999) found that male zebra finches, *Taenicopygia guttata castanotes*, failed to respond to video images of female birds when they were presented on a CRT monitor. A possible explanation for this is that these monitors are designed for human eyes and may actually appear to flicker to animals such as birds, which have evolved to process visual information at much higher critical fusion frequencies (CFF). Humans have a maximum CFF of 60Hz which is lower than that of many birds (e.g. domestic hens 105Hz, Nuboer, Coemans & Vos, 1992;

pigeons 140HZ, Dodt & Wirth, 1953; African grey parrots 55.3 to 105 Hz, Nuboer et al, 1992).

In contrast, TFT liquid crystal displays are flickerless. The colour information of each pixel is retained until the next scanning information arrives (Ohshima, 1998). When Ikebuchi & Okanoya (1999) repeated their zebra finch experiment using a TFT screen they found that their male zebra finches responded to images of females on the screen by emitting directed song. The success of Mottley and Heyes's two-action experiment using this technology suggests it is applicable to social learning studies and may greatly assist in overcoming the problems of stimulus control entailed by use of live demonstrators.

Experiment 3.1

In Experiment 3.1, birds were presented with one stopper. On each of three test days, ten one-minute film clips showing a demonstrator removing the stopper were alternated with ten one-minute test trials. Three groups were used: a Beak group, which saw a bird remove the stopper using its beak; a Foot group, which saw a bird remove the stopper using one of its feet; a Control group, which observed a bird feeding from the test box from which the stopper was absent. The Control group provided the baseline beak and foot response levels to which the experimental groups could be compared. This made it possible to determine whether both the Beak and Foot experimental groups, or only one of these two groups, were learning from their demonstrator.

If observers learned through imitation birds in the Beak group would be expected to use their beak to remove the stopper proportionally more often than birds in the Control group who would use their beaks proportionally more than birds in the Foot group. This result could not be explained by emulation, or observational conditioning, because stopper movement was constant across groups.

Methods

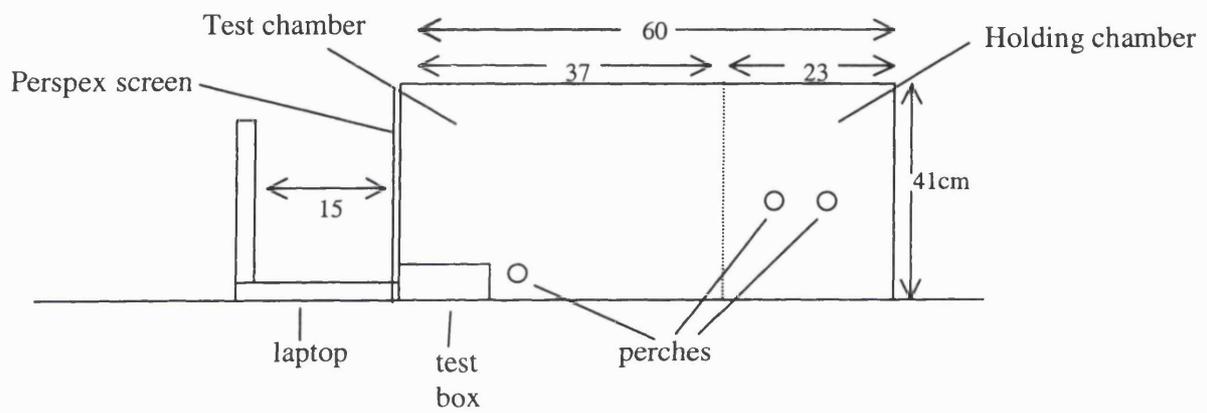
Subjects

Thirty-five juvenile wild type budgerigars of undeterminable sex were used. At the onset of scheduled feeding the birds' mean weight was 35.64gms (SEM=0.82). They were obtained from a commercial supplier. Of the 35 birds, three had served as observers in a previous two-action procedure and were assigned the role of demonstrator. The remaining 32 birds were experimentally naïve and were assigned the role of observer. All birds were allowed to habituate to the laboratory for a period of at least one week prior to the experiment.

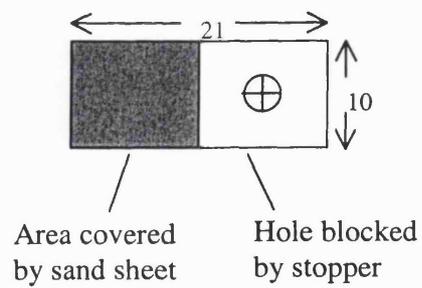
Of the 32 observers, 12 birds observed a video of a conspecific demonstrator using its foot to remove the stopper (group Foot), 12 birds saw a demonstrator use its beak (group Beak), and eight birds saw the magazine training video sequence in which a bird fed from the open hole in the test box (group Control).

Figure 7. Diagram of the basic apparatus used in Experiments 3.1-4.3, showing a) Side view, and b) Overhead view.

a)



b)



Throughout the experiment, demonstrator and observer birds were housed separately in groups of four to eight in large breeding cages (100cm x 50cm and 50 cm high), with free access to water, grit, and cuttlefish. Prior to the experiment, and during initial magazine training, birds were fed ad lib on millet. During the second half of magazine training and the entire test phase birds were placed on a feeding schedule. They were fed 3-6gms millet/bird/day after the completion of training/ testing. Birds were weighed daily and weight was maintained above 90% free feeding weight by the provision of extra food if necessary. The birds were maintained on a 12:12 light:dark cycle (light onset 0800 hours), at a temperature of 22°C (± 2 degrees).

Apparatus

All the birds were trained and tested in the holding room in a modified bird cage (60cm x 32cm and 41 cm high) (see Figure 7a). Three of the cage sides and the roof were constructed of 1cm-gauge wire bars. Bars on the fourth side were replaced with a transparent Perspex plate. The base of the cage was covered with sand sheets. The cage could be divided into two chambers of unequal size (37cm x 32cm and 41cm high; 22cm x 32cm and 41cm high) using a movable wooden partition. The smaller, back chamber, contained two plastic perches (21cm off ground) and was used as a holding chamber for the birds prior to session onset, and between trials during a session. The larger, test, chamber contained the test box and one perch (5cm off ground, 15 cm from front of cage, 5cm from test box). Access to the interior of the cage was through a hatch in this chamber located halfway along one long side. The same side was screened from view using a black plastic sheet.

The test box, present at all times in the test chamber, consisted of an opaque box (21cm x 10cm and 4cm high) placed on the floor next to the Perspex plate (see Figure 7a and 7b). The position of the box was such that its long axis ran parallel to the end wall and the perch. The sides and base of the box were made of thin sheet metal, and the removable lid was made of opaque white plastic. Half the lid, on the left with respect to the observers, was permanently covered by a section of sand sheet (10.5cm x 10cm). The exposed half could be covered with a piece of white card (10.5cm x 10 cm).

The box was filled to a height of 1cm with millet. Budgerigars could reach this millet through a hole (diameter 3.5cm) centrally located in the exposed half of the lid. This hole acted as a receptacle for the stopper (see Figure 7b). The stopper consisted of a shallow hollow cylinder, 0.8cm deep and 3.5cm diameter. The top of this cylinder was replaced with thin plastic lining creating a concave surface and the entire stopper and lining was coloured blue using a permanent marker pen. Two thin wires were crossed over the centre of the stopper, at 90 degrees from each other, to provide a place for the birds to grasp. The stopper could be displaced downwards to gain access to the food. To prevent the stopper being lifted out, two wire arms, consisting of a loop of wire 1cm long, were attached to the underside of the stopper. When in place the stopper was supported by a metal ring, 1cm deep, which surrounded the circumference of the hole on the lower surface of the lid. The inside of the ring, in which the stopper rested, was lined with a thin layer of Velcro (eye side). The depth of the stopper rim and wires was 0.25cm from the surface of the lid. The depth of the base of the stopper was 0.33cm.

During initial bird training an additional mock test box was used. This was constructed entirely of plastic, and was transparent on the sides and opaque white on the lid. Dimensions were 21cm x 10cm and 4cm high. Two holes, both of diameter 3.5cm, were cut in the lid to allow access. The box was completely filled with millet (height 4cm).

The equipment was controlled, and the data were collected manually, by the experimenter, who was positioned, at all times, approximately 1m from the screened side of the cage not visible to the subjects. Demonstrator and observer birds were habituated to the presence of the experimenter during training. All experimental sessions were recorded by an analogue Sony camcorder (model AC-V25A) placed behind the laptop angled down at approximately 60 degrees. The camera was focussed so that the stopper box was central. The angle of filming ensured that both the stopper and the front half of the cage were clearly visible. The camera was connected to a standard Sony TV monitor, which was placed on a shelf below the test cage allowing the experimenter to observe the birds indirectly.

Stimuli

Observers were presented with stimuli consisting of video clips of demonstrator birds. Three clips were used in total, each lasting ten seconds and featuring a different bird. The magazine training clip, which was also presented to the Control group, consisted of a bird feeding from the open hole in the absence of the stopper. The clip started with the bird standing on the edge of the box and then showed the

bird moving his head in and out of the hole a total of eight times. While the head was in the up position the beak was seen to move and husks occasionally fell out. The purpose of the clip was to show a bird feeding but not removing the stopper.

The Beak group was presented with a clip showing a bird flying towards the front of the cage and alighting on the box. The demonstrator bird then used its beak to remove the stopper, which was blocking the hole, before feeding. Before the removal occurred, the stopper was contacted a total of eight times in various places, from the rim to the centre, with removal occurring on the last contact. A period of four seconds elapsed between first contact and the stopper disappearing from view. In the remaining six seconds the bird moved his head in and out of the hole three times. As with the magazine training clip, husks could be seen occasionally falling from the beak when the head was in the up position.

The Foot group was given a very similar clip, except that the demonstrator bird, once it had alighted on the box, used its left foot to push the stopper down before feeding. Before the stopper removal occurred the stopper was contacted a total of seven times in various places, from rim to the centre, with removal occurring on the last contact. A period of just over two seconds elapsed prior to the stopper disappearing from view. In the remaining time the birds moved his head in and out of the hole three times. As with the other two clips husks could be seen occasionally falling from the beak when the head was in the up position.

Stopper removal clips were chosen for the competence with which the demonstrator removed the stopper, and the clarity with which this could be seen. To enable observers to obtain a clear view of the demonstrator's reward, a small bulb powered by an AA battery was placed inside the test box during filming to light up the millet. This was not present during testing, and the bulb was not visible in the clips.

The stimuli were recorded using a Sony digital camcorder (model TRV730E). This was placed in the same position as the camera used during test sessions. Stimuli were edited and played back using a Sony laptop with a 20cm thin film transistor (TFT) screen (model VAIO PCG-FX109K). The software used was Dvgate and Windows Media Player. When presenting the stimuli the laptop screen was positioned parallel to, and approximately 15cm from, the Perspex plate (see Figure 7a). Image size was manipulated to make both the filmed budgerigar and the test box appear life size and the background was set to black to minimise visual distraction. Sound was turned off throughout the experiment to prevent auditory cues affecting learning.

Procedure

All training and testing was conducted in the morning, and timed to coincide with the beginning of the light phase of the birds' light/dark cycle. Before each session began the bird was positioned in the holding chamber of the test cage. Each session commenced when the wooden partition was lifted allowing the bird to access the test chamber, and ended with the bird once again positioned in the holding chamber.

Observer training and testing

Observers underwent magazine training prior to the start of testing. While on ad lib food, birds were fed in their home cage, for four days, from the mock test box. On each of the next four days each bird was placed in the test cage for three separate five minute sessions to allow them to habituate to the cage. The wooden partition was used at the start and end of each of these sessions to restrain the bird briefly within the holding chamber. The test box was present without the stopper in place so birds could feed from the hole, and on the last two of the four days the laptop screen was also present but not switched on. On every day of training and testing birds were placed in the test cage in the same order to allow them to become accustomed to the schedule. The running order was random with respect to group.

After these initial eight days, birds were placed on a feeding schedule and given a further four to eight magazine training sessions. In the first replication, each of these sessions consisted of five trials in which the observers were allowed access to the test box while the magazine training video clip (showing a bird feeding from the open hole of the test box) was played repeatedly. In the second and third replications the sessions were extended to ten trials to increase the number of removal opportunities an observer had. If a bird did not feed, trials lasted one minute. If they did feed they were allowed to do so for 30 seconds before the trial was ended. Birds were moved onto the testing phase of the experiment after four sessions if they had fed on at least 80% of trials in one session. If they had failed to reach this criterion after four days, magazine training continued until the criterion was met, or eight sessions had elapsed. If a bird failed to reach criterion after eight sessions it was

excluded from the experiment. Previous experiments with budgerigars in this laboratory had indicated that non-responding on magazine training was a predictor of non-responding on test.

A test session consisted of ten observation trials alternated with ten test trials. Observation trials lasted one minute during which time observers saw six ten second clips. These clips showed their demonstrator removing the stopper and feeding (Beak and Foot groups) or just feeding (Control group). During observation the test box was present but access to the stopper was prevented with a piece of card placed over the exposed top of the test box. At the end of each observation trial the observer was ushered back into the holding area and restrained there for approximately ten seconds using the wooden partition, while the stopper box was uncovered and the video clip was turned off. The removal of the partition indicated the beginning of a test trial. Test trials ended after one minute had elapsed or, if the bird had made a response, after it had been allowed 30 seconds in which to feed. Tests were administered on three consecutive days.

Videotapes of the observers' behaviour during test trials were scored to provide the data for analysis. Whenever an observer removed a stopper the appendage (beak or foot) which was used to bring about the removal was recorded. Accuracy was checked by comparing the performance of two independent raters across a randomly selected 30% of test trials. The raters were in agreement regarding the appendage used for removal in 98.7% of a randomly selected 30% of test trials.

Results

Beak and foot responses were very uniform across birds. Birds making a beak response would either peck at the stopper several times gradually dislodging it downwards or they would exert a continual downwards pressure using their beaks until the stopper was displaced. Birds making a foot response would either walk over the stopper, in which case their weight would displace the stopper downwards, or, they would stand close to the stopper and stamp on it once with one foot to remove it.

Data were collected from 22 of the initial 32 observer birds (Beak, N=7; Foot, N=9; Control, N=6). In the Foot group one bird was excluded as a result of failing to eat during magazine training, and two others were excluded for failing to make any responses on test. Four birds from group Beak were excluded for failing to respond on test. Testing of three birds, one bird in the Beak group and two in the Control group, was terminated prematurely because their weights became unacceptably low (less than 90% of their free feeding weight).

In order to compare groups in terms of the type of responses they made, an effector discrimination ratio was calculated for each bird across all three test sessions by dividing the number of beak responses by the total number of responses (i.e. beak/ beak + foot). Figure 8 shows the mean effector discrimination ratio for each group. From this it can be seen that the groups differed in the predicted direction, with birds in the Beak group having a higher ratio than birds in the Foot and Control groups.

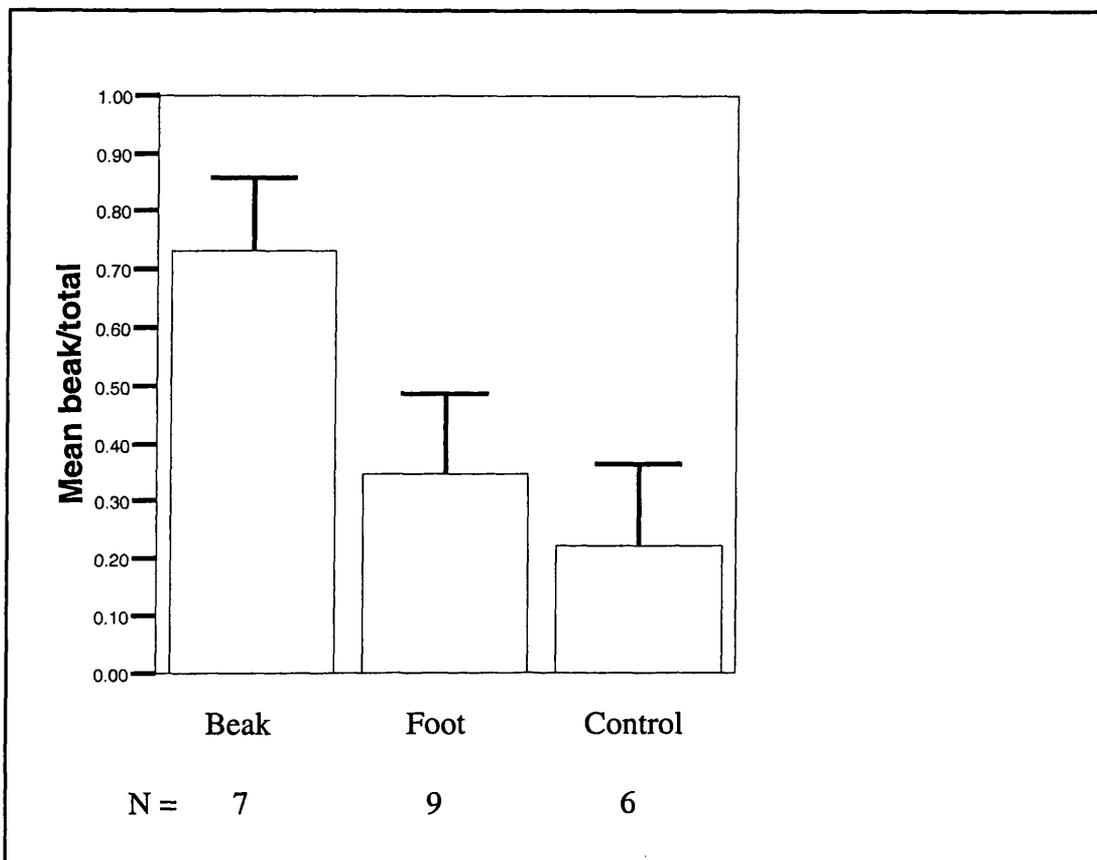


Figure 8: Mean effector discrimination ratio (beak/total) and standard errors of the means across the three tests administered for birds in groups Beak, Foot and Control in Experiment 3.1.

One-way ANOVA indicated a marginal effect of group ($F(2,21) = 3.396, p=0.055$).

When a mixed-model ANOVA was carried out, with group (Beak, Foot and Control) as the between subjects factor, and test (1-3) as the within subjects factor, neither the main effects of group nor the group x test interaction were significant ($F < 1$ both cases), but the effect of test was reliable ($F(1,11)=10.670, p=0.008$). The lack of a group effect in the mixed-model analysis can be attributed to loss of power. Eight birds included in the overall effector discrimination ratios could not be included in the test-by-test analysis because they did not remove the stopper in each of the three tests.

When data from all three tests is examined (see Figure 8) it can be seen that birds in group Beak have a higher ratio of beak removals than birds in either group Foot or group Control which do not differ from one another. The similarity between the performance of birds in group Foot and group Control can be interpreted in two ways. First, it is possible that observation experience had no effect on either group, and birds in both groups were therefore performing the baseline level of beak and foot responses. Second, learning in the Foot group may have been obscured by a low baseline, or floor effect, of beak responding, which resulted in the Control group having an equally low response ratio.

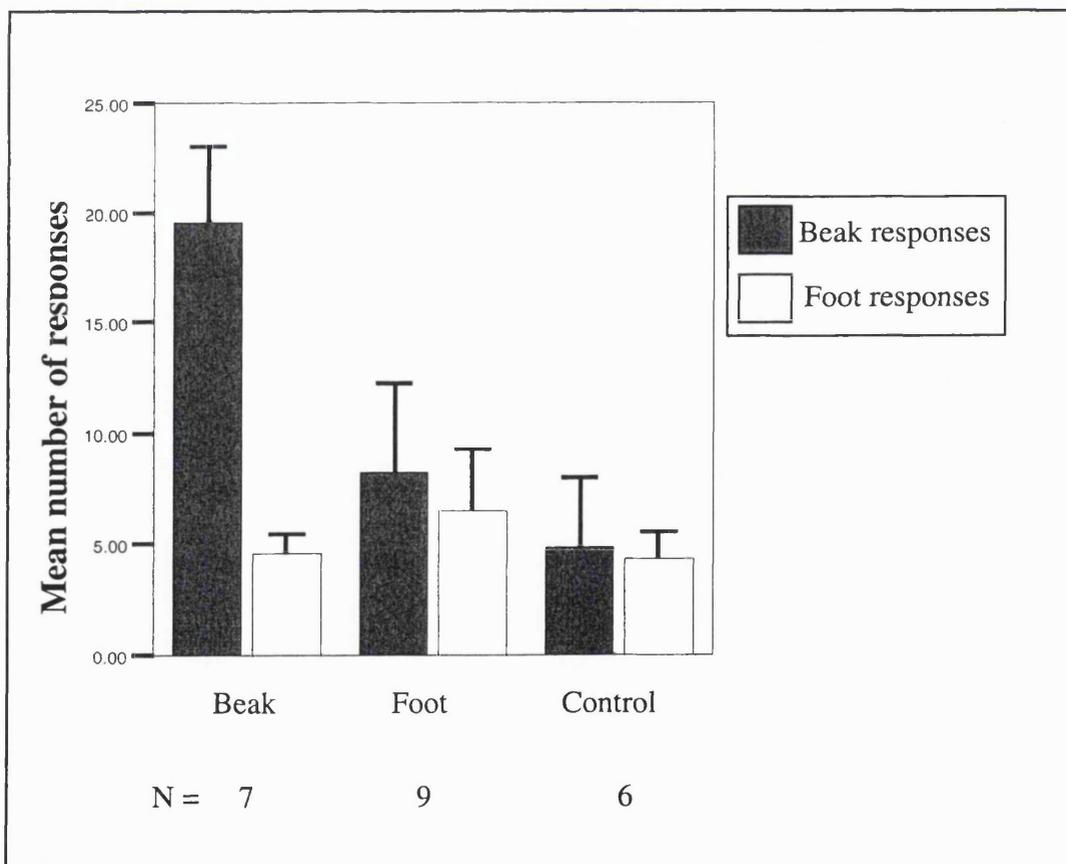


Figure 9: Mean number of beak and foot responses and standard errors of the means made across all three tests administered in groups Beak, Foot and Control in Experiment 3.1.

Frequency data were examined in an attempt to distinguish these possibilities. Figure 9 shows the number of beak and foot responses made by birds in each group. It is apparent that Beak birds made more beak than foot responses, while the Foot and Control groups made equal numbers of foot and beak responses. A mixed-model ANOVA with response (beak or foot) as the within subjects variable and group (Beak, Foot or Control) as the between subjects variable confirmed this. The main effects of response and group were significant ($F(1,19)=4.160$, $p=0.056$, and $F(2,19)=3.809$, $p=0.041$ respectively) and the response by group interaction approached significance ($F(2,19)=2.713$, $p=0.092$). Simple effects analyses revealed a significant difference between the number of beak and foot responses made by Beak birds ($p=0.006$) but no difference within either the Foot or the Control group.

When total number of responses was included as a covariate in a one-way ANOVA with group (Beak, Foot and Control) as the independent variable and ratio (beak/beak+foot) as the dependent variable, group was no longer found to be significant ($F<1$).

Discussion

Initial analyses of the data from Experiment 3.1 indicated that groups differed in the predicted direction in the proportion of beak responses that they made on test. Birds in group Beak were making proportionally more beak responses than birds in groups Foot and Control. When response frequencies were examined, birds in group Beak were found to be making more responses than birds in the other two groups. More

beak than foot responses were made by birds in group Beak, while birds in groups Foot and Control were making equal numbers. When response number was taken into account it was found that groups no longer differed in the proportion of beak responses made.

The results therefore indicate that only birds in group Beak were influenced by their virtual demonstrator. As birds in group Beak showed elevated responding with respect to groups Foot and Control, and the beak response is similar to pecking, it is possible that their responding was brought about as a result of social facilitation of pecking, as opposed to imitation of beak use. Social facilitation was characterised by Thorpe (1956) as occurring when the sight of an animal engaged in a behaviour releases that behaviour in the observer. In Experiment 3.1 the sight of a demonstrator pecking may have released pecking behaviour in the observer. If this effect persisted from the observation trial until the test trial, birds in group Beak may have accidentally pecked the stopper. If this resulted in stopper removal it would have been recorded as a beak response resulting in the elevated beak responding observed.

A large number of studies have investigated socially facilitated, or contagious, pecking in birds, especially domestic chickens, *Gallus domesticus* (e.g. Turner, 1964; Tolman & Wilson, 1965; Suboski & Bartashunas, 1984). Video images have been shown to promote pecking in chicken observers (Keeling & Hurnik, 1993), and attempts have been made to quantify the effect. For example, Keeling & Hurnik (1996) equated pecking rate of chickens, in the presence of a feeding conspecific, with that of food deprived birds. They found that rate was equivalent to a period of

92 minutes of deprivation despite the fact that observers were satiated at the time of testing.

Little attempt has been made to investigate the mechanisms mediating social facilitation. The release of matching behaviours in observers could occur as result of an innate stimulus-response link, also known as a reflex, or it could be a learned stimulus-response connection or habit. In either case, one would expect the effect of demonstrator observation to be immediate and indiscriminate. Thus if birds in group Beak were pecking as a result of social facilitation alone, their pecking would not be expected to be confined to the stopper.

To assess this possibility, the video recordings of observation and test trials in Experiment 3.1 were re-scored for evidence of undirected pecking. In observation trials the number of pecks made to the lid covering the top of the test box were recorded. If social facilitation was occurring, birds in group Beak should show elevated pecking in comparison to birds in the Foot and Control groups. In test trials the number of pecks made to both the stopper and the lid were recorded and a ratio of pecks to the stopper over total was calculated for each bird. If social facilitation alone was occurring birds in group Beak should have a lower ratio than birds in groups Foot and Control. A lower ratio would be expected in birds in group Beak as pecking would be undirected with birds equally likely to peck both the stopper and the lid.

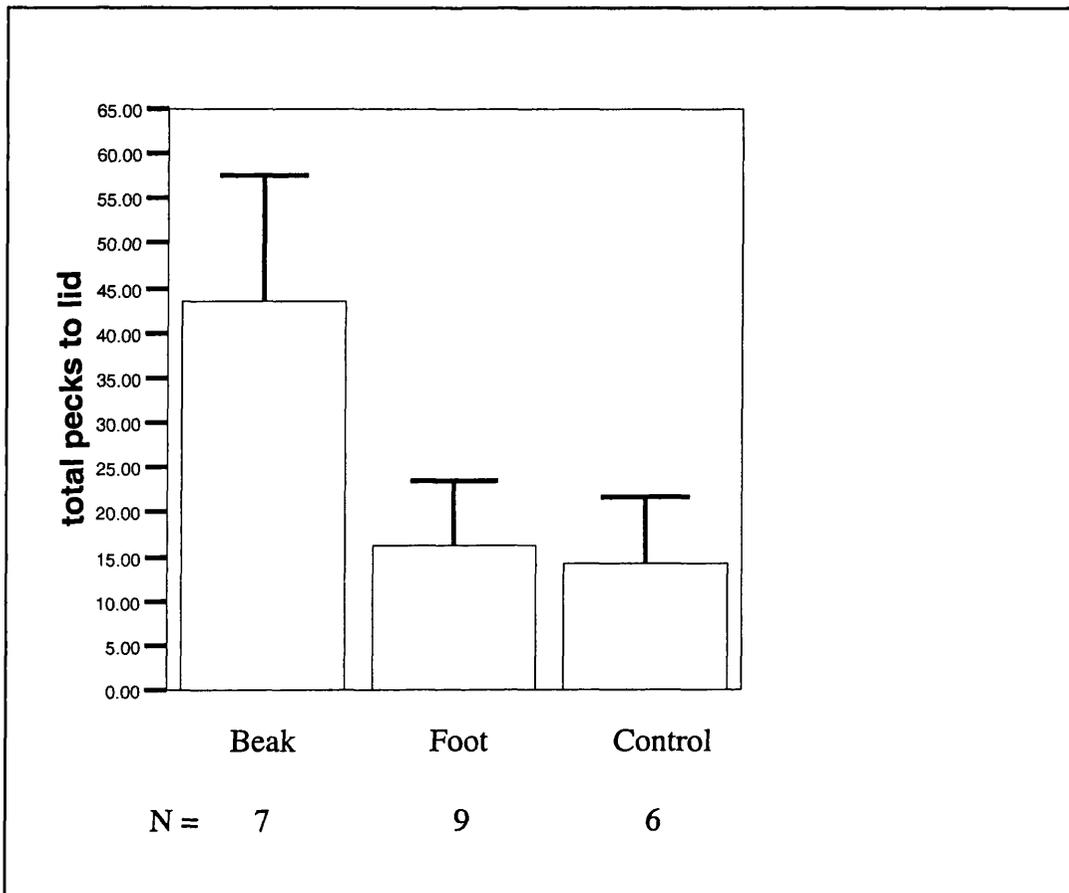


Figure 10: Total number of pecks made to the lid of the test box during observation (and standard errors of the means) by birds in groups Beak, Foot and Control in Experiment 3.1.

Figure 10 shows the number of pecks made to the lid of the test box during observation by birds in each of the three groups. Numerically, the birds in group Beak made more pecks to the lid, but the effect of group was not significant ($F < 1$). Figure 11 shows the pecking ratio (pecks to stopper/total pecks) during test trials for birds in each of the three groups. The ratios for each group are very similar. A one-way ANOVA comparing groups was non significant ($F < 1$).

The tests carried out on the pecking data indicate that birds in the Beak group were not pecking the area around the stopper more than birds in the Foot and Control groups during observation. Furthermore, on test, birds in group Beak were as

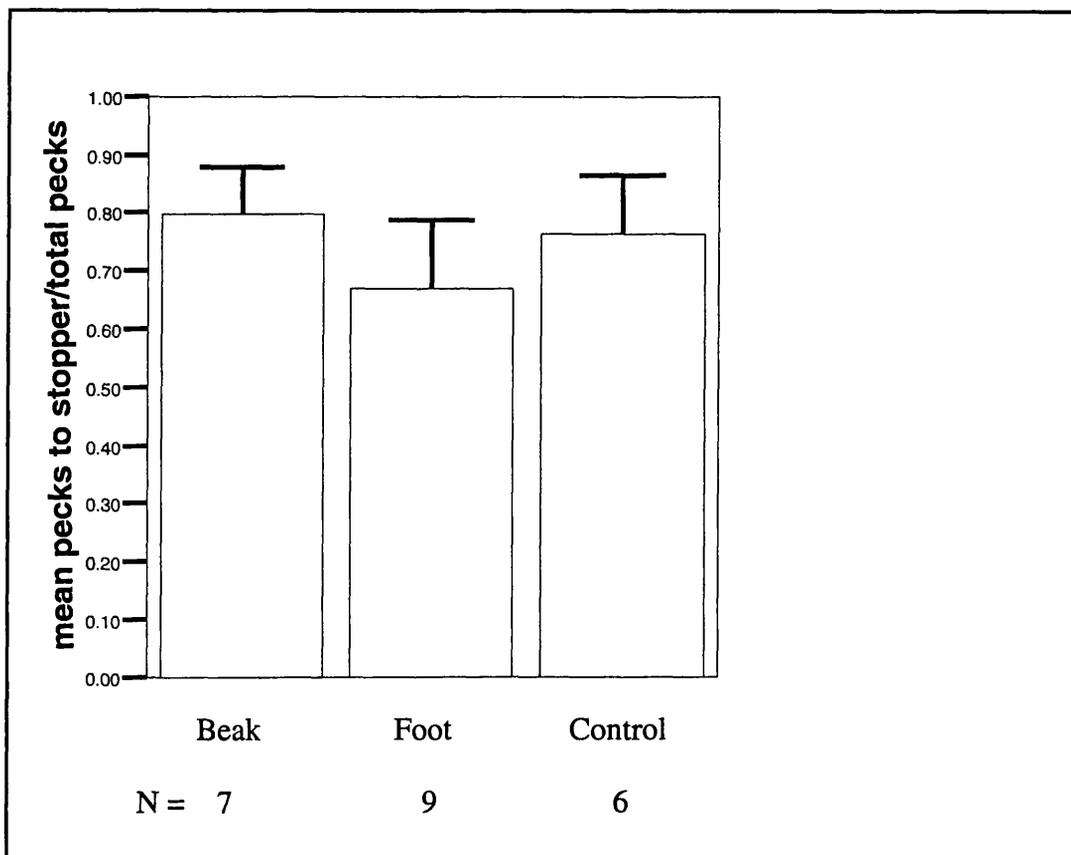


Figure 11: Mean peck discrimination ratio (pecks to stopper/total) and standard errors of the means during test trials for birds in groups Beak, Foot, and Control in Experiment 3.1.

specific in directing their pecks to the stopper as birds in both group Control and group Foot. Social facilitation alone therefore seems an unlikely explanation for the results obtained. It is possible however that social facilitation was occurring in the Beak birds in conjunction with stimulus enhancement. The activity of demonstrators in all groups could have directed the observers' attention towards the stopper location and made it more likely that they would approach the stopper on test. If social facilitation was occurring in the Beak birds in addition to this stimulus enhancement the result would be stopper-specific pecking, which could account for the results obtained. Data from the present experiment cannot be used to rule out this possibility

Results similar to those of the present experiment have been obtained in treadle experiments with quail (Akins & Zentall, 1996; Dorrance & Zentall, 2001). Naïve quail observed a trained demonstrator either peck or step on a treadle and receive a food reward. When tested a significant pecking versus stepping group difference was obtained. However, it is apparent from response frequencies given, but not statistically analysed, that the birds in the pecking group were responding at a much higher rate, and making many more pecking responses, than birds in the stepping group. Although an imitative explanation was given for these results it is possible that they, like the results of the present experiment, can be accounted for by social facilitation in conjunction with stimulus enhancement.

It is encouraging that similar results have been obtained with two different species (budgerigars and quail), using two different two-action procedures (stopper and treadle), especially given that the results were obtained with both live and virtual demonstrators. However, the possibility that the results can be explained by social facilitation in conjunction with stimulus enhancement suggests that further modification of the stopper paradigm is required before imitation effects can be isolated from socially facilitated pecking.

Experiment 3.2

Experiment 3.2 was designed to address the possibility that stimulus enhancement in conjunction with social facilitation could result in stopper specific pecking. In this

experiment birds were presented with two stoppers on test, and during each observation trial they observed a demonstrator making either a foot response to one stopper or a beak response to the other stopper. Half the birds observed a beak response on the right stopper and a foot response on the left stopper (Group RBLF) while the other half observed a beak response on the left stopper and a foot response on the right stopper (Group LBRF). Because observers saw a demonstrator active at both stoppers, one would expect stimulus enhancement of each stopper to be equivalent. If observation of a Beak demonstrator results in social facilitation of beak responses, in conjunction with the stimulus enhancement, beak responses would be expected to be high at both stoppers regardless of the removal type observed, as demonstrators were equally active at each stopper. If beak observers make a greater proportion of beak responses only to the stopper on which they saw beak responses made, this effect could not be explained by social facilitation plus stimulus enhancement.

Methods

The method differed from that of Experiment 3.1 in the following respects:

Subjects

Twenty-four juvenile budgerigars were used. Four were observers in Experiment 3.1 and were assigned the role of demonstrator. The remaining 20 were assigned in equal numbers to Groups LBRF (left stopper beak removal, right stopper foot removal) and RBLF (right stopper beak removal, left stopper foot removal). At the onset of scheduled feeding the birds' mean weight was 36.89gms (SEM=0.69).

Apparatus

The test box was modified to take two stoppers (3.5cm from closest end of box, 7cm from each other). These could be covered when necessary with a piece of white card (21x10cm). Both stoppers were painted a uniform green using standard matt acrylic modelling paint.

Stimuli

Five stimuli videos were used, each lasting ten seconds and featuring a different bird. The magazine training clip, consisted of two birds feeding from the open holes in the absence of the stoppers. The clip started with the two birds landing on the edge of the box and then showed the birds moving their heads in and out of the hole a total of eight times. When the head was in the up position the beak was seen to move and husks occasionally fell out.

Each of groups LBRF and RBLF saw two different stimuli videos. Each featured a bird flying towards the front of the cage, alighting on the test box and then removing one of the two stoppers and feeding. As with the magazine training video when the head was in the up position the beak was seen to move and husks occasionally fell out. Group LBRF saw one clip in which the left stopper was removed with two beak contacts, this took a period of 1 second and was followed by 9 seconds of feeding in which the bird moved its head in and out of the hole four times. The other clip shown to group LBRF featured a bird removing the right stopper with its foot.

Stopper removal required two contacts, which took a period of 3 seconds. In the remaining 7 seconds the bird moved its head in and out of the hole three times.

Group RBLF saw the opposite stopper removal videos. In one clip a demonstrator removed the right stopper with its beak. Stopper removal required two contacts, which took a period of 2 seconds. In the remaining 8 seconds the birds moved its head in and out of the hole a total of five times. In the second clip shown to group RBLF a bird removed the left stopper with its foot. Stopper removal required two contacts, which took 3 seconds. In the remaining 7 seconds the birds moved its head in and out of the hole three times.

Procedure

Within each test session observers were given five observation trials in which they saw one stopper being removed by stepping, and five trials in which they saw the other stopper being removed by pecking (stopper location being determined by group). Order of presentation was randomised within a session and across sessions with the proviso that foot and beak removal clips were not alternated and that birds never saw more than two consecutive presentations of one trial type.

The birds were given four tests in total. The additional test was thought to be necessary because the birds were being given a much harder task and it was thought that additional observation trials may have been required to obtain evidence of conditional discrimination learning.

As in Experiment 3.1, videotapes of the observers' behaviour during test trials were scored to provide the data for analysis. Whenever an observer removed a stopper the raters recorded both the appendage (beak or foot) used to bring about the removal and the location (left or right with respect to the observer's body). Because data were used in an undergraduate project, it was possible to check accuracy by comparing the performance of two independent raters across 100% of test trials. The raters were in agreement regarding the appendage used for stopper removal in 95.4% of all trials, and the side of the stopper removed in 100% of trials.

Results

Response topographies were as described in Experiment 3.1. Data were collected from 18 of the initial 20 birds (LBRF, N=9; RBLF, N=9). Two birds, one from each group, were not tested because they failed to feed from the test box during magazine training.

The summed data from the four test sessions were analysed. Two effector discrimination ratios were calculated for each bird, one for each stopper, consisting of the number of beak removals they made in all four tests divided by the total number of removals. (It was not possible to analyse the data from each test separately because no bird responded to both stoppers on each of the four test sessions). If the observer birds learned a conditional discrimination, the LBRF group would be expected to have a low ratio on the right stopper and a high ratio on the left while for group RBLF the opposite would be expected. The occurrence of social

facilitation in conjunction with stimulus enhancement would be apparent by a high ratio for both groups on both stoppers.

A check on response frequencies prior to analysis of effector discrimination ratios revealed that the birds in both groups responded more to the right stopper (mean=23.67, SEM=2.58, N=18) than the left stopper (mean=4.78, SEM=1.59, N=18). A mixed-model ANOVA with stopper (Left or Right) as the within subjects variable and group (RBLF or LBRF) as the between subjects variable, revealed a significant effect of stopper ($F(1,16)=23.65$, $p \leq 0.00$). No other main effects or interactions were significant ($F < 1$, all cases). To take account of the variation in response direction a spatial discrimination ratio was calculated for each bird, consisting of the number of responses made on the right divided by total responses, and this spatial discrimination ratio was included as a covariate in the subsequent analysis.

Figure 12 shows the effector discrimination ratios for each group on each stopper. It shows that the groups differed in the predicted direction, and suggests that the birds learned the conditional discrimination. Birds in group RBLF had a higher effector discrimination ratio on the right stopper, while the opposite appears to be true of group LBRF. To confirm this, a mixed-model ANOVA with group (RBLF or LBRF) as the between subjects variable and stopper (Left or Right) as the within subjects variable was carried out. As predicted the results indicated a significant interaction between stopper and group ($F(1,9)=5.035$, $p=0.05$). No other main effects or interactions were significant ($F < 1$ all cases), although group approached significance ($F(1,9)=3.536$, $p=0.093$).

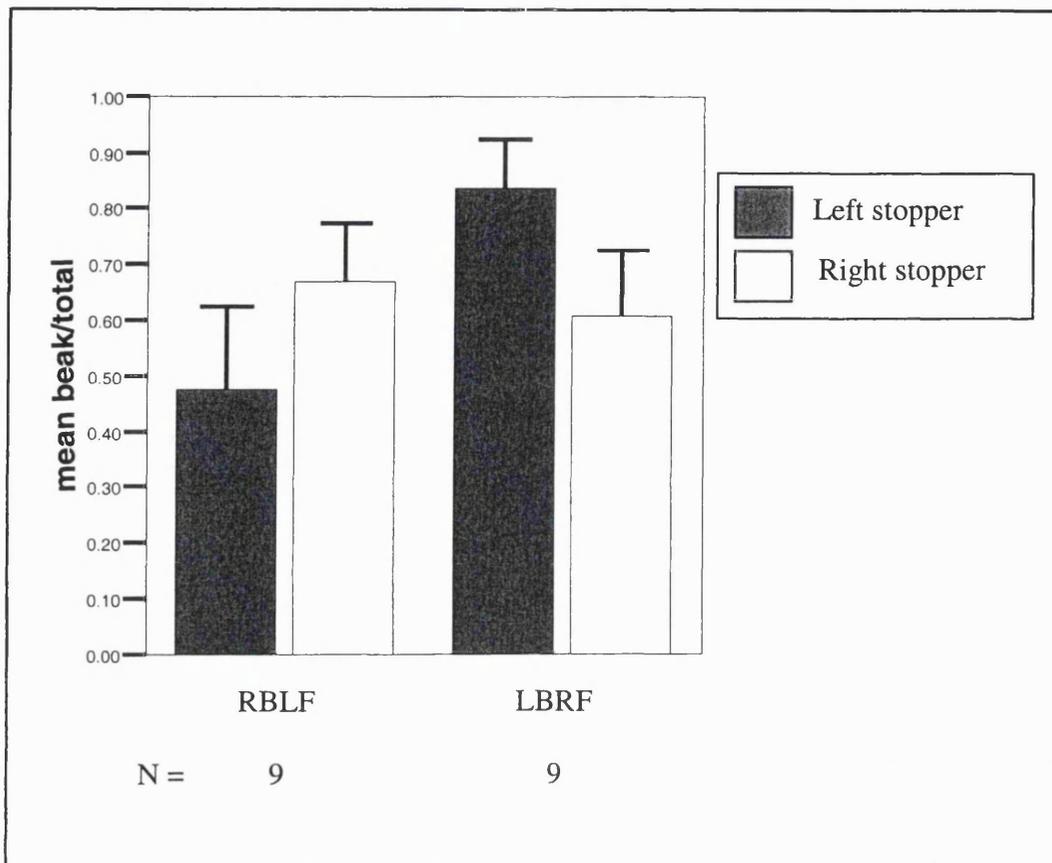


Figure 12: Mean effector discrimination ratio (beak/total) and standard errors of the means for responses made to the left and right stoppers by birds in groups RBLF and LBRF in Experiment 3.2.

The data were additionally analysed on a trial-by-trial basis. As birds saw one type of removal prior to every test trial, it was possible to examine whether birds went to the same or different stopper side as their demonstrator had in each trial, and whether they made the same or different response in each trial. Paired sample t-tests comparing the number 'same' and the number 'different' for side and effector type, on each of the four tests, revealed no significant trend for birds to do the same as they had observed. Interestingly when only the first five trials in each ten trial test were examined, it was found that birds were doing significantly more 'different' side responses in test 2 ($t=-3.117$, $p=0.006$), test 3 ($t=-2.067$, $p=0.055$), and test 4 ($t=-2.650$, $p=0.017$).

Discussion

The results of the primary analysis of Experiment 3.2 suggested that the birds were learning the conditional discrimination. As predicted group LBRF had a higher beak/total effector discrimination ratio on the left stopper, where a beak response had been observed, than on the right stopper, where a foot response was observed. The opposite was seen with group RBLF. As there was no overall beak bias in either group these results cannot be explained by social facilitation in conjunction with stimulus enhancement. It could be argued that for some reason stimulus enhancement of the stopper where beak responses were observed was greater than the stimulus enhancement of the other stopper. This would give the results obtained, but this is not supported by the response rates. The analysis of response rates highlighted the fact that both groups showed a right response bias likely to be due to the position of the experimenter close to the left side of the test cage.

However, without replication the results of Experiment 3.2 must be treated with caution. Sample size was very small and the right response bias meant that the left stopper effector ratio was often based on fewer responses than that for the right stopper. While this probably cannot account for the effect obtained, it would be preferable if the experiment had been balanced with an equal number of responses made to each stopper.

The trial-by-trial analysis did not yield any evidence that the birds tended to use the same effector as their demonstrator on each trial. However, it did show, unexpectedly, a tendency on the part of the observer birds to approach the stopper

not contacted by the demonstrators. This is interesting as it was expected that a bird would respond to the same stopper as a result of stimulus enhancement. It also contrasts with findings from other video experiments in which birds reliably went to the same place where their demonstrator was seen responding or feeding. For example McQuoid & Galef (1992; 1993) showed that Burmese jungle fowl presented with two food bowls, would preferentially feed from the bowl at which they had observed a virtual demonstrator feeding. Similarly, in previous two-action stopper experiments, observers reliably responded at the location where their demonstrator had responded (Campbell et al, 1999; Heyes & Saggerson, 2002; Mottley & Heyes, in press).

There are two possible explanations for this behaviour. First, observers may have been wary of feeding from a location where an unknown bird had been. The gap between observation and testing was very small and so it may not have been apparent that the other bird had gone, and observers were never housed with demonstrators so they were visibly, if not audibly, unfamiliar. Secondly, birds may have been going to the opposite stopper because they wanted to avoid a depleted food source. As trials progressed and birds gained experience with both stoppers this effect would have been reduced. If this is the case the effect would be expected to disappear across tests, but the results indicate that it persisted being present at the start of test 2, 3 and 4. It is possible that birds were incapable of remembering the demonstrator from one test to the next, so the demonstrator was always unfamiliar to the observer at the start of testing. Alternatively, when hungriest at the start of testing the safest feeding strategy was to assume food source depletion.

Experiment 3.3

Experiment 3.3 was designed to overcome the problem of location bias encountered in Experiment 3.2, using an alternative conditional discrimination procedure. In this experiment only one stopper location was used, preventing birds from developing a location bias. The stopper on the right side of the test box was selected because the results of Experiment 3.2 showed that this was where the birds preferred to respond. Instead of discriminating between location, as in Experiment 3.2, birds in Experiment 3.3 were required to discriminate between two stoppers which differed in luminance. As video playback was used, and it is not known how birds perceive colour on TFT (Fleishman, McClintock, D'Eath, Brainards & Endler, 1998), luminance was used instead of colour and maximum contrast was chosen. One stopper was white and one was black and the lid of the test box was painted a uniform mid-grey.

In addition to reducing the number of stoppers present, Experiment 3.3 also differed from Experiment 3.2 in the procedure used. In Experiment 3.2 birds observed both foot and beak removals but on different stoppers and were rewarded on test for all responses made. In 3.3, all birds observed beak removal of the black stopper and foot removal of the white stopper. On test half the birds (group Same) were rewarded for making the same responses as the demonstrator (beak removal of black, foot removal of white) and half the birds (group Different) were rewarded for making the opposite responses (beak removal of white, foot removal of black). This design allows the effects of observation, and also the subsequent training on test, to be examined.

If observers had learned to make black-beak and white-foot responses by imitation, those in group Same should learn the test discrimination faster than those in group Different. This is because birds in group Same were rewarded for doing what they observed, while birds in group Different had to learn to do on test the opposite of what they had observed. If birds were influenced by social facilitation in conjunction with stimulus enhancement they would show elevated beak responding to both the black and the white stoppers irrespective of group. As in Experiment 3.2, all birds observed a beak response and a demonstrator active at both stoppers.

Methods

The method differed from that of Experiment 3.1 in the following respects:

Subjects

Twenty-four juvenile budgerigars were used. Four birds were demonstrators in Experiment 3.1 and were assigned the role of demonstrator in Experiment 3.3. The remaining 20 birds were assigned in equal numbers to groups Same (rewarded for making black beak or white foot responses) and group Different (rewarded for making white beak responses and black foot responses). At the onset of scheduled feeding the birds' mean weight was 37.64gms (SEM=0.67).

Apparatus

The test box lid was painted a uniform mid-grey using standard matt acrylic modelling paint. The same kind of paint was used to paint one stopper white and one stopper black.

Stimuli

Three video clips were used in total, each of which lasted a period of ten seconds and featured a different bird flying towards the front of the cage and alighting on the test box. In the magazine training clip the stopper was absent and after landing on the box the bird fed from the open hole, moving its head in and out of the hole a total of five times.

Birds in both group Same and group Different were shown the same stopper removal clips. One featured a bird removing a black stopper with its beak. Stopper removal required four contacts, which took a period of 4 seconds. In the remaining 6 seconds the bird moved its head in and out of the hole two times. The second stopper removal clip featured a bird removing a white stopper with its feet. Two contacts were required to remove the stopper and this took a period of 5 seconds. In the remaining 5 seconds the bird put moved its head in and out of the hole two times.

Procedure

Birds were given six to eight magazine training sessions. The additional two sessions were given to ensure that birds were more resistant to non-rewarding on test.

During observation, both groups saw clips of a demonstrator removing the black stopper with its beak and the white stopper with its foot. During each one minute observation trial, observers saw six, ten second clips of the demonstrator birds. Five of these clips showed black stopper removal and five showed white stopper removal. The order of presentation of video clips varied randomly in every observation trial

within a test session. The constraints were that the different clips must not alternate and that no clip could be shown more than twice in succession.

Within each test observers were given five opportunities to respond to the black stopper and five to respond to the white. Order of stopper presentation was varied randomly across trials following the same constraints as clip presentation. If birds made an incorrect response according to their group assignment the trial ended immediately and birds were ushered back into the holding chamber ready for the next trial.

Birds were given six tests in total to increase the opportunity the birds had to learn the discrimination. Ideally, testing would have continued until the test discrimination was learned but it was not possible to keep the birds on restricted food for a longer period. Given the small size of budgerigars, prolonged food deprivation is detrimental to their welfare.

Independent raters were in agreement regarding the stopper removal technique used by observers on 98.5% of a randomly selected 30% of test trials.

Results

Response topographies were as described in Experiment 3.1. Data were collected from 12 of the initial 20 birds (Same, N=6; Different, N=6). In group Same, two birds were excluded as a result of failure to feed during magazine training, one was excluded for failure to respond on test, and one was excluded due to illness. In group

Different, two birds were excluded as a result of failure to feed during magazine training and two birds were excluded following illness.

It was predicted that if observers had learned to make black beak and white foot responses by imitation, the performance of those in group Same should improve faster than that of those in group Different. To investigate whether performance improved across tests, data from the first three tests was combined (block 1) and data in the last three tests was combined (block 2). (It was not possible to analyse the data from each test separately because no bird responded to both stoppers in each of the six test sessions). For each of the two blocks a ratio was calculated of correct responses (responses birds were rewarded for) over total, for every bird, for both the black and the white stoppers separately. If group Same learned the test discrimination faster than group Different, then the difference between blocks 1 and 2 should be greater for group Same than for group Different.

Figure 13 shows that on the black stopper, group Same showed better discrimination in block 2 than in block 1, whereas the reverse was true of group Different. This was as predicted. However it is also clear from the graph that the opposite pattern is seen with the white stopper. That is, on the white stopper, group Same showed worse discrimination in block 2 than in block 1, whereas the reverse was true of group Different. This was confirmed using a mixed-model ANOVA in which group (Same or Different) was the between subjects variable and stopper luminance (black or white) and block (1 or 2) were the between subjects factors. A significant three-way interaction was obtained ($F(1,9)=11.731, p=0.008$). No other main effect or

interaction was significant ($F < 1$ all cases, except; group, $F = 3.220$; block x group, $F = 3.727$; stopper, $F = 1.429$).

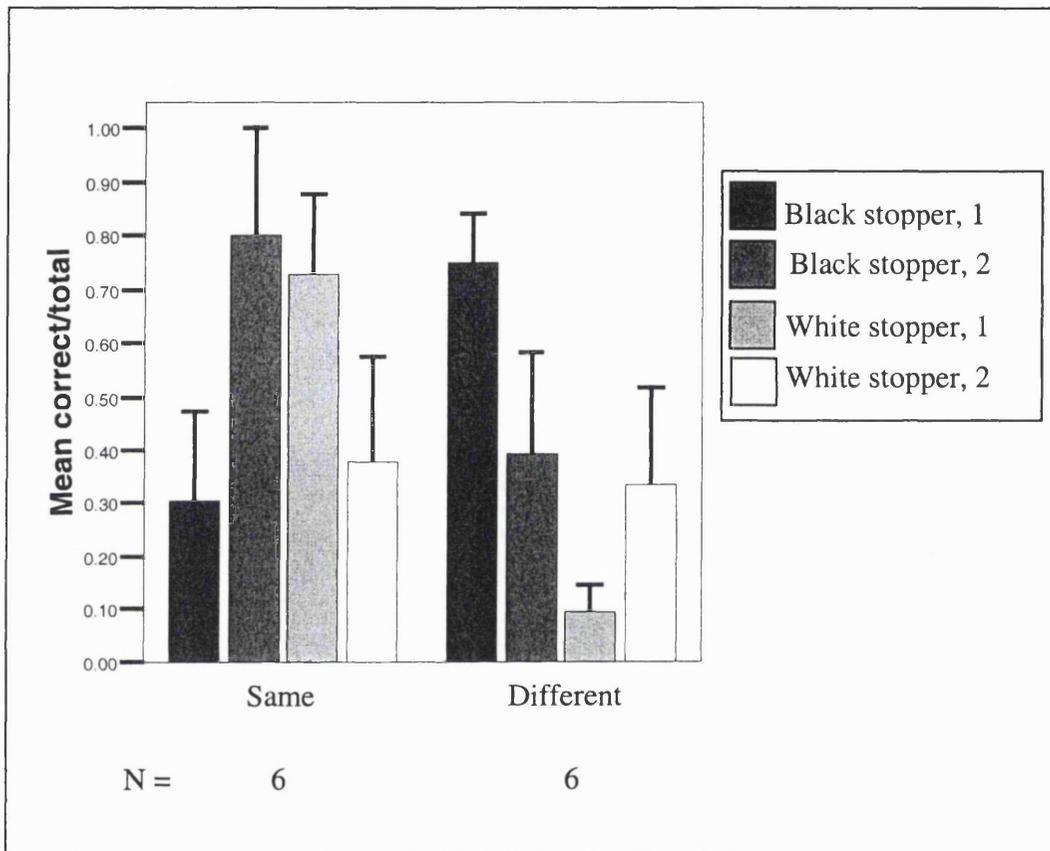


Figure 13: Mean correct discrimination ratio (correct/total) and standard errors of the means for responses made to the Black and White stoppers in Blocks 1 and 2, by birds in group Same and group Different in Experiment 3.3.

To investigate the three-way interaction the number of beak responses birds made in groups Same and Different were examined. For each of the two blocks a ratio was calculated of the number of beak responses over total, for every bird, for both the black and the white stoppers separately. Figure 14 shows these ratios and it is clear that birds in both groups are making more beak responses to both stoppers in block 2 than in block 1. This was confirmed by a mixed-model ANOVA in which group (Same or Different) was the between subjects variable and stopper luminance (black or white) and block (1 or 2) were the between subjects factors. Only the main effect

of test was significant ($F(1,9)=11.731$, $p=0.008$; In all other cases $F<1$, except; group, $F=1.429$; stopper, $F=3.220$; stopper x group, $F=2.390$; stopper x block, $F=3.727$).

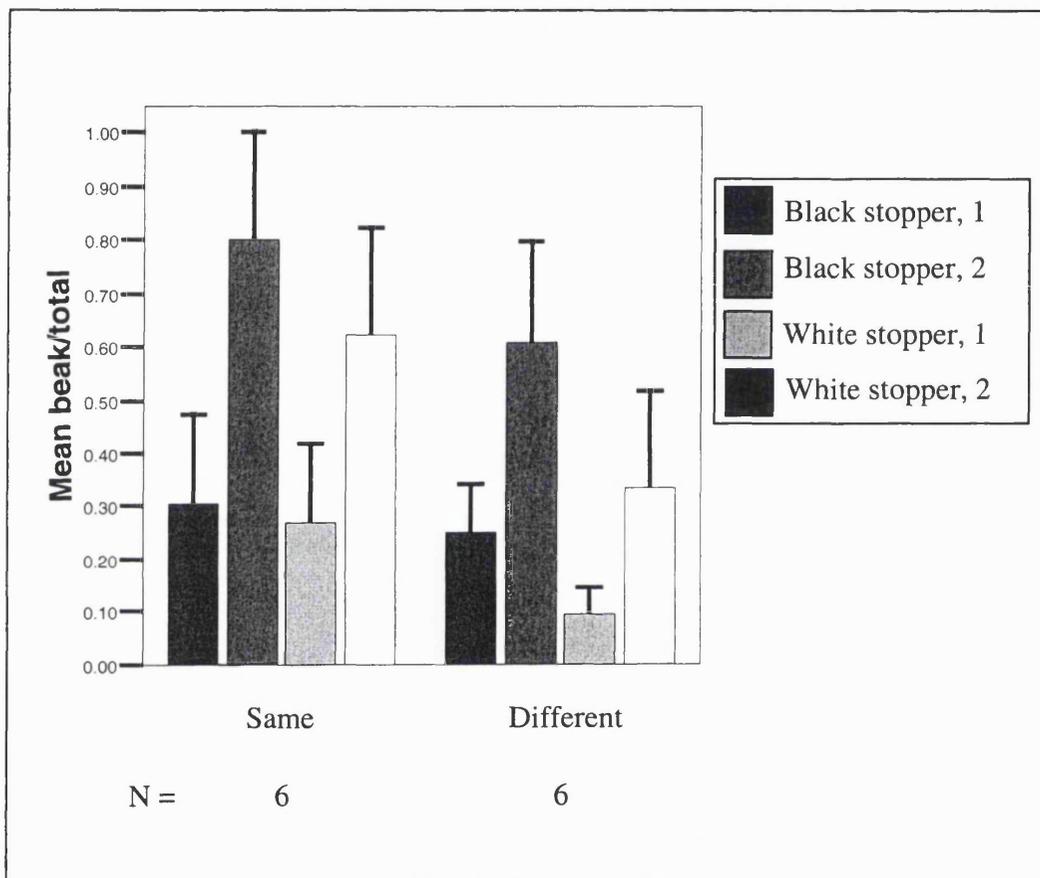


Figure 14: Mean effector discrimination ratio (beak/total) and standard errors of the means for responses to the Black and White stopper in Block 1 and 2, for birds in group Same and group Different in Experiment 3.3.

The increase in beak use between blocks 1 and 2 can account for the significant interaction between group, stopper and luminance obtained when correct discrimination ratios were examined. For the black stopper, where birds observed beak stopper removal, the increase in beak use is correct for group Same but not for group Different. This makes it look as if group Same learned the discrimination faster than group Different on the black stopper. However the opposite is true for the

white stopper, where birds observed foot stopper removal. On this stopper beak removals were correct for group Different so the increase in beak removals made it look like this group learned the discrimination faster than group Same.

Discussion

When the number of beak responses made by birds in each group are taken into account it is clear that Experiment 3.3 provided no evidence that birds in either group Same or group Different learned the discrimination. As tests progressed birds in both groups were making more beak than foot responses irrespective of stopper colour, or reward contingencies. This beak use displayed by both groups is compatible with social facilitation plus stimulus enhancement. The sight of the demonstrator removing the black stopper with his beak, combined with the activity of both demonstrators at the same stopper location, may have released pecking in the observers and drawn their attention to the stopper. Alternatively it is possible that the equipment was biased in some way towards beak responding, however neither explanation detracts from the fact that the conditional discrimination was not learned.

The analysis also makes it clear that there was a flaw in the design. The two groups should have observed either black-beak and white-foot demonstrations, or white-beak and black-foot demonstrations and then been rewarded for performing black-beak and white-foot on test. To fully counterbalance the test two additional groups are needed in which observers see either black-beak and white-foot demonstrations, or white-beak and black-foot demonstrations and are rewarded for white-beak and

black-foot. The flaw in Experiment 3.3 was the fact that birds in both groups saw the same demonstrations but each group was rewarded for different responses. This design does not allow the effects of observation to be separated from the effects of experience on test. Had the predicted results been obtained with birds in group Same learning the discrimination faster than birds in group Different it could have been due to imitation, but this cannot be distinguished from the possibility that birds in both groups simply preferred to make beak responses to the black stopper and foot responses to the white stopper.

3.4. Summary and Conclusions

The experiments in Chapter 3 introduced a variant of an existing two-action paradigm, in which budgerigars observed a demonstrator removing a stopper from a food box with its beak or its feet. As the stopper followed the same downwards trajectory for both beak and foot removals, emulation was excluded as a potential explanation for matching behaviour. This two-action test was implemented using a fixed trial procedure and 'virtual' demonstrators.

In Experiment 3.1 birds were shown virtual demonstrators removing a stopper with their beak (group Beak), their foot (group Foot) or eating from an open hole (group Control). On test, the proportion of beak responses made by birds in each group was found to be different, with birds in group Beak making proportionally more beak responses than birds in either the Control or the Foot group. This was consistent with imitation. However, further investigation revealed that birds in group Beak were making more responses in total than birds in groups Foot and Control, and were

making more beak than foot responses. This raised the possibility that social facilitation of pecking, as opposed to imitation, was occurring in the Beak group.

To investigate the possibility of social facilitation, observation and test trials were re-scored looking for non-specific pecking in the Beak birds. This would have indicated social facilitation but was not found. However, it was possible that social facilitation was occurring along with stimulus enhancement of the stopper. This would result in stopper specific pecking in the Beak birds and therefore elevated beak responses as observed.

The next two experiments, Experiments 3.2 and 3.3, adopted two different conditional discrimination designs to distinguish social facilitation plus stimulus enhancement from imitation. It was argued that, if birds could learn not only the beak response but also where to make the response, then social facilitation with stimulus enhancement, could not account for the result. Experiment 3.2 provided some evidence that birds were learning to link their responses to the appropriate stopper. However, all birds in Experiment 3.2 developed a strong bias in favour of responding to the right stopper, which meant that the result was based on a small sample of responses to the left stopper. This combined with the small number of birds in Experiment 3.2 means that the result must be interpreted with caution.

Experiment 3.3 attempted to overcome the location bias by limiting responding to one stopper location. One of two stoppers, which were of differing luminance (one black, one white), was positioned in the stopper location at any one time. All observers saw beak removal of the black stopper and foot removal of the white

stopper. On test, half the birds were rewarded for making black beak and white foot responses (group Same), while the other half were rewarded for making white beak and black foot responses (group Different). If birds in group Same improved the number of rewards they obtained on test faster than birds in group Different, then this would have been interpreted as evidence of imitation. On test, however, it was found that all birds increased the number of beak responses made as tests progressed irrespective of stopper luminance or reward contingencies. It is possible this was due to social facilitation plus stimulus enhancement.

Conditional discrimination experiments were developed here in an attempt to separate out the effect of social facilitation plus stimulus enhancement from that of imitation. Some success was obtained in Experiment 3.2 but this was undermined to some extent by a side bias developed in the observers. This side bias in conjunction with the results from the bidirectional procedures strongly argues against using any experiment design with budgerigars that is based on responses made in different locations. The birds would appear to be highly sensitive to room cues, particularly the position of the experimenter.

Experiment 3.3 avoided the problem of location bias but failed to provide any evidence of learning despite the extended period of testing. The difficulty in running conditional discrimination experiments, especially in terms of the length of time observers are required to be on a restricted feeding schedule, made persistence with this design untenable. A similar experiment carried out on pigeons by Dorrance & Zentall (2001) also failed to get discrimination during the acquisition stage despite birds being given up to 20 test sessions. It is therefore proposed that alternative

modifications must be made to the stopper box design in order to further investigate imitative abilities in budgerigars while excluding social facilitation plus stimulus enhancement.

Chapter 4

Imitative learning in the budgerigar using a two-action stopper paradigm II.

The previous chapter reported three two-action experiments based on a stopper box design. Birds observed a virtual demonstrator remove a stopper from a test box using either their feet or their beak. If, on test, observers used the same stopper removal technique as had their demonstrator then this would provide evidence of imitation. Emulation was excluded as the stopper moved in the same way for both foot and beak removals. Results from the initial experiment, Experiment 3.1, were compatible with social facilitation plus stimulus enhancement, as only birds observing beak learned and they showed elevated levels of responding. Two conditional discrimination experiments, Experiments 3.2 and 3.3, were run to try to isolate imitation from social facilitation plus stimulus enhancement. However, a stopper location bias in Experiment 3.2 and a beak responding bias in Experiment 3.3 suggested this line of study was not a useful approach for studies of imitation in budgerigars.

The experiments reported in Chapter 4 sought to distinguish imitation from social facilitation plus stimulus enhancement using a delay rather than a conditional discrimination procedure. Social facilitation, as characterised by Thorpe (1956), occurs when a behaviour, in this case pecking, in one animal releases the same behaviour in an observer. The nature of social facilitation is that one would expect the effect to be transitory and not confined to one location. The psychological

mechanism involved could be an innate stimulus-response link also known as a reflex, or it could be a learned stimulus-response connection or habit. In both cases the direct nature of the link between the stimulus and the response means that the effect of the stimulus is immediate and undirected.

The issue of location specificity was addressed in Experiments 3.2 and 3.3 with marginal success. The experiments in Chapter 4 in contrast take advantage of the transitory nature of social facilitation. If observing a virtual demonstrator use its beak to remove a stopper releases pecking behaviour in birds then this effect would be immediate. If birds were tested immediately after observation it is possible that elevated pecking rates could persist resulting in more beak responses in these birds. If, however, a significant delay is imposed between observation and testing, elevated pecking rates would not be expected to persist for the duration of the delay. Any beak removals made on test by birds in group Beak after such a delay could not therefore be due to social facilitation.

There has been no specific investigation into the duration of socially facilitated behaviour once it has been released. Therefore, it is not possible to determine what would constitute a significant delay. There is some indirect evidence however from a treadle experiment carried out with quail by Dorrance & Zentall (2002). In this experiment observers saw demonstrator birds step or peck a treadle for a food reward. The experimenters were interested in how the motivational state of observers at the time of observation and testing affected imitative learning. The two groups of interest were hungry at the time of observation and were either tested immediately, or after a 30 minute delay. In both groups pecking observers were found to make

proportionally more peck treadle responses than stepping observers. Interestingly, however, pecking observers when tested immediately showed an elevated level of responding (mean number of responses of 164 compared with 42 for stepping observers, over a 10 minute test session), which could reflect social facilitation of pecking. The difference in response rates for birds tested after a delay was much smaller (pecking observers, mean 35.7 compared with 16.7 for stepping observers) suggesting that social facilitation, if it had occurred at all, was decaying or 'wearing off'.

This chapter outlines three experiments imposing a delay between observation and testing. In the first experiment the design was similar to that in Experiment 3.1, with the addition of a 30 minute delay. In the second half of this experiment and then in the two subsequent experiments the design was then modified: 1) observation session length was increased from 5 minutes to 1.5 hours; 2) birds observed in small groups as opposed to individually; and 3) the delay between observation and individual testing was extended to 24 hours.

The three modifications were introduced to increase the likelihood that observers would learn from their demonstrators, while reducing the chance that social facilitation would promote beak use in the Beak group. Increasing observation time increased the opportunity observers had to learn from their demonstrator. There is some existing evidence that increased observation time may be required if a delay is imposed before testing. McQuoid & Galef (1993) allowed Burmese jungle fowl to observe videos of demonstrators feeding from one of two bowls. When testing was immediate, observers reliably went to the same bowl as their demonstrator. When the

delay was extended to 48 hours, this effect could be obtained only if the observation time was doubled.

Group observation was introduced to provide a more natural environment for social learning. In addition, isolation induced fear and vigilance in animals is reduced in groups, which may give observers more time to devote to observation of the demonstrator. For example, Sullivan (1984) found that as group size in woodpeckers increased, rate of head cocking decreased and rate of feeding increased. Finally, extending the delay to 24 hours was believed to be optimal for two reasons. First, a period of 30 minutes may not be long enough for the effect of social facilitation to decay. In Dorrance & Zentall's (2002) experiment, response levels were still slightly higher in the Beak birds after a delay of 30 minutes (Beak observers, mean 35.7 compared with 16.7 for Foot observers). Second, a delay of 24 hours allows observers to return to their home cage and perform a variety of behaviours, such as roosting and grooming, which would be likely to disrupt socially facilitated pecking. Third, time of day is a component of the context in which (observational) learning took place. Therefore a delay of 24 hours, allowing birds to be tested at the same time of day at which they observed, may facilitate performance by assisting retrieval of information obtained during observation.

Experiment 4.1

Experiment 4.1 was a pilot study for the delay paradigm. It was carried out in two parts. In Part A, observers were initially given a test 30 minutes after observing, for 5 minutes, a virtual demonstrator perform stopper removals. A period of 30 minutes

was chosen following its initial successful use in Dorrance & Zentall's experiment (2002). In Part B, which was run due to lack of responding in Part A, and which involved the same birds as A, observation time was increased to 1.5 hours and birds were allowed to observe in groups. They were then tested individually a full 24 hours later.

Observers were divided into two groups. Group Beak observed a demonstrator remove the stopper using its beak. Group Foot observed a demonstrator remove the stopper using its foot.

Methods

Subjects

Fourteen juvenile budgerigars obtained from a commercial supplier were used. At the onset of scheduled feeding the birds' mean weight was 39.40gms (SEM=1.33). Birds were allowed to habituate to the laboratory for a period of at least one week prior to the onset of training. Throughout the experiment birds were housed in two groups of seven in large breeding cages (100 X 50 x 50cm high). For details of housing and feeding see Experiment 3.1.

Of the 14 observers, seven observed a video of a conspecific demonstrator using its foot to remove the stopper (Group Foot) and seven birds observed a demonstrator use its beak (Group Beak). The experiment was run in one replication and birds were

randomly assigned to groups. Group assignment did not vary between Part A and Part B.

Apparatus

The apparatus was the same as that used in Experiment 3.1. The stopper was blue, and the test box was opaque white. The stopper was positioned on the right hand side of the test box with respect to the observer. For full details see Experiment 3.1 methods.

Stimuli

Observers were presented with stimuli consisting of video clips of demonstrator birds. Three clips were used, each lasting 10 seconds and featuring a different bird flying towards the front of the cage, alighting on the box, and then either feeding from the open hole (magazine training), or using its feet (group Foot) or beak (group Beak) to remove the stopper prior to feeding. The clips used were the same as those in Experiment 3.1.

Procedure

All training and testing was conducted in the morning, and timed to coincide with the beginning of the light phase of the birds' light/dark cycle. Before each session began the bird was positioned in the holding chamber of the test cage. Each session

commenced when the wooden partition was lifted allowing the bird to access the test chamber, and ended with the bird once again positioned in the holding chamber.

Magazine training

Observers underwent magazine training prior to the onset of testing. While on ad lib food birds were fed, for four days, in a plastic box mimicking the test box. On each of the next four days each bird was placed in the test cage for two 5 minute sessions, 30 minutes apart to allow them to habituate to the cage. The divide was used at the start and end of each of these sessions, the test box was present minus the stopper, and on the last two of the four days the laptop screen was also present.

After these initial eight days birds were placed on restricted food and given a further two days of magazine training. On each day observers were given two 5 minute sessions 30 minutes apart. Each session consisted of five trials in which the observers were allowed access to the test box while the magazine training video clip was playing continuously. Each trial lasted 1 minute unless the bird fed in which case the bird was allowed 30 seconds in which to feed before the trial ended.

Part A observer training and testing

On each of the following three days birds were given an observation session lasting a period of 5 minutes, followed 30 minutes later by a 5 minute magazine training session. This was carried out to give the observers experience with the test procedure. In the observation sessions birds saw a demonstration clip played repeatedly. Prior to the onset of the experiment a second experimenter relabelled the demonstration clips '1' or '2'. This enabled the main experimenter to be blind to

group assignment on test. At the start of the observation session clip 1 or clip 2 was started, and the experimenter immediately left the room. Half the observers were shown clip 1 and half were shown clip 2. While the demonstration clip was playing observers were allowed to move freely around the cage and the test box was absent. The magazine training session occurred as before but no clip was played.

On the next four days birds which had responded on the magazine training sessions progressed to testing. They were given a 5 minute observation session as described above, and then 30 minutes later they were returned to the test cage and given a 5 minute test session in the absence of any video. This consisted of five discrete trials in which the observer was allowed access to the test box with the stopper in place. A test trial ended after 1 minute, or if a bird made a response, 30 seconds after the stopper was removed. This was repeated on the fifth day but testing was extended to ten trials in an attempt to increase the incidence of responding.

Part B observer training and testing

Analysis of the data from Part A indicated very low response rates (see below). Therefore the test procedure was changed. In preparation for this, and in order to increase response levels, one hour after the fifth test session, all observers were given an additional magazine training session. This consisted of ten trials. The test box was present, but no stoppers, and no video was playing. Each trial ended after 1 minute had elapsed, or 30 seconds after the onset of feeding.

On the following six days birds were given alternating observation and test days. On an observation day birds were placed in the test cage and allowed to observe their

demonstrator clip (1 or 2) for 1.5 hours. Birds underwent observation in groups of two to four. During the observation sessions the test box was not present. A total of three observation sessions were given.

Birds were tested individually approximately 24 hours after each observation session. The test sessions consisted of ten trials in which the observers were allowed access to the test box while the magazine training video (bird feeding from the open hole of the test box) was played repeatedly. Each trial lasted 1 minute unless the birds removed the stopper in which case the bird was allowed 30 seconds in which to feed before the trial ended. Birds were given a total of three test sessions.

Independent raters were in agreement regarding the effector used by observers to remove the stopper in 94.5% of a randomly selected 30% of test trials.

Results

Part A:

Data were examined from 12, out of the original 14, birds (group Beak, N=5; group Foot, N=7). Two birds in group Beak were excluded, one as result of illness on test and another as a result of failure to feed during magazine training.

Across the five tests responding in all birds was very low. Two birds in the Beak group and two birds in the Foot group made no responses at all. The remaining eight birds made only foot responses. The mean number of foot responses made by birds in the Beak group was, 2.40 (SEM=1.91, N=5), and in the Foot group the mean was

4.14 (SEM=2.14, N=7). The maximum number of responses that could have been made was 30. A one-way ANOVA revealed no significant difference between the two groups in terms of the total number of responses made ($F < 1$).

Part B:

Response levels improved in Part B, but an additional bird in group Beak had to be excluded because it still failed to respond on test (group Beak, N=4; group Foot, N=7). The mean number of responses, made in all three administered test sessions in Part B only, was 14.5 (SEM=7.33), for the Beak group and 12.00 (SEM=5.60) for the Foot group. A one-way ANOVA confirmed that there was no significant group difference in response rates ($F < 1$). This can be contrasted with the results of Experiment 3.1 in which the Beak group had elevated levels of responding. Thus the response rate data from Part B of Experiment 4.1 provided no evidence of socially facilitated pecking in the Beak observers.

The data from Part B were further analysed using an effector discrimination ratio calculated for each bird by dividing the number of beak responses made by the total number of responses across the three test sessions. The mean effector discrimination ratios for group Beak and group Foot can be seen in Figure 15, which shows that birds in the Beak group were making proportionally more beak responses than birds in the Foot group. One-way ANOVA indicated that the effect of group approached significance ($F(1,11) = 4.640$, $p = 0.060$). The mean effector discrimination ratio was also calculated for each bird on each of the three test sessions. A mixed-model ANOVA with test (1,2 or 3) as the within-subject factor and group (Beak or Foot) as the between-subjects factor revealed a significant effect of test

($F(1,9)=10.770, p=0.010$) with ratio increasing from test 1 to test 3 (mean test1=0.09, SEM=0.30, N=11; test 2= 0.05, SEM=0.11, N=11; test 3=0.50, SEM=0.41, N=11). The effect of group approached significance ($F(1,9)=4.128, p=0.073$) and there was no group by test interaction ($F < 1$).

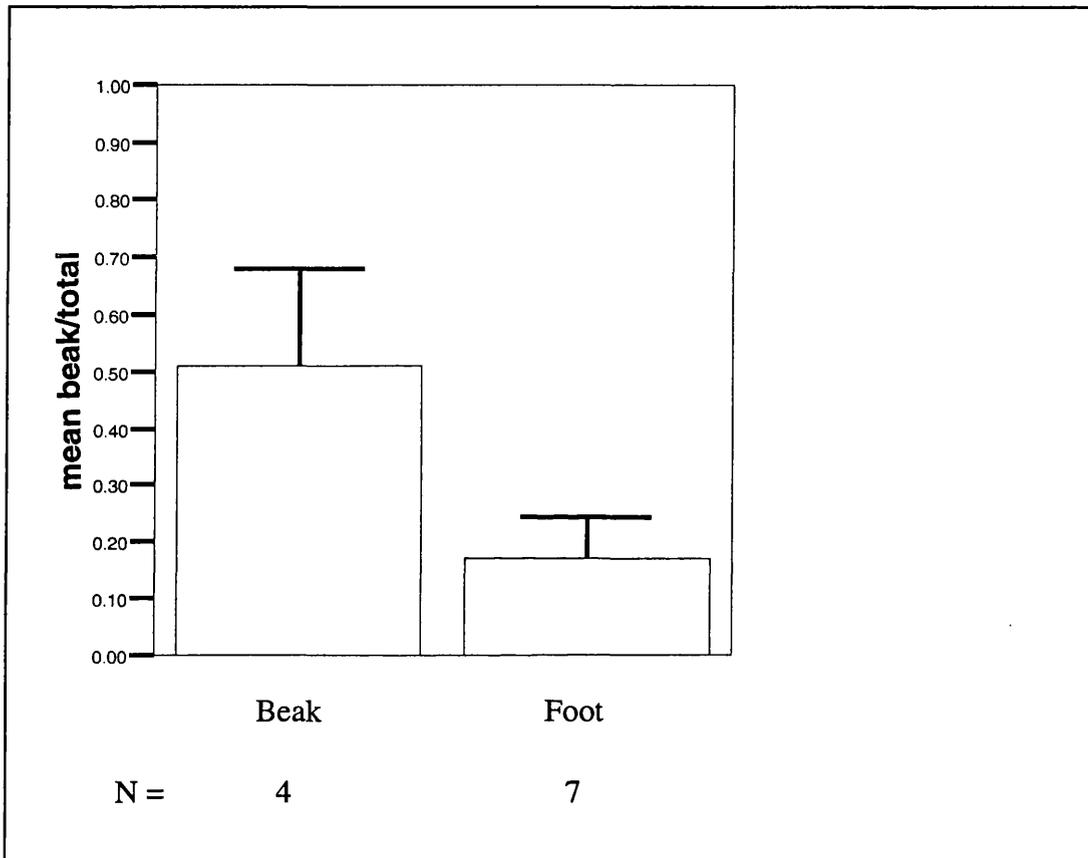


Figure 15: Mean effector discrimination ratio (beak/total) and standard errors of the means for groups Beak and Foot in Experiment 4.1.

These results indicate that birds in both groups increased the proportion of beak responses made from test 1 to test 3. There is also some evidence, when data from the three test sessions were combined, that the groups differ in the ratio of beak/total responses. This was further investigated by examining the frequency of each response type. Figure 16 shows the frequency of beak and foot responses for each group. The figure suggests that the groups did not differ in the total number of beak or foot responses made, but that within the Foot group birds were making more foot

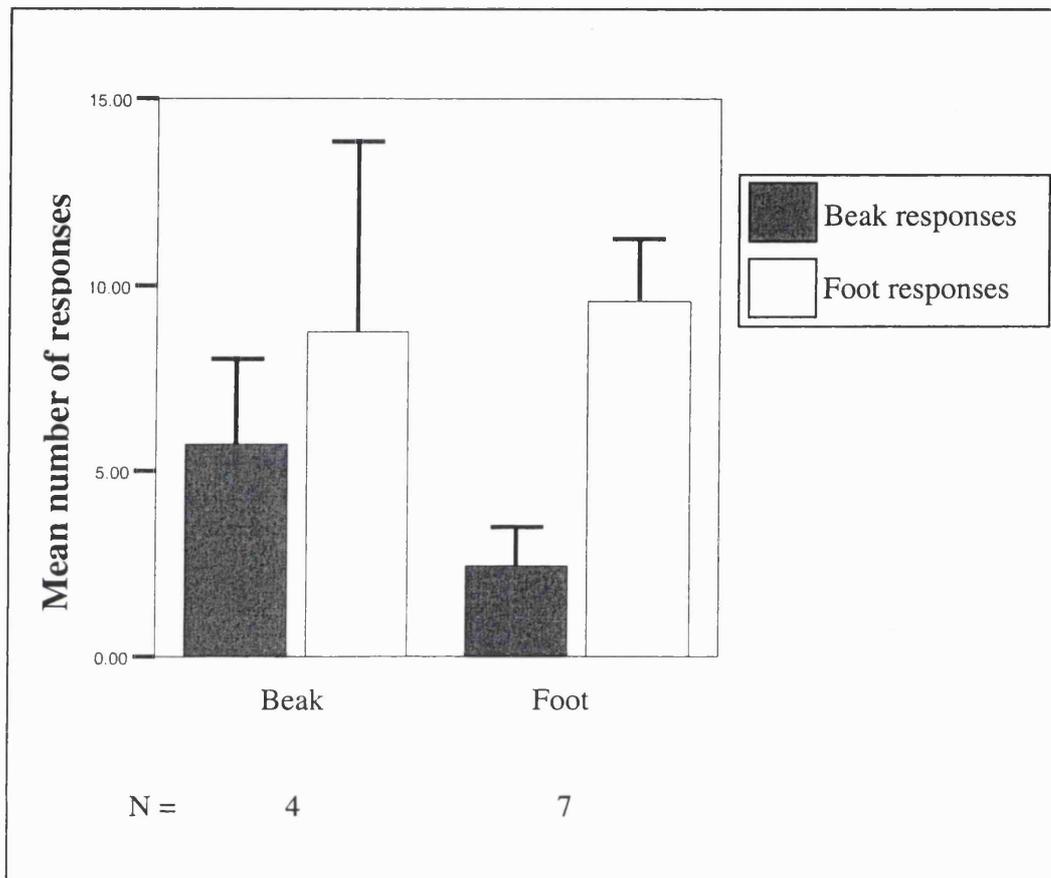


Figure 16: Mean number of beak and foot responses and standard errors of the means made across all three tests administered in groups Beak and Foot in Experiment 4.1.

than beak responses. It was not possible to confirm this as a mixed-model ANOVA investigating this revealed no significant main effects or interactions ($F < 1$, all cases), preventing further within group analysis using simple effects.

Discussion

Part A was not successful, with birds responding only with their feet and at very low frequencies, irrespective of group. As both observation and test sessions were very short in Part A, it was possible that birds were not allowed enough time to recover

from the stress of handling and cage changes, to make it possible for them to respond on test. In addition the delay of only 30 minutes meant that birds were handled and moved around a lot within a short period of time, which may have contributed to their stress. The design of the experiment was therefore modified in Part B, with observation time increased to 1.5 hours and undertaken in groups, with test sessions increased to 10 minutes, and with a delay of 24 hours between observation and testing.

The results of Part B were encouraging, despite the fact that the birds underwent five initial tests responding at a very low level, and a complete change of test design, it seems that to some extent they were able to learn from what they observed.

Interestingly, although it could not be tested statistically, there is some evidence that it may have been birds in the Foot group learning to do foot responding, rather than birds in the Beak group learning to do beak responses. When the frequency of beak and foot responses were examined birds in group Foot look like they are making more foot than beak responses while there is no difference for birds in group Beak. Importantly birds in group Beak made the same number of responses as birds in group Foot which along with the lack of learning in this group suggests that social facilitation plus stimulus enhancement was not occurring. The results are instead consistent with of imitation of foot use.

Without a control group it is not possible to draw firm conclusions about whether birds in groups Beak or Foot were learning from their demonstrator in this experiment. A control group would have provided the baseline level of beak and foot responding, which could have been used to determine whether birds in the Beak,

Foot, or Beak and Foot groups were learning. This along with the lack of a significant finding, and the small number of birds in group Beak, weakens the conclusions that can be drawn from this experiment. The results from Experiment 4.1 were therefore encouraging but they do not provide conclusive evidence of imitative learning in the budgerigar.

Experiment 4.2

Experiment 4.2 was an exact replication of Part B, Experiment 4.1, with the addition of a Control group, and an increase in sample size. If observers were capable of learning through imitation, birds in group Beak should make proportionally more beak responses on test than birds in group Control, who would make proportionally more beak responses than birds in group Foot.

Methods

The method used in Experiment 4.2 differed from that of Experiment 4.1 in the following respects:

Subjects

Thirty-eight juvenile budgerigars were used. At the onset of scheduled feeding the birds' mean weight was 38.85gms (SEM=0.70). Three to five birds were housed together in small breeding cages (60cm x 30cm, and 30cm high). Birds were housed with other members of their experimental group, with two cages making up each

group. This was necessary as birds observed in groups and it was thought that familiar cage mates would be less of a distraction during observation sessions.

Birds were run in two replications. In replication 1, 18 birds were assigned to groups as follows: Beak, N=9; Foot, N=9. In replication 2, 20 birds were assigned as follows; Beak, N= 7; Foot, N=7; Control, N=6. (The second replication was necessary as a result of a large number of birds being excluded from group Beak in the first replication, as a result of illness and failure to respond in either magazine training or on test).

Stimuli

The magazine training, beak and foot clips were the same as those used in Experiment 4.1. The Control clip was a random sequence of ten, ten second clips. Two different clips were used, one showing a beak responding demonstrator and one showing a foot responding demonstrator. To form the clips the original beak and foot clips from Experiment 3.1 were edited, using Adobe Premier 6, to remove the section of the clip in which the stopper is removed and replace it with a paused bird. This meant the Control birds observed a bird flying down onto the test box, which had the stopper in place, pausing for a few seconds, and then eating from the hole with no stopper in sight. The advantage of this was that Control birds would see the same stimuli as the birds in groups Beak and Control with the exclusion of the stopper removal. Importantly Control birds would see the stopper, and the demonstrator approaching it. Therefore stimulus enhancement of the stopper should be equal across groups.

Procedure

The initial eight days of training occurred as in Experiment 4.1. Restricted food magazine training lasted a period of four days. All birds were given the same number of sessions despite variations in performance as it was necessary that all birds started the observation and test phase of the experiment at the same time, due to the group observation design.

Once magazine training was completed birds were given alternating observation and test days for six days. On an observation day all the birds in one cage (N= 3 to 5) would be placed together in the test cage for a period of 1.5 hours during which their group's stimuli would be continually playing. As in Experiment 4.1 the main experimenter was blind to group assignment. This was achieved by a second experimenter randomly labelling the control, foot and beak clips, as clips 1,2 and 3, prior to the onset of the experiment.

Independent raters were in agreement regarding the stopper removal technique used by the observers in 100% of a randomly selected 30% of test trials.

Results

For details of response topographies see Experiment 3.1.

Data were obtained from 29 out of the 38 birds (Beak, N=8; Foot, N=16; Control, N=5). In the Beak group three birds were excluded as a result of illness, two due to lack of feeding in magazine training, and three as a result of failure to make any responses on test. In the Control group one bird was excluded as a result of illness.

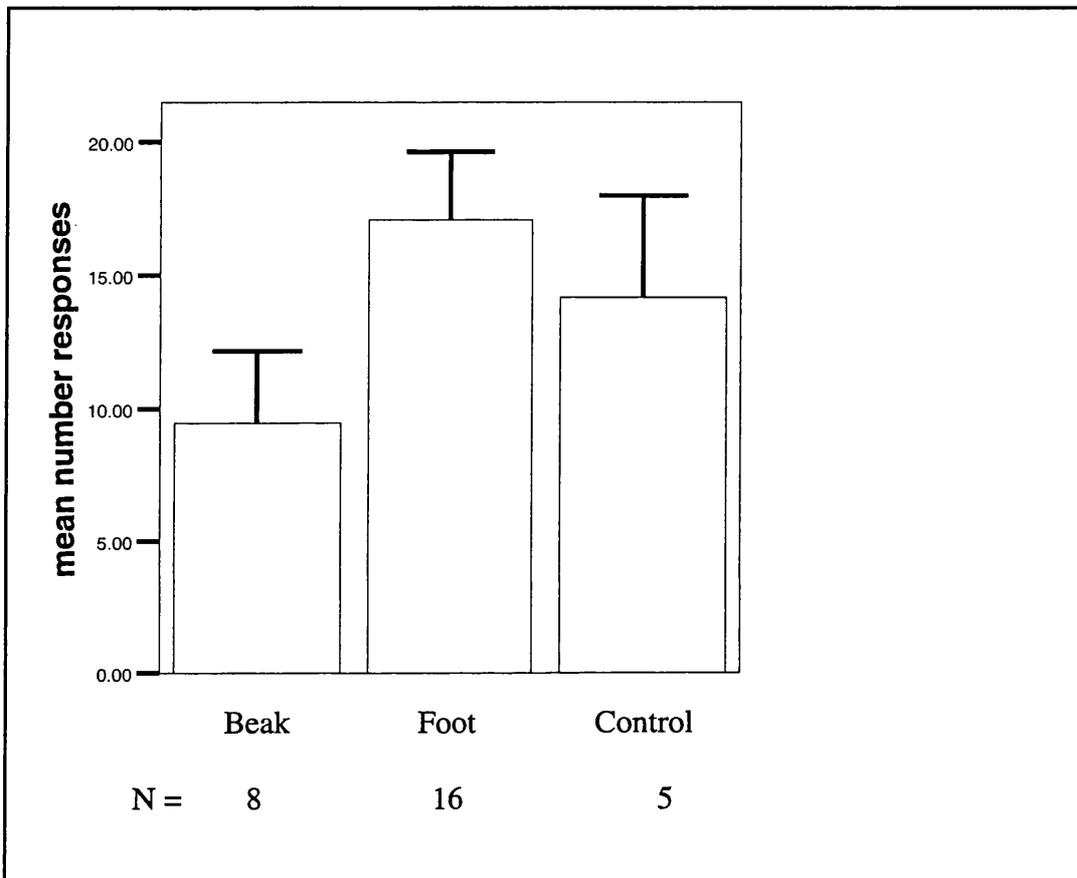


Figure 17: Mean number of responses and standard errors of the means made in all three tests administered by groups Beak, Foot, and Control in Experiment 4.2.

Figure 17 shows the mean number of responses made by birds in Groups Beak, Foot, and Control across the three tests administered. Birds in group Beak appear to have made fewer responses than birds in the Foot and Control groups. However, when tested with ANOVA in which number of responses was the dependent variable and group and replication were the independent variables, neither the main effects nor the interaction were significant ($F = 2.550$ for group, $F < 1$ all other cases).

Figure 18 shows the mean effector discrimination ratios calculated across all three test sessions. It is apparent that, regardless of group, all birds showed a strong foot response bias. ANOVA in which group and replication were the independent variables revealed no significant effects ($F < 1$ all cases). A mixed-model ANOVA with test (1,2 or 3) as the within-subjects variable, and group (Beak, Foot or Control) and replication (1 or 2) as the between subjects variable, confirmed this result. No main effects or interactions were significant ($F < 1$ all cases).

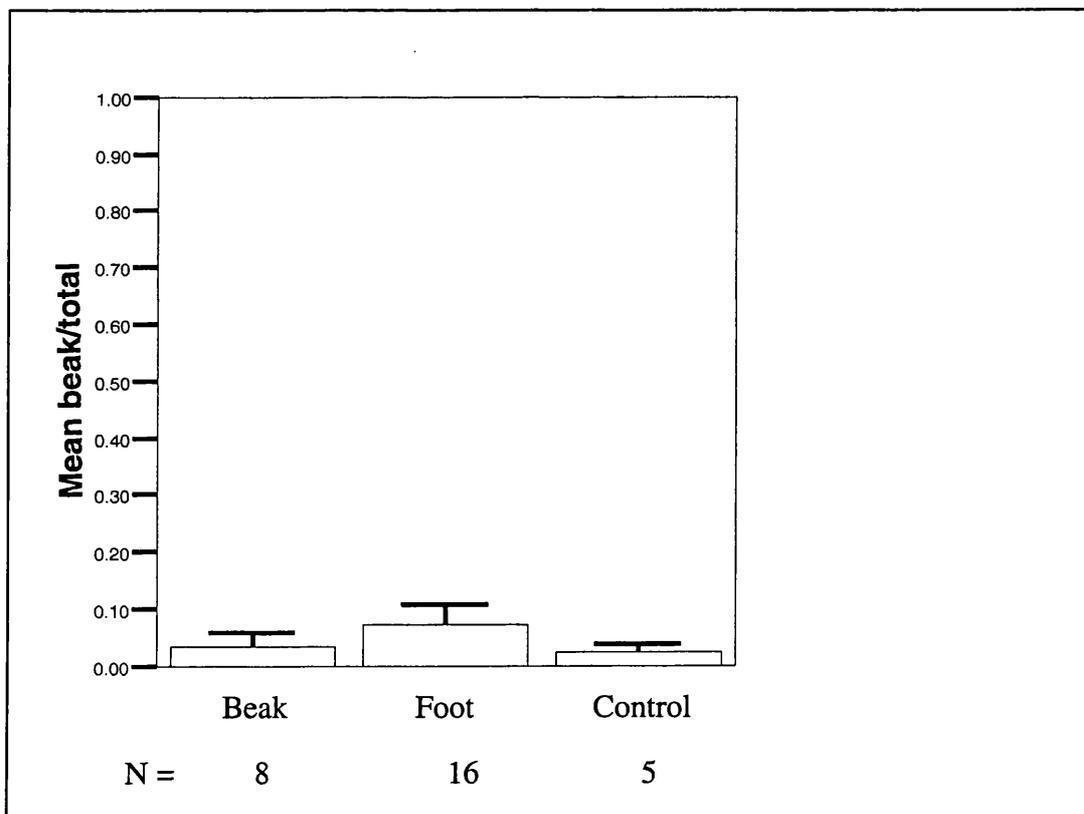


Figure 18: Mean effector discrimination ratio (beak/total) and standard errors of the means across the three tests administered for birds in groups Beak, Foot and Control in Experiment 4.2.

Discussion

The results of Experiment 4.2 did not support those obtained in Experiment 4.1. All birds, irrespective of group, displayed a strong foot bias. This meant that Experiment

4.2 was ineffective as a means of testing for imitation. It is not clear what caused this foot bias. Experiment 4.1 had a very similar design to that of 4.2 and yet provided some evidence of imitative learning in observers. The major difference between the two was that in Part A of Experiment 4.1, observers were given individual observation sessions and tested after a delay of only 30 minutes. This suggests that the 24 hour delay and extensive group observation used throughout in Experiment 4.2 may have been responsible for the foot bias.

Before the potential causes of the foot bias are considered in more detail it is important to note that initial foot responding in Experiment 4.1 may have been the result of 'accidental' stopper displacements. The surface of the test box was horizontal enabling birds to walk over it. If the stopper was stepped on as birds walked around the lid this could displace the stopper and be recorded as a foot response. Low motivation, distraction or excitement in observers could all increase the number of these foot responses made.

Low motivation in observers in Experiment 4.2 could have occurred as a result of the 24 hour delay design. Observation of a demonstrator could increase motivation for a test session but in Experiment 4.2 the delay of 24 hours between observation and testing could have made it likely that this motivation would have 'worn off'. In addition the delay between the last magazine training session and the first test session was 48 hours for observers in Experiment 4.2, so they did not have any recent experience of obtaining food from the test box.

In conjunction with low motivation or on its own, distraction or excitement by the magazine training video could have elevated foot responses. In Experiment 4.2 the magazine training video was playing continuously during test sessions. If observers were watching this they would have less time to respond, and may also have been attracted onto the test box to get a better view. When on the test box accidental responses could occur as previously described. The extended periods of time spent observing birds during observation sessions, may have made this distraction during testing more likely, as it would have given birds extensive experience of watching, while not responding.

To summarise, therefore, low motivation on test and/or distraction or excitement caused by the magazine training video seem the most likely explanations for the foot bias observed, although this cannot be known for sure. Given that the delay paradigm has the potential to isolate imitation from social facilitation in budgerigars, it was worth persisting with it. Before this could be done, however, it was necessary to modify the design of 4.2 to reduce foot response level and give a baseline level of beak: foot responding closer to 50:50. This would maximise the chance that learning in the Foot and Beak groups could be distinguished from one another and from the Controls.

A series of pilot experiments were run in an attempt to find a suitable paradigm for the delay design. Two different approaches were taken. Firstly the possible causes of the foot response bias were addressed. The magazine training video was eliminated from test trials to minimise distraction and/or excitement and 1 minute clips of the video were instead alternated with the 1 minute test trials. It was thought this would

increase motivation/activity in the observers. Alternating observation and test trials were used in the experiments reported in Chapter 3 and birds responded with both their beaks and their feet.

The second approach was to manipulate stopper depth. In all stopper experiments the stopper was held in place using Velcro pads attached to a ring fixed below the test box lid. The depth of the stopper's rim from the surface of the lid was fixed at 0.25cm. It was hypothesised that increasing the depth would increase the proportion of beak responses made by birds, as they would be less likely to accidentally step on the stopper and it would make foot responses more difficult to make. Galef et al (1986) report, in their replication of Dawson & Foss's (1965) experiment with budgerigars, that adjusting the height of the lid birds had to remove, affected the proportion of beak and foot responses used.

Four pilots were run in total using four to nine birds. All birds were given magazine training as in Experiment 4.2 prior to being tested. Stopper depths of 0cm, 0.5cm, 1.0cm, and 1.5cm were tested in conjunction with alternation of observation of magazine training and test trials. No conclusive results could be drawn given the small sample size. However, the alternating design appeared to increase levels of both beak and foot responding, while number of foot responses made did seem to decrease as depth of stopper increased. Levels of foot and beak responding approached 50:50 with the alternating design, at the original stopper depth of 0.25cm.

Experiment 4.3

Experiment 4.3 used the results of the pilot studies in an attempt to obtain evidence of imitation in a delay paradigm. The design used was essentially the same as that in Experiment 4.2, except that in test sessions 1 minute clips of the magazine training video were alternated with 1 minute test trials. One further modification to encourage elevated response levels was adopted from Mottley & Heyes (in press). In this experiment, if a bird failed to respond on two consecutive test trials it was given an additional magazine trial in which the stopper was absent allowing the bird free access to the food inside the box. This was considered to be a useful addition to Experiment 4.3 as it would help retain the observers' interest in the stopper and box, and therefore help reduce the number of sessions in which birds did not respond at all.

As in Experiment 4.2, it was anticipated that imitative learning would result in group Beak making proportionally more beak responses than birds in group Control, who would make proportionally more beak responses than birds in Group Foot.

Methods

The method used in Experiment 4.3 differed from that of Experiment 4.1 in the following respects:

Subjects

Twenty-four juvenile budgerigars were used. They were a mixture of wild type and show birds. At the onset of scheduled feeding the birds' mean weight was 49.79gms

(SEM=1.08). The birds were run in two replications. In each replication, 12 birds were assigned to groups as follows: Beak, N=4; Foot, N=4; Control, N=4. Birds observed and were housed in the groups of four.

Procedure

The initial eight days of training were the same as in Experiment 4.1. Restricted food magazine training was extended to last a period of five (replication 1) or six (replication 2) days. The number of magazine sessions was increased to maximise the number of birds that would learn to feed from the stopper box.

Each test session included a minimum of twenty trials in which the observers were allowed access to the test box every other trial. Starting with the first trial and alternating after this, observers were allowed to watch a 1 minute clip of the magazine training video. During this period the stopper box was present but access to it was prevented with a piece of card covering the lid. At the end of this trial birds were returned to the holding chamber, the test box was uncovered, and the magazine training clip was turned off leaving the laptop screen blank. Birds were then allowed forward for their test trial.

If a bird failed to remove the stopper on any two consecutive test trials it was given a 1 minute magazine trial in which the stopper was not present. As in test trials, birds were allowed to feed for 30 seconds. If no feeding occurred birds were given another magazine trial. If after this there was still no feeding birds were removed from the test cage and given another test once all the other birds had been tested.

Independent raters were in agreement regarding the stopper removal technique used by observers in 96.2% of a randomly selected 30% of test trials.

Results

For details of response topographies see Experiment 3.1.

Data were collected from 22 of the original 24 birds (Beak, N=8; Foot, N=7; Control, N=7). One Foot bird and one Control bird were excluded as a result of failing to make any responses on test. The response levels of the remaining birds were consistently high. Only four birds required an additional test session (Beak, N=1; Control, N=4). The number of additional magazine training trials administered was low in all groups: Beak, mean=1.25, SEM=0.98; Foot, mean=0.57, SEM=0.37; Control, mean=1.43, SEM=0.57. One-way ANOVA confirmed there was no significant group difference.

The total number of responses made across the three test sessions can be seen in Figure 19. This shows that birds in each group made approximately the same number of responses. This was confirmed with ANOVA in which number of responses was the dependent variable and group and replication were the independent variables. Neither the main effects nor the interaction were significant ($F < 1$ for all cases except group, $F = 2.331$). The overall mean number of responses was 25.18, SEM=1.56. This is higher than that in Experiments 4.2 (mean=14.03, SEM=1.75, N=29), and 4.1 (mean=12.91, SEM=1.82, N=11). Thus, it would appear that the alternating trial

design and/or additional magazine trials, had a positive effect on responding. The response data of Experiment 4.3 provided no evidence of socially facilitated pecking in the Beak observers.

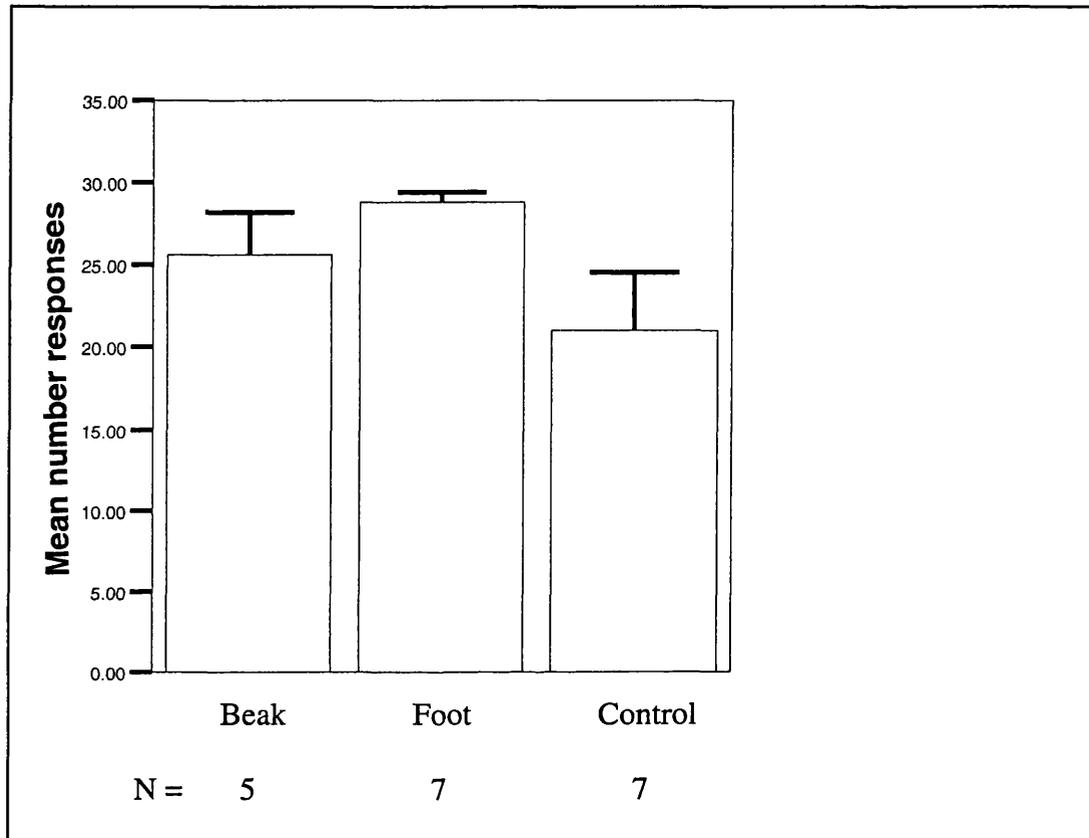


Figure 19: Mean number of responses and standard errors of the means made in all three tests administered by groups Beak, Foot, and Control in Experiment 4.3.

The mean effector discrimination ratio for each group on each of the three test sessions can be seen in Figure 20. It is apparent that in group Beak the mean effector discrimination ratio increased from test 1 to test 3. The ratio remained relatively constant across the three tests for the Foot and Control groups. Consequently by test 3, birds in the Beak group appeared to be making proportionally more beak responses than birds in the other two groups. This was tested with a mixed-model ANOVA in which test (1, 2 or 3) was the within-subject factor and group (Beak, Foot or Control) and replication (1 or 2) were the between-subjects factors. The main

effect of test ($F(1,14)=11.726$, $p=0.004$) and the test x group interaction ($F(2,14)=6.863$, $p=0.008$) were significant. No other main effect or interaction was significant (group, $F = 1.751$; replication, $F=1.373$; test x replication, $F=1.205$; test x group x replication = 0.229). Simple effects analyses investigating the test by group interaction revealed a significant difference between Beak and Foot groups on test 3 ($p=0.014$) and a significant difference between the Beak and Control groups on test 3 ($p=0.009$).

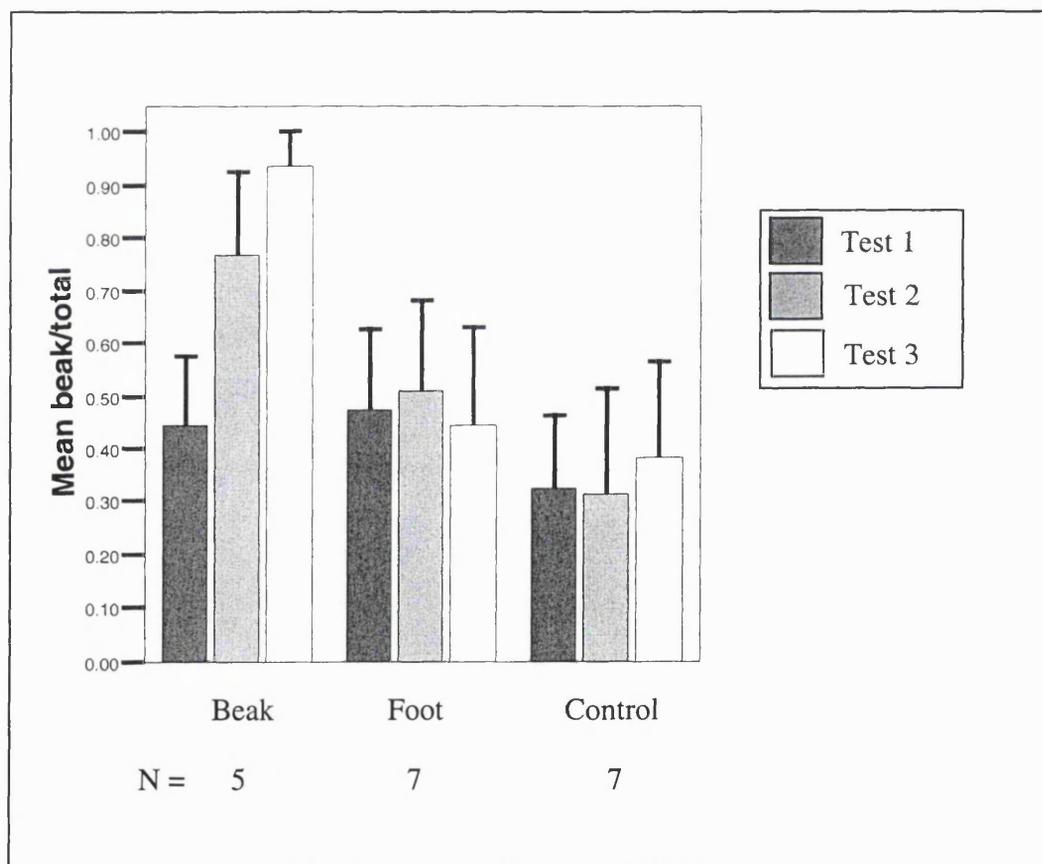


Figure 20: Mean effector discrimination ratio (beak/total) and standard errors of the means in each of Test 1, 2, and 3 for birds in groups Beak, Foot and Control in Experiment 3.3.

Discussion

The results of Experiment 4.3 suggest that observation of virtual demonstrators' behaviour influenced the behaviour of birds in the Beak group. By test 3, birds in the Beak group were making proportionally more beak responses than birds in either the Foot or Control groups, which did not differ from one another. This effect was not apparent on test 1 when all the birds were behaving in a similar way. Birds in Group Beak increased the proportion of beak responses they made as tests progressed.

It is possible that the birds in group Foot learned to make foot responses through demonstrator observation but that this effect was masked by an overall foot bias, i.e. a floor effect. The proportion of beak responses made by birds in both the Foot and Control groups was low which means that there was not much 'room' for the Foot birds to make proportionally fewer beak responses than the Controls. However, the mean effector discrimination ratio across tests was numerically higher for the Foot birds than for the Controls (Foot, 0.44 ± 0.19 ; Control, 0.38 ± 0.18 ; Beak, 0.94 ± 0.63). The mean effector discriminations also show that birds in both the Foot and Control groups have ratios which are only just lower than 0.5, which is the ratio resulting from equal numbers of beak and foot responding. This makes it likely that in Experiment 4.3 only birds in the Beak group were learning from their virtual demonstrators.

Learning in the Beak birds cannot be accounted for by emulation, observational conditioning or social facilitation plus stimulus enhancement. The stopper design ensured that both beak and foot responses moved the stopper downwards through the

same trajectory. If emulation or observational conditioning were occurring then birds in all three groups would be expected to respond in the same way. Social facilitation plus stimulus enhancement were prevented by the 24hr delay between observation and testing. If pecking behaviour were released in birds who had observed a demonstrator using its beak to remove the stopper, then this effect would be transitory and would not persist over the period of 24 hours between observation and testing. Elevated response levels in the Beak group, which would have been indicative of social facilitation, were not seen on test. If anything, the Foot birds made marginally more responses in total than the Beak birds.

Insofar as the procedure used in Experiment 4.3 excludes these non-imitative forms of social learning, the results imply that the birds in the Beak group learned by observation to remove the stopper using their beak, i.e. that they engaged in imitative learning. If so, lack of learning through observation in the Foot group may have resulted from a number of factors. For example, lack of clarity in the video used for this group or lack of opportunity to practise the foot response on test given that only three sessions were administered. Another possibility is that the ability to imitate is dependent on the birds having previously had experience of performing the action while others were performing it. It is likely that during communal feeding birds would have had extensive experience of using their beak while other birds were using their beaks. They may have had insufficient correlated experience of observation and execution of foot responding, which would have prevented birds in group Foot from learning the foot response from their demonstrators.

4.4. Summary and Conclusions

This chapter has detailed a series of two-action experiments in which a delay was imposed between observation and testing in an attempt to isolate imitation in the budgerigar from behavioural matching due to social facilitation plus stimulus enhancement.

Experiment 4.1 was carried out in two parts. In Part A, which was abandoned as a result of low responding in all birds, a delay of 30 minutes was imposed between observation and testing. In Part B the delay was extended to 24 hours, and observation sessions were extended to 1.5 hours and carried out in groups. Results from Part B suggested that it was only the Foot birds that had learnt with birds in this group making more foot than beak responses. Birds in the Beak group in contrast were responding with equal levels of foot and beak responses. This, and the fact that there was no group difference in response levels, provides evidence against a social facilitation explanation. Instead Experiment 4.1 provided tentative evidence of imitative learning in the Foot group.

Experiment 4.2 was a replication of Experiment 4.1 but with a 24 hour delay design from the outset. It was run with more birds than Experiment 4.1 and a Control group to provide a baseline beak and foot response rate. Its purpose was to improve the evidence obtained from Experiment 4.1. However no group effect was obtained because responding on test was predominantly with their feet.

Building on the outcome of pilot studies investigating the foot bias, test sessions in Experiment 4.3 consisted of test trials alternating with trials in which the magazine

Chapter 5

General Discussion:

The methodological and substantive implications of imitation experiments with budgerigars.

Imitation is a form of social learning, which has been defined as learning to do an act from seeing it done (Thorndike, 1898). It is considered to be unique as in order to imitate animals must somehow translate visual information about the body movements of others into matching motor outputs, solving what is known as the correspondence problem (Nehaniv & Dautenhahn, 2001). It is argued by many that this ability requires complex cognitive processing and as a result the ability to imitate is limited to humans, and possibly other apes (e.g. Meltzoff & Moore, 1977; Whiten, 1996; Tomasello & Call, 1997). In contrast others argue that the correspondence problem can be solved by associative learning processes, and therefore that imitation should be within the capabilities of a wider range of species (e.g. Heyes & Ray, 2000).

The distribution of imitative abilities could therefore provide an indication of whether the mechanism for imitation is complex, or simple. In order to determine the distribution well controlled experiments are required to isolate imitation from a range of social influences and non-imitative social learning which can result in matching behaviour (Whiten, 2000; Tomasello & Call, 1997; Visalberghi & Fragaszey, 1990). In recent years the two-action test has shown the potential for isolating imitation, and has been used with a variety of species, but controversy

exists over interpreting many of the results (Caldwell & Whiten, 2002). Emulation in particular has proved difficult to eliminate and may explain the results of most of the two-action experiments run with birds (e.g. Dawson & Foss, 1965, budgerigars; Campbell et al, 1999, starlings; Heyes & Saggerson, 2002, budgerigars). Evidence for imitative abilities is therefore currently limited to apes (Custance et al 1995, chimpanzees; Miles et al 1996; Call, 2001, orangutans), and monkeys (Voelkl & Huber, 2000, marmosets).

The experiments presented in this thesis sought to use the two-action procedure to obtain conclusive evidence of imitative abilities in a species of bird, the budgerigar. If budgerigars can imitate it suggests that the correspondence problem must be solved without the involvement of complex cognitive processing. In addition if a paradigm to show imitation in this species was designed it may then be possible to adapt the paradigm to investigate the psychological mechanism of imitation.

This chapter is divided into four parts. In Part 1 the results obtained from the eight experiments reported in the thesis are summarised. These results have a number of methodological and substantive implications, which are discussed in Parts 2 and 3 respectively. Finally, in the light of these implications, Part 4 re-examines the evidence of imitation from experiments carried out with primates.

5.1. Summary of experimental results

Eight experiments were run in total in an attempt to isolate imitative learning in the budgerigar. The first two, reported in Chapter 2, were bidirectional control

procedures which were initially developed for investigating imitation in rats (Heyes & Dawson, 1990). The remaining six experiments reported in Chapters 3 and 4 were two-action tests, based on a stopper paradigm.

5.1.1. The bidirectional control procedure

Chapter 2 presented two bidirectional control procedures designed to identify whether birds were carrying out transpositional or mirror imitation, or whether they were carrying out emulation. In the first experiment, Experiment 2.1 naïve observers faced a trained demonstrator as he pushed a pole, which was suspended horizontally across the test cage, to the left, with respect to the actor. On test observers were seen to push the pole to the left with respect to their own bodies, suggesting that they were carrying out transpositional imitation, coding pole movement with respect to the actor's body. However, when the experiment was replicated (Experiment 2.2) with both left and right pushing demonstrators it was clear that the observers' behaviour was not influenced by that of their demonstrators. Instead it appeared that room cues, most likely the position of the experimenter were affecting direction of pushing. All birds, irrespective of group, showed a bias in pushing away from where the experimenter was positioned. Asymmetries in both the design and implementation of Experiment 2.1 mean that it is possible that room cues can also account for the results of this experiment.

5.1.2. The two-action stopper paradigm

Experiments presented in Chapters 3 and 4 were based on a stopper paradigm. In the first experiment, Experiment 3.1, observers saw a virtual demonstrator use its feet or its beak to dislodge a stopper down into a test box to gain access to food. A control group saw a demonstrator feeding from the open hole in the absence of the stopper. On test it was found that birds which had observed beak removals made proportionally more beak removals on test. This was confounded however with elevated response levels in the Beak group. It is possible that their responding was brought about as a result of social facilitation of pecking, as opposed to imitation of beak use. Social facilitation is a type of social influence and was characterised by Thorpe (1956) as occurring when the sight of an animal engaged in a behaviour releases that behaviour in the observer. Given that on test pecking in the Beak birds was concentrated on the stopper it is likely that if social facilitation was occurring it was in conjunction with stimulus enhancement of the stopper.

Experiments 3.2 and 3.3 were based on the same stopper design but were run as conditional discrimination experiments. It was reasoned that if birds could not only learn the removal response but also where to make it then social facilitation plus stimulus enhancement could not be responsible. In Experiment 3.2 birds were found to learn the conditional discrimination although a strong side bias weakened this finding. Experiment 3.3 failed to show any learning of a conditional discrimination with all birds developing a beak response bias as tests progressed.

The stopper experiments in Chapter 4 approached the problem of social facilitation plus stimulus enhancement using a delay inserted between observation and testing. It

was argued that if observing a virtual demonstrator using its beak to remove a stopper releases pecking behaviour in birds then this effect would be immediate due to the transitory nature of social facilitation. In Experiment 4.1 a delay of 30 minutes was initially used but this was later extended to 24 hours. It was found that birds in group Beak made proportionally more beak removals than birds in group Foot, although this effect was not statistically significant. Experiment 4.2 was run as a direct replication but all birds showed a strong foot response bias irrespective of group.

The reason for the foot response bias in Experiment 4.2 cannot be known for sure. However a series of pilots studies revealed that both foot and beak responding could be elevated in birds on test through the alternation of test trials with 1 minute observation sessions in which the magazine training clip was playing constantly. The final experiment, 4.3, took advantage of these results and on test birds in group Beak were found to make proportionally more beak stopper removals than birds in either groups Foot or Control which did not differ from one another. This suggests that only birds in group Beak were learning stopper removal technique through observation.

5.2. Methodological Implications

The eight imitation experiments run with budgerigars had several methodological implications. The principle implications concern the suitability of budgerigars for social learning work, along with both the design of experiments and the equipment used to carry them out.

5.2.1. Suitability of budgerigars for social learning work

Budgerigars were initially chosen as a model species for imitation work for five reasons: 1) two-action tests with this species had already indicated potential imitative abilities (Dawson & Foss, 1965; Galef et al 1986; Heyes & Saggerson, 2002; Mottley & Heyes, in press); 2) budgerigars are a social species and as such may be more likely to learn socially (e.g. Templeton, Kamil, & Balda, 1999); 3) they are easily available; 4) there is a substantial literature relating to budgerigar neurobiology (e.g. Jarvis & Mello, 2000), which would be important for investigations into the neural basis of imitation, and 5) budgerigars could be used in the future to investigate the link between vocal and motor imitation as they acquire their calls through vocal imitation (Farabaugh, Linsenbold, & Dooling, 1994; Hile, Plummer, & Streidter, 2000; Hile & Streidter, 2001).

The experiments reported in this thesis provide further evidence that budgerigars are capable of social learning, perhaps even imitation. They also went further and confirmed Mottley & Heyes' (in press) findings that budgerigars could learn complex responses from a virtual, as opposed to live, demonstrator. This combined with the ease with which budgerigars were obtained and maintained, along with the potential for neural and vocal learning investigations, suggest that budgerigars are highly suitable for social learning experiments.

However, there is some need for caution. Firstly some budgerigars did have to be excluded from testing as a consequence of either failing to feed on magazine

training, or failing to respond on test. Overall data was obtained from 86% of the birds used, and although this is not excessively low it would have been preferable if data could have been obtained from more birds. It is possible that some birds will never respond on test, however it may be possible to elevate the number responding by making alterations to the magazine training and testing. For example in Experiment 4.3 the number of magazine training sessions administered was increased and during test sessions, test trials were alternated with 1 minute clips of the magazine training video. In this experiment only two birds out of the original 24 had to be excluded.

A second, and potentially more serious, reason for caution concerns the fact that some birds had to be excluded as a result of their weight falling unacceptably low while on restricted food. Budgerigars are a very small species of bird, and as a consequence a very careful feeding and weighing schedule was necessary to maintain the birds above 90% free feeding weight. Experiments also had to be planned to restrict the amount of time an individual bird was on restricted food as for ethical reasons it was not possible to keep the birds on extended periods of food deprivation.

One way round the problem of restricted feeding would be to reward budgerigars with a highly palatable food which they would be willing to work for in the absence of a restricted feeding schedule. For example in Campbell et al's (1999) experiment with starlings, birds were rewarded with live mealworms, *Tenebrio molitor*, which they found highly appetising. As a consequence only 1 hour of food deprivation prior to testing was required to get the starlings to respond on test. Identifying an

equivalent food reward for budgerigars however is problematic. When presented with both standard millet and honey coated 'treat' millet in the home cage, birds were observed to consume equal amounts of each, indicating no preference for the treat food (pilot study, own laboratory). Budgerigars are incredibly keen on millet sprays but these cannot be easily presented as a reward on test. While although apples or other green foodstuffs would work in the short term, extended use over testing could potentially result in gastroenteritis (personal communication with UCL veterinary surgeon).

One final problem with budgerigars is that although birds rapidly became accustomed to being picked up and handled, the results from the bidirectional control procedures (2.1 and 2.2) and the first conditional discrimination experiment (3.2) suggested that birds perceived the experimenter, or at least the sounds of the experimenter, as a negative stimulus. This is problematic for two reasons. Firstly, the results of Experiments 2.1, 2.2, and 3.2 were directly affected with birds responding away from the experimenter. This meant there was no evidence of social learning in the bidirectional control procedures, and that the significant finding from 3.2 was undermined. Secondly if the budgerigars are so sensitive to the presence of the experimenter then it is possible that the experimenter could have consciously or sub-consciously cued the budgerigars, for example making a disturbing noise when the wrong response was made, thereby 'fixing' the results.

The problem of demonstrator cuing was directly addressed in Experiments 4.1, 4.2, and 4.3 as the use of virtual demonstrators made it possible for the experimenter to be blind to bird group assignment. For the development of experimental design it

was useful and more economic to have the experimenter present. However the potentially significant effect of the experimenter suggests that in future experiments completely automated apparatus should be used enabling the birds to observe and be tested in the absence of the experimenter. If this was not possible additional magazine training may also help reduce the effect of the experimenter by increasing habituation. This would need to be combined with a blind experimenter to prevent inadvertent cuing.

5.2.2. Experimental Design

Bidirectional control procedures

Bidirectional control procedures investigate imitative abilities by looking at whether observers copy the direction an action was performed in either with respect to themselves (mirror imitation) or with respect to the demonstrator (transpositional imitation). It is therefore vitally important that cues which could influence direction, either in conjunction with demonstrator performance (emulation or observational conditioning), or on their own, can be eliminated from these procedures.

Experiments 2.1 and 2.2 were carefully designed with the intention of excluding both cage and room cues which could affect observer learning. However the results obtained suggest that despite the precautions, the observers' behaviour can be explained in terms of the position of the experimenter on test. The performance of the demonstrator in contrast seemed to have no influence on observers' behaviour.

A bidirectional control procedure with quail (Akins et al, 2002) claimed to have provided evidence of imitative learning. However in this experiment cues were not controlled for and so emulation or observational conditioning could explain the results. In addition this experiment was also affected by experimenter position, with birds showing a bias in responding in the opposite direction to where the experimenter was located. Furthermore when the procedure was run with rats it was found that responding in these animals was influenced by scent cues deposited by their demonstrator during observation sessions (Mitchell et al, 1999).

The results of these four experiments combined suggest that bidirectional control procedures are not a useful technique in the investigation of imitation. In order to exclude emulation and observational conditioning care has to be taken to either eliminate cues, which the animals could use to code movements, or make the use of cues apparent. As described in Experiments 2.1 and 2.2 this is not easy to do, while the series of bidirectional control procedure run with rats prior to the discovery of the possible role of scent cues highlights the fact that cues may not always be obvious to experimenters (e.g. Heyes & Dawson, 1990; Heyes et al, 1992). Finally both the experiments with budgerigars and quail indicate that the experimenter is an important cue, and one, which for at least the budgerigars was more salient than demonstrator responding.

Stopper two-action paradigm

The stopper two-action paradigm developed in the experiments reported in Chapters 3 and 4 proved to be highly adaptable. It was originally based on a design used to

investigate imitation in starlings (Campbell et al, 1999) and later budgerigars (Heyes & Saggerson, 2002; Mottley & Heyes, in press). In these experiments the actions used to remove the stopper was confounded with direction the stopper moved in when displaced, which meant that emulation was a possible explanation for the results obtained. In the experiments reported in Chapters 3 and 4 it was possible to modify the design to prevent emulation.

Design flexibility was confirmed with further modifications that were made to the stopper paradigm in Experiments 3.2 through to Experiment 4.3. These modifications were necessary because one of the actions used in this paradigm, beak stopper removal, may be socially facilitated, owing to its possible similarity to pecking behaviour. Although this is one potential disadvantage of the stopper two-action paradigm it would be very difficult to design a two-action experiment for birds in which the beak not used. The beak is the primary means by which most birds influence the world, and is used in a similar way to how primates used hands to reach, grasp, and manipulate objects (Deich & Balsam, 1994). As a consequence most bird two-action experiments use at least one action based on the beak (e.g. Dawson & Foss, 1965; Akins & Zentall, 1996; Campbell et al, 1999; Mottley & Heyes, 2002).

Conditional discrimination procedures

Two conditional discrimination experiments (3.2 and 3.3) were designed and run using the stopper paradigm. It was reasoned that they had the potential to separate the effects of imitation from those of social facilitation and stimulus enhancement

which could not account for birds learning both what response to make and where to make it. Although there was some success with Experiment 3.2, Experiment 3.3 failed to reveal any learning in the observers. This may have been due to the length of the test phase as opposed to inability to learn. In Experiment 3.3 the result of interest was the rate at which birds in each group acquired the conditional discrimination so testing should have continued until all birds had demonstrated that the discrimination had been learned. However, owing to the small size of budgerigars it was only possible to administer six tests to the birds in this experiment before they had to be taken off the restricted feeding schedule.

Further test sessions in Experiment 3.3 may therefore have revealed a different rate of learning in birds in each group, but any form of extended testing will never be viable with budgerigars unless restricted feeding can be replaced with the use of a highly palatable food reward. Even if extended testing were possible, and the conditional discrimination were learned, there may be no observable effect of the demonstrator. Dorrance & Zentall (2001) ran a similar conditional discrimination experiment with pigeons and found that although the discrimination was learned it took up to 20 test sessions, and no effect of demonstrator was observed. The difficulty in running conditional discrimination experiments, in terms of the extended periods of restricted food required, in conjunction with the lack of success with using them in birds suggests that they are not the most effective way to investigate imitation in budgerigars.

Delayed test procedures

The experiments reported in Chapter 4 used a delay between observation and testing, as opposed to a conditional discrimination design, to address the problem of social facilitation. The results from Experiment 4.3 indicate that this is an effective means of controlling for social facilitation in two-action procedures. Although it was only birds in group Beak which appeared to be learning in Experiment 4.3, birds in this group did not show elevated levels of responding, in comparison with birds in the Foot and Control groups, which would have been expected if social facilitation was occurring.

Little work has been done on the persistence of socially released behaviour so it was not possible to determine exactly how long the delay between observation and testing should be to prevent social facilitation from effecting behaviour on test. The initial part of Experiment 4.1 used a delay of only 30 minutes but this was later extended to 24 hours. Birds failed to respond with a delay of 30 minutes, possibly as a result of the amount of handling and cage changes that were necessary with this design. A quail treadle study, which incorporated a delay of 30 minutes showed that pecking observers still had an elevated level of responding relative to stepping observers suggesting that social facilitation had not yet 'worn off' (Dorrance & Zentall, 2002). For both these reasons a delay of 24 hours is preferable.

5.2.3. Experimental Apparatus

Virtual technology

Following successful use of ‘virtual’ demonstrators by Mottley & Heyes (in press) they were used as an alternative to real ones in the stopper paradigm experiments (3.1 to 4.3). This technology has great potential, which has yet to be fully exploited. In the stopper experiments using a virtual demonstrator made it possible to present every observer within a group, and across experiments, with exactly the same stimulus presentation. It also enabled larger sample sizes to be run, and more importantly made it possible to give birds extended observation sessions. The 1h30 observation sessions administered in Experiments 4.1, 4.2 and 4.3 would not have been possible with live demonstrators who would have become satiated and/or fatigued a long time before 1h30 had elapsed. As mentioned earlier using a virtual demonstrator also made it possible for the experimenter to be blind to group assignment.

Given that there is some evidence that birds can learn from virtual demonstrators in the future it would interesting to be more adventurous with the technology. In the experiments reported in Chapters 3 and 4 birds in each group only saw one video clip, which was played repeatedly. It may be that several video clips showing stopper removals from different angles and with different techniques may improve responding in observers. For example video clips were chosen for the clarity of removal response from a human perspective. It may be that the angle and removal used were not the clearest from a budgerigar’s perspective. In addition varying the video clips used may reduce habituation in the observers, especially given the 1h30 observation sessions administered in Experiments 4.1, 4.2 and 4.3. Habituation may

have reduced the amount of time birds observed the video clips and thereby reduced the opportunity they had to learn.

As well as showing different demonstrations the use of a virtual demonstrator makes it possible to manipulate exactly what the observers see. For example in Experiments 4.2 and 4.3 it was possible to edit the video clips shown to the Beak and Foot groups to produce a specially designed video clip for the Control group. This video clip consisted of the beak removal clip followed by the foot removal clip, but stopper removals were deleted and replaced with a paused bird. This meant that the Control birds saw everything that the Beak and Foot birds did except the actual stopper removal. Importantly this meant that stimulus enhancement of the stopper should be equal across groups. Editing the video clips was made possible using Adobe Premier 6 software which enabled the video to be examined and altered on a frame by frame basis. It therefore has great potential for further manipulating what the observers see. For example, using this technology it would be relatively easy to alter the contingency between the response and the reward.

5.2.4. Summary and Conclusion of methodological implications

Six different methodological implications of the experiments reported in this thesis have been outlined and discussed, concerning the species used for the work and both the design and apparatus used. Regarding the species, budgerigars are suitable for social learning work, having the advantage that they are easy to maintain and showed the ability to learn from virtual demonstrators. The disadvantages of using budgerigars, the failure of some to respond on test and the sensitivity to the

experimenter, should be relatively easy to address by extending magazine training and using an automated test apparatus. It could prove more difficult to overcome the problems associated with restricted feeding and as a consequence another larger species, such as pigeons, should be used for experiments, such as conditional discrimination ones, in which extended periods of testing are required.

In terms of experimental design the problems associated with the bidirectional control procedure suggest that two-action stopper paradigm is a better design to investigate imitation. In particular it has been found to be relatively flexible allowing changes to be implemented in attempts to isolate imitation from social influences and non-imitative social learning. Using a two-action stopper paradigm combined with delayed testing has proved to be capable of eliminating any potential effect of social facilitation on test. Given that most two-action experiments with birds involve beak use, and pecking is a socially facilitated it is recommended that this delay should be adopted in other bird two-action paradigms. Finally the use of TFT technology to show observers virtual demonstrators has great potential in social learning work and should perhaps be used in favour of live demonstrators.

5.3. Substantive Implications

Along with methodological implications, the experiments reported in this thesis had two important substantive implications, concerning the occurrence of effector matching in budgerigars and the potential explanation for it.

5.3.1. Effector matching

In the experiments reported in this thesis the strongest evidence for effector matching, which cannot be attributed to emulation or social facilitation plus stimulus enhancement, was seen in Experiment 4.3. In this two-action stopper experiment, it was found that birds, which had observed beak removals made proportionally more beak removals on test than birds, which had observed foot removals, or the control birds, which simply observed a feeding bird. These results indicate that effector matching can occur in budgerigars using a fixed trial procedure, a virtual demonstrator, and when a delay of 24 hours is placed between observation and testing.

In Experiment 4.3 the effector matching appears to be restricted to birds observing beak removals. In 4.3 birds observing foot removals were making an equivalent proportion of beak responses as birds in the Control group. It is possible that learning in Foot birds in this experiment was masked by a floor effect caused by a relatively low baseline level of beak responding. However, this is unlikely given that birds in the Foot group were actually observed to make a slightly higher proportion of beak responses than birds in the Control group. It is therefore more likely that birds in the Foot group failed to learn to remove the stopper with their feet.

It is interesting that the treadle experiments carried out with pigeon and quail also lack conclusive evidence of imitation of foot use. In these experiments, as detailed previously, birds saw a demonstrator either peck or step on a treadle for a food reward. In the quail experiments (Akins & Zentall, 1996; Akins & Zentall, 1998; Dorrance & Zentall, 2001) similar results were obtained to those in Experiment 3.1

training video was playing and access to the test box was prevented with a card lid. This procedure was successful in increasing overall response levels and decreasing foot bias in all three groups. The results from the experiment indicated that only birds in the Beak group were learning. It is possible that learning in Foot birds was masked by the relatively low baseline level of beak responding, which was revealed by the Control group. As emulation, observational conditioning and social facilitation plus stimulus enhancement, cannot account for the learning in the Beak group, Experiment 4.3 provides tentative evidence of imitation in this group.

with birds in the Pecking group making more peck responses on test, when compared to birds in the Stepping group. It was concluded that birds in both groups were displaying imitative learning. However when Akins & Zentall (1998) included a Control group, which saw a demonstrator being rewarded but no treadle interaction, it is apparent from the figures presented, but not statistically tested, that there was no difference between Stepping and Control groups in terms of the proportion of pecks made. As in Experiment 3.1 the birds in the Pecking group may have been influenced by social facilitation, while birds in the Stepping group failed to learn from their demonstrator.

Problems also exist with the treadle experiments carried out using pigeons. Zentall et al (1996) found that on test all birds that saw stepping stepped, while five out of the ten birds that saw pecking pecked. This result was statistically significant but it is possible that all birds were biased towards stepping and that pecking occurred in some of the pecking observers as a result of social facilitation. To investigate these claims two control groups were run by Kaiser, Zentall & Galef (1997). One group saw a naive demonstrator, while the other saw a naïve demonstrator trained to feed from the feeder at variable intervals. Data from these birds were compared with those from the stepping group in the first experiment and it was concluded that a stepping demonstrator was essential in order for observers to learn to step. Even if the cross experiment comparison is ignored this conclusion is suspect. Neither control group would have drawn the observers' interest to the stopper through stimulus enhancement as the responding demonstrator would have done. It is possible that the activity of a bird on the treadle would have been enough to result in stepping through stimulus enhancement and trial and error in the observers.

Results from the quail, pigeon and budgerigar experiments suggest that birds are unable to learn foot responses through observation. It is possible that in both the treadle and stopper paradigms foot use by the demonstrators was not obvious to the observers. This is more likely for the stopper experiment as birds were shown a virtual demonstrator and only one removal was seen, admittedly many times. In the treadle experiments however live demonstrators were used so observers were presumably exposed to many different foot responses, which they could observe from many different angles. Lack of opportunity to learn from the demonstrator is therefore an unlikely explanation in the treadle experiments.

As an inability to learn foot responding was observed in more than one experiment, and in more than one paradigm, it suggests that the explanation may be more than one of experimental design. It is possible that the ability to imitate is dependent on the birds having previously had experience of performing the action whilst others were performing it (Heyes & Ray, 2000). It is likely that birds would have had a lot of experience of using their beak, while others were using their beak. However, they may have had insufficient correlated experience of observation and execution of foot responding, which would have prevented birds in group Foot from learning the foot response from their demonstrators. It would be interesting to give birds correlated experience of observation and execution of foot responding prior to observation and testing, to see whether foot use was promoted in Foot observers.

5.3.2. Potential explanation for effector-matching

The effector matching seen in the Beak group in Experiment 4.3 cannot be attributed to emulation or social facilitation plus stimulus enhancement. Emulation was prevented as direction of stopper movement following a removal response was not confounded with the type of removal used. While social facilitation plus stimulus enhancement was prevented by the 24 hour delay inserted between observation and testing. Even if observation of beak removals resulted in socially facilitated pecking it would be incredibly unlikely that this effect could persist over an interval of 24 hours until the bird was tested.

However, although emulation and social facilitation plus stimulus enhancement cannot account for the effector matching seen in Experiment 4.3 there is an alternative explanation to imitation. It is possible that higher order conditioning of the stopper was occurring (Rescorla, 1973). During pre-experimental social feeding the sight of a conspecific pecking (S2) signals receipt of food by observer (S1), therefore sight of a conspecific pecking becomes a conditioned reinforcer. In Experiment 3 the sight of the stopper in observation (S3) occurs in closer temporal and spatial contiguity with the sight of a demonstrator pecking than in the other two groups, therefore one might expect the stopper to become a conditioned reinforcer. To summarise for Group Beak the stopper is paired with the food directly, but also indirectly via S2. This could make the stopper more attractive and as a consequence Group Beak may peck it more on test.

Higher order conditioning could not explain a difference between Groups Foot and Control as it is unlikely that any prior experience of the birds would result in stepping becoming a conditioned reinforcer. Higher order conditioning can only

explain learning in the Beak group if the stopper manipulation by the Beak demonstrators is seen as pecking by the observers. Given the complexity of pecking and the flexibility of beak use in various behaviours (Hörster, Krum, Mohr, & Delius, 2002) use of the beak to displace the stopper may not resemble pecking behaviour exhibited during feeding. However until more is known about how birds perceive beak use, imitation and higher order conditioning are both valid explanations for the results obtained in Experiment 4.3.

5.3.3. Summary and Conclusions of substantive implications

The experiments reported in this thesis addressed the problem of emulation which can potentially explain the results of many two-action experiments carried out with birds. The experiments in Chapter 4 also succeeded in excluding social facilitation and stimulus enhancement, which could potentially account for the results of the treadle experiments with pigeons and quail along with the results of the stopper Experiment 3.1. However despite the final experiment, Experiment 4.3, providing evidence of effector matching this was limited to birds which had observed beak removals and as a consequence these results could possibly be explained using higher order conditioning.

The experiments with budgerigars therefore failed in their aim to provide conclusive evidence of imitative abilities in birds, instead identifying the need to control for both social facilitation and higher order conditioning in imitation experiments. Given, the failure to exclude all social influences and non-imitative social learning there is currently no conclusive evidence of imitative abilities for any species of bird.

In future experiments it will be important to attempt to obtain imitation of foot use in addition to copying of beak use. It may be that this will only be possible if birds are given experience of simultaneously using their feet and observing foot use.

5.4. Imitation in Primates

Given the rigour with which imitation experiments with birds have been examined it is important that the same strict criteria are applied to the data from primate imitation studies. In Chapter 1 data from primates was considered and it was concluded that if emulation was considered to be a serious alternative to imitation in experiments in which manipulandum movement is confounded with demonstrator action, then evidence for imitation in primates currently comes from the two-action experiment with marmosets (Voelkl & Huber, 2000) and the do-as-I-do experiments with chimpanzees and orangutans (Custance et al 1995; Miles et al 1996; Call, 2001). These data will be re-examined in more detail, in the light of the experiments run with budgerigars.

5.4.1. Marmoset two-action experiment

The marmoset experiment run by Voelkl & Huber (2000) was presented in Chapter 1 as providing the only evidence of imitative abilities in monkeys. Observers in this experiment watched trained demonstrators remove the lid of a film canister to obtain a food reward using either its mouth or its hand. On test, observers that had seen the hand technique only used their hands, while observers of the mouth opening technique used their mouths as well. A control group showed that this effect was not

due to scent cues deposited by the demonstrators on the film canisters, suggesting that the observers were carrying out imitation.

When the data are examined in more detail it is clear that hand opening is the preferred opening technique in marmosets. In the first test mouth opening was shown by four out of the six animals who observed a mouth opening demonstrator and by none of the five animals who observed hand opening. In the non-exposed control group and the olfactory control group only two out of eleven and one out of fourteen animals, respectively, used their mouths to open the canisters. This suggests that hand opening did not have to be learnt through conspecific observation but that mouth opening did. Imitation is one explanation, however, it is possible that higher order conditioning, as in the budgerigar experiments, was occurring (Rescorla, 1973).

Higher order conditioning of the canister in the marmoset experiment can be explained in a similar way to higher order conditioning of the stopper in the budgerigar experiment; During pre- experimental social feeding the sight of a conspecific putting something in its mouth (S2) could have signalled the receipt of food by observer (S1), therefore sight of a conspecific putting something in its mouth becomes a conditioned reinforcer. In the canister experiment the sight of the canister in observation (S3) occurs in closer temporal and spatial contiguity with the sight of a demonstrator eating in the mouth opening group, than in the hand opening and control groups, therefore one might expect the canister to become a conditioned reinforcer. To summarise for the mouth group the canister is paired with the food directly, but also indirectly via S2. This could make the canister more attractive and

as a consequence the mouth group may be more likely to put it in their mouth. As with the results of Experiment 4.3 imitation is only one possible explanation.

5.4.2. Do-As-I-Do experiments

The do-as-I-do experiments with chimpanzees and an orangutan (Custance et al 1995; Miles et al 1996; Call, 2001) were presented in Chapter 1 as providing the only evidence of imitation in apes other than humans. The apes were trained to copy the actions of a human demonstrator before being asked to copy novel gestures. The range of actions used and the absence of actions on objects ensure that imitation is successfully isolated. It is unlikely that either social facilitation or higher order conditioning can be invoked as alternative explanations to imitation for these experiments.

In Custance et al's (1995) do-as-I-do experiment two human reared chimpanzees were trained to imitate 15 gestures and were then tested on 48 novel gestures. Independent observers correctly identified a significant number of the chimpanzees imitations (13 responses for one animal and 17 for another). It is explained however that when the actions produced were examined in more detail, some either appeared to be replications of an action already in the repertoire or they were modifications of previously performed actions. For example one chimpanzee's response to 'touch stomach' was the 'pat stomach' response it had previously been taught during the training phase. Altogether 13 out of the 18 responses performed by one chimpanzee, and 13 out of the 17 responses performed by the other chimpanzee, could have a non-imitative explanation. However it is not clear how the remaining responses, five

for one chimpanzee and four responses for the other, can be explained without using imitation.

Detailed analysis of the chimpanzees' responses has important implications for the studies ran with the orangutan, Chantek (Miles et al 1996; Call, 2001). The chimpanzee do-as-I-do study highlights the importance of knowing what actions the animals already had in their repertoire at the time of testing. Call (2001) replicated Custance et al's (1995) experiment with Chantek and impressively found that the orangutan produced a full reproduction 58.3% of the time. However, these results are contaminated to a certain extent by the long experimental history of Chantek and the previous two-action experiments run with him (Miles et al, 1996, Call & Tomasello, 1995). It is possible that Chantek had previously been exposed to the majority of actions he was asked to reproduce, and as consequence he may have been reproducing actions already in his repertoire, as opposed to carrying out imitation.

5.4.3. Summary and Conclusions of primate imitation evidence

If data from imitation experiments with primates is examined with the same rigour as that from experiments with birds it becomes apparent that higher order conditioning, which may account for the results of Experiment 4.3, is also a potential explanation for the imitation experiment carried out with marmosets (Voelkl & Huber, 2000). Imitation does however remain the most likely explanation for some of the action copying seen in the do-as-I-do experiment run with chimpanzees and possibly those run with the orangutan, Chantek (Custance et al 1995; Miles et al 1996; Call, 2001).

When non-imitative explanations are considered for the results of imitation experiments with a variety of species it would appear that there is currently only evidence for imitation in species of ape. This provides some evidence for theories which assume that imitation is a cognitively complex form of learning (e.g. Meltzoff & Moore, 1977; Whiten, 1996; Tomasello & Call, 1997). The experiments reported in this thesis, however, have highlighted how difficult it is to exclude all forms of social influence and non-imitative social learning from imitation experiments. Until this can be achieved the distribution of imitation cannot be known for certain. Two-action experiments with birds have shown potential, but further work is needed before imitation can be successfully isolated.

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., Klein, E. D. & Zentall, T. R. (2002). Imitative learning in Japanese Quail (*Coturnix japonica*) using the bidirectional control procedure. *Animal Learning and Behaviour*, 30, 275-281.

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.

Anisfeld, M. (1991). Neonatal imitation. *Development Review*, 11, 60-97.

Anisfeld, M. (1996). Only tongue protrusion modelling is matched by neonates. *Development Review*, 16, 149-161.

Bekkering, H., Wohlschläger, A. & Gattis, M. (2000). Imitation of gestures in children is goal directed. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, 53, 153-164.

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, 26, 325-338.

Boesch, C. & Tomasello, M. (1998). Chimpanzee and human cultures. *Current Anthropology*, 39, 591-614.

Boysen, S. T. & Himes, G. T. (1999). Current issues and emerging theories in animal cognition. *Annual Review of Psychology*, 50, 683-705.

Byrne, R. W. (1994). The evolution of intelligence. In P J B Slater and T R Halliday (Eds). *Behaviour and Evolution*, pp. 223-265. Cambridge: Cambridge University Press.

Byrne, R. W. (1998). Comments on C. Boesch and M. Tomasello 'Chimpanzees and human cultures'. *Current Anthropology*, 39, 604-605.

Byrne, R. W. (2003). Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society London. B.*, 358, 529-536.

Byrne, R. W. & Russon, A. E. (1998). Learning by imitation: a hierarchical approach. *Behavioural and Brain Sciences*, 21, 667-721.

Bugnyar, T. & Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour*, 54, 817-831.

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

Caldwell, C. A. & Whiten, A. Evolutionary perspectives on imitation: is a comparative psychology of social learning possible? *Animal Cognition*, 5, 193-208.

Call, J. (2001). Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernetics and Systematics: An International Journal*, 32, 97-119.

Call, J. & Tomasello, M. (1995). Use of social information in the problem solving of orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 109, 308-320.

Campbell, F.M., Heyes, C. M. & Goldsmith, A. R. (1999). Stimulus learning and response learning by observation in the European starling, in a two-object/two-action test. *Animal Behaviour*, 58, 151-158.

Carpenter, M., Akhtar, N. & Tomasello, M. (1998). Fourteen- through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behaviour and Development*, 21, 315-330.

- Chartrand, T. L. & Bargh, J. A. (1999). The chameleon effect: the perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, 76, 893-910.
- Clayton, D. A. (1978). Socially facilitated behaviour. *Quarterly Review of Biology*, 53, 373-391.
- 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.
- Custance, D. (1998). Apes ape! *Behavioural and Brain Sciences*, 21, 118-119.
- Custance, D., Whiten, A. & Bard, K.A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, 132, 837-859.
- Custance, D., Whiten, A. & Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 113, 13-23.
- Dawson, B. V. & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour*, 13, 470-474.

D'Eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews*, 73, 267-292.

D'Eath, R. B. & Dawkins, M. S. (1996). Laying hens do not discriminate between video images of conspecifics. *Animal Behaviour*, 52, 903-912.

Deich, J. & Balsam, P. (1994). Development of prehensile feeding in ring doves (*Streptopelia risoria*). In M. Davies & P. Green (Eds.). Perception and motor control in birds, pp. 160-181. Heidelberg, Germany: Springer- Verlag.

Doty, E. & Wirth, A. (1953). Differentiation between rods and cones by flicker electroretinography in pigeon and guinea pig. *Acta Physiologica Scandinavica*, 30, 80-89.

Dorrance, B. R. & Zentall, T. R. (2001). Imitative learning in Japanese quail depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology*, 115, 62-67.

Dorrance, B. R. & Zentall, T. R. (2002). Imitation of a conditional discrimination in pigeons. *Journal of Comparative Psychology*, 116, 277-285.

Farabaugh, S. M., Linzenbold, A. & Dooling, R. J. (1994). Vocal plasticity in budgerigars: Evidence for social factors in the learning of contact calls. *Journal of Comparative Psychology*, 108, 81-92.

Fawcett, T. W., Skinner, A. M. & Goldsmith, A. R. (2002). A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour*, 64, 547-556.

Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainard, D. H. & Endler, D. A. (1998). Colour perception and the use of video playback experiments in animal behaviour. *Animal Behaviour*, 56, 1035-1040.

Fredman, T. & Whiten, A. (2002). The nature and function of observational learning of tool use by capuchin monkeys (*Cebus apella*) in relation to human and conspecific models. Unpublished poster, Perspectives on Imitation Conference, Royaumont Abbey.

Fritz, J. & Kotrschal, K. (1999). Social learning in common ravens, *Corvus corax*. *Animal Behaviour*, 57, 785-793.

Galef, J. R. (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. (1990). Tradition in animals: Field observations and laboratory analyses. In M. Bekoff and D. Jamieson (Eds.), *Interpretations and explanations in the study of behaviour: Comparative perspectives*, pp. 74-95. Boulder, CO: Westview Press.

Galef, J.R. (1996). Introduction. In C. M. Heyes and B. G. Galef (Eds.), *Social Learning In Animals: The Roots of Culture*, pp. 3-16. New York: Academic Press.

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

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

Hart, N. S., Partridge, J. C. & Cuthill, I. C. (2000). Retinal asymmetry in birds. *Current Biology*, 10, 115-117.

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. 267-286. New York: Academic Press.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioural and Brain Sciences*, 21, 101- 148.

Heyes, C. M. (2001). Causes and consequences of imitation. *Trends in Cognitive Science*, 5(6), 253-261.

Heyes, C. M. & Dawson, G. R. (1990). A demonstration of observational learning using a bi-directional 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, 81-92.

Heyes, C. M. & Ray, E. D. (2000). What is the significance of imitation in animals? *Advances in the Study of Behaviour*, 29, 215-245.

Heyes, C. & Saggerson, A. (2002). Testing for imitative and nonimitative social learning in the budgerigar using a two-object/two action test. *Animal Behaviour*, 64, 851-859.

Hile, A. G. & Striedter, G. F. (2001). Call convergence within groups of female budgerigars. *Ethology*, 106, 1105-1114.

Hile, A. G., Plummer, T. K., & Striedter, G. F. (2000). Male vocal imitation produces call convergence during pair bonding in budgerigars. *Animal Behaviour*, 59, 1209-1218.

Hosey, G. R., Jacques, M. & Pitts, A. (1997) Drinking from tails: social learning in a group of ring-tailed lemurs (*Lemur catta*). *Primates*, 38, 415-422.

Huffman, M. A. (1996). Acquisition of innovative cultural behaviours in nonhuman primates: A case study of stone handling, a socially transmitted behavior in Japanese macaques. In C. M. Heyes and B. G. Galef (Eds.), *Social Learning In Animals: The Roots of Culture*, pp. 267-286. New York: Academic Press.

Hunt, G.R. (2000). Human-like population- level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London, B*, 267, 403-413.

Ikebuchi, M. & Okanoya, K. (1999). Male zebra finches and Bengalese finches emit directed song to the video images of conspecific females projected onto TFT display. *Zoological Science*, 16, 63-70.

Itani, J. & Nishimura, A. (1973). The study of infrahuman culture in Japan. In E. W. menzel Jr (Ed.), *Symposia of the Fourth International Congress of Primatology*, Vol. 1, pp. 26-60. Basel: Karger.

Janik, V. M. & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, 60, 1-11.

Jarvis, E.D. & Mello, C. V. (2000). Molecular mapping of brain areas involved in parrot vocal communication. *Journal of Comparative Neurology*, 419, 1-31.

Jones, S. S. (1996). Imitation of exploration? Young infants' matching of adults' oral gestures. *Child Development*, 67, 1952-1969.

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.

Kawai, M. (1965). Newly acquired pre-cultural behaviour of a natural troop of Japanese monkeys on Koshima Island. *Primates*, 6, 1-30.

Keeling, L. J. & Hurnik, F. (1993). Chickens show socially facilitated feeding behaviour in response to a video image of a conspecific. *Applied Animal Behavioural Science*, 36, 223-231.

Keeling, L. J. & Hurnik, F. (1996). Social facilitation acts more on the appetitive than the consummatory phase of feeding in domestic fowl. *Animal Behaviour*, 52, 11-15.

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

Masure, R. H. & Allee, W. C. (1934). Flock organisation of the shell parakeet *Melopsittacus undulates* Shaw. *Ecology*, 15, 388-397.

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

Mcquoid, L. M. & Galef, B. G. (1993). Effects of access to food during training on social learning by Burmese red hunglefowl. *Animal Behaviour*, 46, 13-22.

Meltzoff, A. N. (1995). Understanding of the intentions of others: re-enactment of intended acts by 18-month-old children. *Developmental Psychology*, 31, 838-850.

Meltzoff, A. N. & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science*, 198, 75-78.

Miles, H. L., Mitchell, R. W. & Harper, S. E. (1996). Simon says: The development of imitation in an enculturated orangutan. In A. E. Russon, K. A. Bard and S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes*, pp. 278-299. Cambridge: Cambridge University Press.

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

Moore, B.R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour*, 122, 231-263.

Morimura, N. & Matsuzawa, T. (2001). Memory of movies by chimpanzees. *Journal of Comparative Psychology*, 115, 152- 158.

Mottley, K. & Heyes, C. (in press). Budgerigars (*Melopsittacus undulates*) copy 'virtual' demonstrators in a two-action test. *Journal of Comparative Psychology*.

Mowrer, O. H. (1960). *Learning Theory and the Symbolic Processes*. New York: Wiley.

Nagell, K., Olguin, R. S. & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 107, 174-186.

Nehaniv, C. & Dautenhahn, K. (2001). Imitation in natural and artificial systems. *Cybernetic systems*, 32, 1-10.

Nuboer, J. F. W., Coemans, M. A. & Vos, J. J. (1992). Artificial lighting in poultry houses: do hens perceive the modulations of fluorescent lamps as flicker? *British Poultry Science*, 33, 123-133.

Ohshima, A. (1998). *Visual guide for the anatomy of personal computers*, Vol. 2., Tokyo: Softbank Books.

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

Rescorla, R. A. (1973). Second-order conditioning: Implications for theories of learning. In F. J. McGuigan and D.B. Lumsdem (Eds.). *Contemporary approaches to conditioning and learning*, pp. 127-150. Washington: W. H. Winston and Sons.

Rogers, L. J. & Workman, L. (1993). Footedness in birds. *Animal Behaviour*, 45, 409-411.

Rowley, I. & Chapman, G. (1986). Cross-fostering, imprinting and learning in two sympatric species of cockatoo. *Behaviour*, 96, p.1-16.

Russon, A. E. & Galdikas, M. F. (1993). Imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 107, 147-161.

Russon, A. E. & Galdikas, M. F. (1995). Constraints on great ape's imitation: Model and action selectivity in rehabilitant orangutan (*Pongo pygmaeus*) imitation. *Journal of Comparative Psychology*, 109, 5-17.

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

Stoinski, T.S., Wrate, J.L., Ure, N. & Whiten, A. (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology*, 115, 272-281.

Suboski, M. D. & Bartashunas, C. (1984). Mechanisms for social transmission of pecking preferences to neonatal chicks. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 182-194.

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

Sumita, K. Kitahara-Frisch, J., & Norikoshi, K. (1985). The acquisition of stone tool use in captive chimpanzees. *Primates*, 26, 168-181.

Tanaka, I. (1998). Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Animal Behaviour*, 56, 1229-1236.

Tayler, C.K. & Saayman, G.S.(1973). Imitative behaviour by Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in captivity. *Behaviour*, 44, 286-298.

Templeton, J. J., Kamil, A. C. & Balda, R. P. (1999). Sociality and social learning in two species of corvids: The Pinyan jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). *Journal of Comparative Psychology*, 113, 450-455.

Thorndike, E. L. (1898). Animal intelligence. *Psychological Review Monographs*, 2, 8.

Thorndike, E. L. (1911). *Animal Intelligence*. New York: Macmillan.

Thorpe, W. H. (1956). *Learning And Instinct In Animals*. London: Methuen.

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

Tolman, C. W. & Wilson, G. F. (1965). Social feeding in domestic chicks. *Animal Behaviour*, 13, 134-142.

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 Development Perspectives, pp. 271-311. Cambridge: Cambridge University Press.

Tomasello, M. (1996). Do Apes Ape? In C. M. Heyes and B. G. Galef (Eds.), *Social Learning In Animals: The Roots of Culture*, pp. 267-286. New York: Academic Press.

Tomasello, M. (2000). Culture and cognitive development. *Current Directions In Psychological Science*, 9 (2).

Tomasello, M. & Call, J. (1997). *Primate Cognition*. New York: Oxford 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.

Tomasello, M., Gust, D. & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates*. 30, 35-50.

Tomasello, M. Kruger, A. C. & Ratner, H. H. (1993a). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development*, 64, 1688-1705.

Tomasello, M., Savage-Rumbaugh, S. & Kruger, A. C. (1993b). Imitative learning of actions on objects by children, chimpanzees and enculturated chimpanzees. *Child Development*, 64, 1688-1705.

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

Visalberghi, E. & Fragaszy, D. M. (1990). Do monkeys ape? In S. T. Parker and K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives*, pp. 247-273. Cambridge: Cambridge University Press.

Voelkl, B. & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60, 195-202.

Wallbott, H. G. (1991). Recognition of emotion from facial expressions via imitation? Some indirect evidence for an old theory. *British Journal of Social Psychology*, 30, 207-219.

Wapner, S. & Cirillo, L. (1968). Imitation of a model's hand movements: Age changes in transposition of left-right relations. *Child Development*, 39, 887-894.

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

Whiten, A. (1996). Imitation, pretense and mindreading: Secondary representation in comparative primatology and developmental psychology? In A. W. Russon, K. A. Bard, and S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes*, pp. 300-324. Cambridge: Cambridge University Press.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, 24, 477-508.

Whiten, A. & Custance, D. M. (1996). Studies of imitation in chimpanzees and children. In C. M. Heyes and B. G. Galef (Eds.), *Social Learning In Animals: The Roots of Culture*, pp. 291-318. New York: Academic Press.

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

Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behaviour*, 21, 239-283.

Wood, D. (1988). How children think and learn. London: Basil Blackwell.

Wyndham, E. (1980). Diurnal cycle, behaviour and social organization of the budgerigar. *Emu*, 80, 25-33.

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

Zajonc, R. B. (1969). *Animal Social Psychology*. New York: Wiley.

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. 221-244. New York: Academic Press.

Zentall, T. R. (2001). Imitation in animals: evidence, function and mechanisms. *Cybernetics and systems: An international Journal*, 32, 53-96.

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