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**Summary of Thesis:**

A series of experiments was conducted in order to evaluate a theory proposed by Heyes and Saggerson (2000) of how one animal is able to imitate the action of another animal. A fundamental assumption of the theory is that animal's are able to discriminate between the natural movements of other animals on the basis of dynamic cues created by the transition from one posture to another. The results from Experiment 1 to 3 revealed for the first time that pigeons and budgerigars are indeed sensitive to the dynamic cues created by different movements. These cues were shown to be effective with inverted images (Experiment 4), but not degraded, point-light images (Experiment 5). A further assumption of the theory is that imitation will be evident whenever one animal has the opportunity to observe the actions of another animal. This assumption gained support from the results of Experiment 7, but not Experiment 6. Overall the results lend strong support to the theory.

# **Evaluation of a Theory of Imitation**

**Rosetta Suet Ying, Mui**

**Submitted in partial fulfillment of the requirements of  
the degree of Doctor of Philosophy  
at the  
School of Psychology,  
Cardiff University  
UK.  
September, 2008**

**Supervisor: John M. Pearce (Cardiff University)  
Cecelia M. Heyes (University College London)**

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Experiment 1, 2, and 3 described in Chapter 2 and 3 are published as: Mui, R., Haselgrove, M., McGregor, A., Fetter, J., Heyes, C., Pearce, J.M. 2007. The discrimination of natural movement by budgerigars (*Melopsittacus undulates*) and pigeons (*Columba livia*). *Journal of Experimental Psychology: Animal Behaviour Process*, 33(4):371-80.

## **Abstract**

A series of experiments was conducted in order to evaluate a theory proposed by Heyes and Saggerson (2000) of how one animal is able to imitate the action of another animal. A fundamental assumption of the theory is that animal's are able to discriminate between the natural movements of other animals on the basis of dynamic cues created by the transition from one posture to another. The results from Experiment 1 to 3 revealed for the first time that pigeons and budgerigars are indeed sensitive to the dynamic cues created by different movements. These cues were shown to be effective with inverted images (Experiment 4), but not degraded, point-light images (Experiment 5). A further assumption of the theory is that imitation will be evident whenever one animal has the opportunity to observe the actions of another animal. This assumption gained support from the results of Experiment 7, but not Experiment 6. Overall the results lend strong support to the theory.

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## Chapter 1

Environments change rapidly. However, evolutionary changes take at least a few generations' time to occur. To adapt to the fast changing environment, acquiring information and techniques through learning, can be a good alternative solution to the time lag required for evolutionary changes. Changing genetically or physiologically may not be the best solution to accommodate to a fast changing environment.

Developing a neurosystem with plasticity may allow faster, fitter adaptations.

However there are pros and cons of individual learning. Animals have to encounter many dangerous situations to learn. It may be too risky to learn by trial-and-error *per se*. Social learning provides a useful intermediate step between genetic predepositions and individual trial-and-error learning, maintaining much of the flexibility of individual learning, while reducing the likelihood of possible aversive consequences associated with making errors (see Zentall, 2003). Imitative learning, in which an individual learns to reproduce the behaviour pattern of another, has attracted considerable attention as a potentially powerful form of social learning (Fawcett, Skinner & Goldsmith, 2002).

In many situations, individual learning by trial-and-error may be more costly than social learning in term of energy, time and risk. The extra cost required for individual learning must be borne by the individual solely, whereas the acquired information potentially benefits everyone via the cultural knowledge pool (Kameda & Nakanishi 2003). Social /cultural learning allows us to acquire useful information without costly individual learning by trial-and-error. One major adaptive advantage

usually ascribed to such cultural learning is its uncertainty-reduction function (Kameda & Nakanishi 2003). Individual needs to suffer the metabolic cost of trying, cost of making errors (Heyes 1993), and remember what happened on its previous trials. Sometimes it can be lethal to make a mistake and the individual will not have its second chance to try.

Imitation, which can be defined as a form of social learning that involves the acquisition of a new behavior after observing another animal perform that behavior (Dorrance & Zentall 2001), differs from other forms of social learning in terms of what is learned as a direct result of observation or interaction with another animal or its products (Heyes 1993). It requires a more complex brain for an animal to apply other's experience to its own behavior. Imitation is considered to be a more advanced way to learn because it greatly reduces the risk and the energetic cost of learning through trial-and-error. Individuals can learn without experiencing errors. In the past, primates were thought to be the only nonhuman animals being capable of non-vocal or motor imitation (Thorndike 1898). However, recently imitation has been said to occur in other species: rodents (Heyes 1993, 1994), zebra finches (Benskin, Mann, Lachlan & Slater 2002), quail (Dorrance & Zentall 2001, Dawson & Foss 1965), pigeons (Epstein 1984), starlings (Fawcett, Skinner & Goldsmith 2002), common ravens (Fritz & Kotrschal 1999), budgerigars (Heyes & Saggerson; Galef, Manzig & Field 1986), keas (Huber, Rechberger & Taborsky 2001), fish (Dugatkin 2000), and even octopus (Fiorito & Chichery 1995).

If animals are capable of imitation, then this ability poses two fundamentally profound challenges to our understanding of learning in animals. On the one hand,

there is the question of explaining how an animal is able to copy the response that is made by another animal. To be more specific, if an animal observe another animal press a lever, how does the observer know what action to perform in order to behave in the same way as the demonstrator? On the other hand, there is the question of explaining why the animal should repeat the action it has just observed. Theories of instrumental conditioning maintain that the likelihood of a response being made by an animal will increase if it is followed by reward. In the case of imitation, however, there is often no tangible reward for the response that is copied which makes it hard to understand why the response is repeated. The purpose of this thesis is to explore the implications of one theory that has been developed to answer these questions: The Associative Sequence Learning theory of Heyes and Ray (2000, see also Heyes, 2001, 2005). Before going further into this theory, I shall first review the evidence that animals are capable of imitation. Some of the most compelling evidence of imitation by animals has come from studies with birds. Accordingly, I shall concentrate on the findings from these studies.

Fisher and Hinde (1949) found that blue tits are capable of piercing the metal foil on milk bottles in order to drink the milk. This bottle opening behavior was initially found within a small group of birds, and later it was found to spread over a much larger population. One explanation for the spread of the behavior is that this milk bottle opening behavior was spread by imitation. However, the spread can also be explained by simpler mechanisms, like stimulus enhancement (e.g. Galef, 1988) or local enhancement (e.g. Thorpe, 1956). Local enhancement refers to drawing attention to a particular place or location, whereas the term stimulus enhancement is often used when the activity of the demonstrator draws the attention of the observer to a particular object. In the case of opening milk bottle tops by blue tits, this activity could be acquired through imitation, but it could also be a consequence of stimulus enhancement. The observer's attention may be drawn to the milk bottle top by virtue of seeing another blue tit pecking at the top. This increase in attention may then encourage the observer to approach the top of a milk bottle top itself, and once there it might peck at the top and, by accident, open it. Quite often in the study of imitative learning, the object in question is at a fixed location, so local enhancement and stimulus enhancement are indistinguishable (Zentall 2006).

Apart from stimulus enhancement and local enhancement, emulation poses another problem to the study of imitation. Emulation is a type of non-imitative social learning about an object's property. For example, seeing the crumpled, opened foil of the milk bottle may suggest to an observer that the foil can be pecked through, which may be enough to encourage the observer to peck at the foil when it has the chance. In this process, because no other animal is involved, emulation cannot be categorized as a social learning mechanism, not to mention imitation. To solve the problem of emulation, the two-action method was developed to test for imitation.

*Two-action method.* Using the two-action procedure (e.g. Dawson & Foss, 1965), the same manipulandum can be operated in more than one way, and lead to the same outcome. For example a treadle can be pressed down by either being pecking at it, or stepping on it. In both case the same object (the treadle) is manipulated in the same manner (pressed down). Both actions produce the same effect upon the manipulandum. Thus, the two-action method can control for explanations of apparent imitation in terms of both stimulus enhancement and emulation. However, it could be argued that the likelihood or the ease of performing the different action (pecking or

stepping) are not the same. Pecking, for example, is generally more readily performed in social feeding birds.

*Bidirectional Control.* The bidirectional design (e.g. Akins, Klein, & Zentall, 2002), on the other hand, can control for the difficulties of the required actions, as well as the explanation of stimulus enhancement, because the same object, for example a panel covering a food hopper, is manipulated. The likelihood and the difficulty of performing the two actions, for example, pushing the panel to the left or right, is generally the same. However, it is now possible that emulation can explain any apparent effect of imitation. That is, observing a bird push a panel to the left might enable the observer to learn that panels can be pushed to the left and, when given the opportunity, it will perform this action to achieve its goal.

Now that the problems of identifying whether or not imitation has taken place have been identified, and possible solutions to the problems have been introduced, I shall examine the results from experiments which have investigated whether birds are capable of imitation. The first laboratory experiment to employ the two-action method was by Dawson and Foss (1965). Dawson and Foss allowed observer

budgerigars to watch another budgerigar use one of the three ways of removing a container's lid to get food: push the lid off with the beak, twist it off with the beak, or grasp it with the foot and pull it off. When given the opportunity to operate the lid, observers opened the lid in the same way as their demonstrators. In this case the experimental design has controlled for alternative explanations like stimulus enhancement, because all the demonstrators contacted the lid, and the observers manipulated the lid in the way they observed but not the other ways. However, emulation suggests that the sight of the opened lid at a different position alone may be enough to generate the same result. The sight of the lid on the side (resulted from being twisted off), at the back (resulted from being pushed off), or at the front (resulted from being pulled off) may be enough to encourage the observer to push the lid to that particular direction.

Lefebvre, Templeton, Brown, and Koelle (1997) performed a study similar to that by Dawson and Foss (1965) with Carib grackles. Observer grackles were allowed to watch the demonstrator removing a stopper on a test tube to gain food either by pushing the stopper away from itself, or pulling the stopper towards itself. Lefebvre *et al.*'s experiment revealed that grackle observers use the same motor technique to open

the feeder as their tutor. Yet, due to the differences in the end position of the stopper, this experiment result can again be explained by emulation.

Imitation in pigeons has been studied with the two action method. Zentall, Sutton, and Sherburne (1996) let naïve pigeons observe a conspecific demonstrator either pecking at or stepping on a treadle in order to gain food. The experiment results showed that of the ten pigeons who observed pecking, five pecked and five stepped; and of the ten pigeons that observed stepping, nine stepped on the treadle and none pecked at it. Asymmetry in the tendency to perform these movements may account for some of the results, which nonetheless are difficult to explain in terms of stimulus enhancement and emulation.

Several imitation experiments with Japanese quail have been conducted using the two-action design. With a similar methodology to that used by Zentall *et al.* (1996), Akins and Zentall (1996) reported that birds who observed pecking demonstrations made more pecking than stepping responses; and birds that observed stepping demonstrations made more stepping than pecking responses. However, although the quail imitated both actions, the frequency of imitating pecking is greater than that of stepping. Akins and Zentall explained that the differences may be due to how convenient it is to perform the two actions.

Dorrance and Zentall (2001) used the two-action control to investigate the influence of motivational state on imitation, again with Japanese quail. In their study, observers were allowed to observe another quail gain food by either pecking or stepping at the treadle. Imitation was evident in birds who were hungry during the observation period, but not in birds who were satiated.

By using the bidirectional design, Akins, Klein and Zentall (2002) allowed tutor quail to slide a screen in front of a food hopper in a specific direction in order to gain food. When observers were given the chance to manipulate the screen, they moved the screen in the direction they had observed significantly more often than in the opposite direction. To control for the possibility that this outcome was a consequence of emulation learning, Akins *et al.* employed a “ghost” control group. This group observed only the screen movements but without the demonstrator pushing it (the screen was moved unobtrusively by the experimenter). On test, the control group did not show a preference for pushing the screen in the direction it had observed the screen being pushed.

The bidirectional design was also adopted by Campbell, Heyes and Goldsmith (1999). Campbell *et al.* let observer European starlings watch demonstrators removing one of the two different colored plugs by either pulling it up or pushing it

down. It was found that juvenile starlings preferred to remove the plug that was the same colour as the one manipulated by the demonstrator. Furthermore, they manipulated this plug in the same manner as the demonstrator. Stimulus enhancement can explain the preference for one plug over the other. The fact that the observer performed the same response as the demonstrator can be explained by either imitation or emulation.

Following Campbell *et al.* (1999), Heyes and Saggerson (2002) modified the starling experiment to test for emulation or imitation in budgerigars. In their experiment, observers watched a demonstrator removing one of the two different colored stoppers by either pulling it up or pushing it down. Heyes and Saggerson found that the observers not only tended to manipulate the same stopper that its demonstrator manipulated, but also the observers used the same technique to remove the stopper. Emulation or imitation can both explain these results.

Dorrance and Zentall (2002) used a rather complex version of the two-action control to provide a good example of imitation in pigeons. Observer birds were first trained to peck on a treadle in order to gain food in the presence of a red light, and to step on the treadle in order to gain food in the presence of a green light. The observers were then required to learn the reverse of this discrimination: step during

red, peck during green. Prior to each reversal session, the birds were given the opportunity to watch demonstrators performing a discrimination. Observers in the consistent group saw demonstrators step for food during red, and peck for food during green. Those in the inconsistent group watched demonstrators pecking during red, and stepping during green. Any tendency to imitate the actions that were being performed would then facilitate the acquisition of the reversal in the consistent group, and hinder it in the inconsistent group. The results described by Dorrance and Zentall were consistent with this prediction. It is not possible to explain this outcome by stimulus enhancement, local enhancement or emulation. Instead, the most plausible explanation for its findings is that the observers imitated the actions they observed being performed by the demonstrators. A convincing replication of this study has been reported by Saggerson, George and Honey (2005). For a related finding see McGregor, Saggerson, Pearce, and Heyes (2006).

In conclusion, despite the problems in providing a clear demonstration of imitation, there is at least some evidence to suggest that birds are capable of imitation. I now turn to consider how this imitation might take place.

## 1.1 A theory of imitation

Even though it has been accepted for some considerable time, by at least some researchers, that animals are capable of imitation, there have been rather few convincing explanations of how imitation takes place. Heyes and Ray (2000) review some of the earlier theories and argue that they are rather vague and thus hard to test. The theories are also criticised for being incomplete. As a consequence, Heyes and Ray, see also Heyes (2001, 2005), put forward a new theory of imitation – Associative Sequence Learning theory. The theory is based on established principles of associative learning, and can be regarded as a development of earlier associative theories of imitation (Mowrer, 1960).

At the heart of Associative Sequence Learning theory is the assumption that any action is composed of a number of component actions, or as Heyes and Ray refer to them “action units”. Thus the response of pecking a key would be treated as a sequence of discrete postures, with each posture being regarded as an action unit.

When an observer watches a demonstrator pecking a key, it will then break down the action into its component units and form a memory, or sensory representation of each unit. Furthermore, because the units occur in the same sequence, over and over again as the response is repeated, associations will form between the memories of

successive action units. In other words, observing a response being performed will result in the acquisition of a sensory representation of the response, and the nature of this representation is of a number of action units linked together by associations in the order in which they occur.

There is another important component to this theory. Suppose that a bird is pecking for food. Saggerson and Heyes (2002) have argued that this action will be a consequence of the activation of a sequence of motor action units. They further argued that if this response is being performed while observing another bird pecking, then the sensory representations of the action units activated by the sight of pecking will fire at the same time as the motor units that are responsible for pecking are activated. The simultaneous firing of these sensory and motor action units will then result in associations developing between them. As a consequence, if the observer should subsequently observe a bird pecking, the sensory representations of the appropriate action units will fire. This firing will in turn activate the motor units for pecking, through the previously acquired conditioned links, and encourage the observer to peck.

The implication of this theory, therefore is that imitation of pecking, say, will be possible only if the subject has previously engaged in pecking while observing

another bird pecking. With this implication in mind, Heyes and Ray (2000, see also Saggerson *et al.*, 2005) have argued that because birds such as pigeons feed in groups, they will have ample opportunity to associate the sight of a conspecific pecking with the action of themselves pecking. A similar line of argument has been developed to suggest that birds might also form associations between the sensory representations activated by seeing a bird step, and the motor units responsible for eliciting stepping in the observer. If these claims are accepted, it then follows that the theory of Heyes and Ray (2000) predicts that pigeons will be capable of imitating both pecking and stepping. Of course, they should be incapable of imitating actions they observe for the first time, or that they have never performed before.

Associative Sequence Learning theory is an ingenious attempt to explain how imitation takes place. Moreover, the findings from experiments by, for example, Dorrance and Zentall (2001), Saggerson *et al.* (2005) and McGregor *et al.* (2006) are consistent with this theory by showing that pigeons are capable of imitating pecking. To my knowledge, however, there has been no attempt to test specific predictions from this theory. In view of the potential importance of this theory, therefore, the purpose of my thesis is to evaluate some of the assumptions on which it is based.

## **1.2 Two predictions from Associative Sequence Learning Theory**

It has just been noted that an important feature of Associative Sequence Learning theory is the assumption that an action can be broken down into a sequence of action sub units and that internal representations of these units enter into an associative sequence. This sequence will then allow the animal to recognise the action if it is going to see it again. If animals are able to recognise different movements, then they should be able to discriminate between them and, most critically, this discrimination should be based upon an ability to discriminate between different sequences of postures. One purpose of the experiments to be described in Chapters 2, 3, 4 and 5 is to test this prediction, and to explore further its implications.

A second prediction from the theory is that imitation should be completely automatic. All that is necessary for imitation to take place is for the suitably experienced observer to see a demonstrator performing an action. The mere sight of this action will then be a sufficient condition for the observer to make the response. With this in mind, it is surprising that the techniques reviewed above have revealed imitation in rather complex circumstances. According to the Associative Sequence

Learning theory, it should also be possible to observe imitation with relatively simple tasks. This prediction is tested in Chapter 5.

Before describing the experiments, the remainder of this chapter will be devoted to two issues. First, I shall review the evidence to determine whether animals are able to discriminate between different natural movements made by another animal.

The second issue concerns a shortcoming that relates to all the experiments I have reviewed thus far. All of the aforementioned studies used live demonstrators which means that individual observers experienced different treatments. In theory, this problem can be overcome by using video presentations of the actions, and by using an automated method for recording different actions. Saggerson *et al.* (2005) have developed an automated method for recording different actions, which will be described in Chapter 5. In the final part of this chapter, I shall examine whether it will be feasible to use video displays for exposing experimental subjects to different actions performed by demonstrators or models.

### **1.3 The discrimination of movement**

All living things, both animal and plant, are able to detect their environment and respond accordingly. One major sense that is used for detecting movements of

others is vision. The psychological study of animal behavior and discrimination learning has concentrated primarily on examining stationary visual stimuli such as colours, patterns, and stationary pictures. However, locomotion plays a very important role in animals' daily life, and thus, motion perception is also very important. "It is necessary for animals to detect and discriminate among such movements to interact socially with conspecifics, to escape from their predators, to catch prey, and to move efficiently within their environments" (Goto & Lea, 2003). Recognition of complex biological movements – such as locomotion, gestures, facial expressions and motor actions – is biologically important as the following examples show. Burmese jungle fowl are more likely to peck at a distinctive dish if they have observed conspecifics engage in the same activity (McQuoid & Galef 1992, 1993); budgerigars who observe another budgerigar remove a stopper from a box to obtain food tend to copy this action (Mottley & Heyes 2003); and the courtship behavior of a bird such as the western grebe can be intricately related to the behaviour of its partner (Nuechterlein & Storer 1982).

The obvious implication of these examples is that animals are able to tell the difference between the various actions and movements of other animals and to react accordingly. Given this conclusion, the question then arises as to how such

discriminations are made. When any animal engages in a natural movement it can be regarded as executing a sequence of postures. It is possible that an animal discriminates between the actions of another animal on the basis of the information provided by a single posture from this sequence. For example, the sight of a bird bent over with its beak touching a container might have been sufficient to make the observers in the study by McQuoid and Galef (1993) perform the same response. In the study by Mottley and Heyes (2003), the observers may have simply copied the relevant postures of the models, rather than entire movements. Similarly, a stance offered during a courtship display may be sufficient to encourage the partner to react in a certain manner.

A particular posture can be described as a static cue, because it does not depend upon the movement of the model for it to occur. All that is necessary is for the observer to detect a single posture within an activity, and to use this posture to identify the activity. Of course, sufficient information for the discrimination to be successful could be derived from either the single posture as a whole, or from a relevant fraction of it. It is not of present concern to choose between these alternatives, and we shall thus regard static cues as emanating from individual postures of the model, without considering their nature in more details.

Instead of referring to static cues, the actions of a model might be identified by the movement that is created, as assumed by Heyes and Saggerson (2000). Any activity will generate what we shall refer to as dynamic cues, which depend upon changes in posture for their existence. Thus it might have been the sight of a model's beak moving towards and away from the bowl that had an effect on the behavior of the observers in the study by McQuoid and Galef (1992, 1993), or the sight of the model actually moving the stopper in the study by Mottley and Heyes (2003) that encouraged the observers to engage in this activity, or the sight of an elaborate sequence of postures in a courtship display that resulted in a response by the partner (Neuchterlein & Storer 1982). A major concern of the present article is to determine whether animals make use of such dynamic cues when discriminating between the actions of other animals.

The first demonstration in the laboratory that one animal can solve a discrimination based on the movements of another animal was reported by Dittrich, Lea, Barrett, and Gurr (1998). They found that a pigeon could master a discrimination between video clips showing another pigeon either pecking or walking (see also Lea and Dittrich, 2000, for a similar finding with bantam hens using the same stimuli). Since the postures of a model who is pecking will differ from those of a model who is

walking, it is impossible to know whether the discrimination was based on static or dynamic cues. Results described by Jitsumori, Natori, and Okuyama (1999) lend support to the first of these possibilities. The design of one of the reported experiments was similar to that used by Ditttrich *et al.* (1998), except that the video clips were of models engaged in either key pecking or turning in circles. Once the discrimination between these activities had been acquired, test trials revealed that it was maintained when subjects were shown individual frames of different postures from the two clips. This outcome would be expected if the discrimination between the two activities was based on static cues. In a further experiment, Jitsumori *et al.* (1999) showed subject pigeons two video clips of a pigeon engaged in different activities. Subsequent test trials in which the clips were played in the opposite direction to that used for training had no impact on the discrimination. If birds solved the discrimination by referring to the sequence of movements within a clip, then it might be thought that reversing this sequence would impair the discrimination. Instead, the results again imply that the birds solved the discrimination by learning about the significance of particular postures from the clips. In support of this conclusion, additional test trials revealed that birds were able to discriminate accurately between still frames from each of the two video clips.

Many studies of the perception of human movement have involved point-light displays (e.g. Johansson 1973, 1975). Blake (1993) used similar stimuli in a study with cats, who were given a discrimination between a point-light animation of a cat walking forwards on a treadmill and the same animation but with the points rearranged so that they no longer corresponded to the shape of a cat. The cats acquired the discrimination, which transferred to a test with a sequence based on a cat running and, after a small amount of training, to an animation based on a human walking. Blake concluded from these results that cats can perceive biological motion created by moving points of light. Given the nature of the stimuli that were used, it is not possible to determine from Blake's results whether cats can go one step further and discriminate between different types of biological motion using point-light stimuli. In an attempt to address this issue, Dittrich *et al.* (1998) gave pigeons a discrimination using point-light stimuli that depicted pigeons walking or pecking. Four out of the eight birds acquired the discrimination, which suggests that at least some animals are capable of discriminating different types of biological motion depicted by point-light displays. This finding is difficult to interpret because it is likely that the two natural movements created different configurations of points of light. The discrimination could thus have been based on either static cues created by

the different configurations, or by dynamic cues derived from the movement of the points of light (Beintema & Lappe 2002).

In another experiment, Ditttrich *et al.* (1998) trained pigeons to discriminate between model birds that were either walking or stepping. The birds were then shown point-light versions of the models and they demonstrated a small but significant discrimination between the two movements. Although Ditttrich *et al.* (1998) concluded that this successful transfer demonstrates that birds used dynamic cues to solve the discrimination, it is noteworthy that subjects were rewarded for responding during the correct but not the incorrect point-light display. It is thus possible that the successful discrimination during testing was due to new learning based on static cues provided by the point-light images, rather than on any control by dynamic cues acquired during the initial training. There is, therefore, rather little evidence that animals refer to dynamic cues when discriminating between different natural movements of other animals. Since it follows from Associative Sequence Learning theory that animals should be able to solve a discrimination on the basis of dynamic cues, the experiments in Chapters 2 and 3 will examine whether they have this ability.

For the experiments in Chapters 2 and 3, as well as the others in my thesis, it will be necessary for observers to watch another animal engaged in a particular activity. For reasons already noted, it would be preferable for these activities to be

displayed by means of a video recording. In the next, and final, section of this chapter I consider the merits of adopting this technology.

## **1.4 The use of video technology for experiments involving live demonstrators**

Originally, live animal demonstrators were commonly used in social learning experiments. However, there are certain drawbacks for experiments using live demonstrations. The major problem is that the performance made by the live demonstrator is not under control of the experimenter. First of all, each demonstration performed is different. Sometimes the view of the observer of a critical action may be blocked because the demonstrator turned around. The quality of the demonstrations – speed and accuracy of the movement – cannot be guaranteed.

As technology develops and becomes more easily available, researchers have started to use video techniques to study social learning in animals. Advances in video and computer technology give the experimenter full control of the stimuli each subject will receive. Video images can be selected and edited, and the demonstration can be presented repeatedly to the same and/or different animals (D'earth 1998, Mcquoid & Galef 1993). For example, sequences of events can be manipulated, objects and/or their movements can be hidden or added, and the relative timing of events can be changed (Morimura & Matsuzawa 2001). Using video images also permits sophisticated analysis of visual stimuli producing socially induced

modifications of behaviour that would not otherwise be possible (Mcquoid & Galef 1993). Lastly, replacing live stimulus animals with video recordings can facilitate research by reducing variability inherent in direct interactions between individuals, disruption of normal behavior caused by handling, and the number of subjects needed for experiments (Ophir & Galef 2003).

There are a few problems, however, with the application of video stimuli. Apart from the lack of interaction between video stimulus and the subjects (Ophir & Galef 2003; Shimizu 1998), the most obvious potential problems with the use of video stimuli concerns the quality and nature of the image. Different species have different visual system. It is not clear if monitors designed for human vision provide the same kind of information to other animals. Monitors only emit frequencies of lights that are visible to human, but not UV or infra red light that most birds can perceive; monitors also have a flicker rate that is too low for birds. Light sources perceived as continuous to human eyes might induce distortion to the eyes of fast moving animals such as bees, spiders, lizards, birds (>100 Hz), and certain fish, as they have much higher flicker-fusion frequency than human (50Hz) (as cited in Mottley & Heyes, 2003). This flicker frequency problem was later solved by using the recently developed thin film transistor (TFT) liquid crystal display that does not produce this kind of distortion (Mottley & Heyes, 2003).

Despite these shortcomings, there is a growing body of evidence that video displays can be effective cues. Some of this evidence comes from studies showing that images on a screen can elicit social behavior from animals. Chickens engaged in socially facilitated feeding in response to a video image of a conspecific (Keeling &

Hurnik 1993). Red junglefowl showed socially enhanced feeding site preferences for the type of food dish after they saw videotapes of conspecific feeding from it (Mcquoid & Galef 1993). Other social behaviors like dustbathing have been shown to be triggered sooner when shown a video image of a dustbathing hen compared to a standing hen (Lundberg & Keeling 2003). Finally, male pigeons performed courtship displays to the video stimuli of female pigeons in the same way (and duration) as they do to real life females (Shimizu 1998).

Ophir and Galef (2003) report a thorough investigation of the influence of video stimuli on the social behavior of quail. Previous research had shown that females will increase the time they spend with a non-preferred male after they have seen him mating with another female (Galef & White 1998). Ophir and Galef (2003) let the focal female observe either 1) a live non-preferred male court and mate with a model female (live mating), 2) a life-size mute digital video sequence of the non-preferred male standing alone (video alone), or 3) a life-size mute digital video sequence of a model female courting and mating with the non-preferred male (video mating). Their results showed that there was a significant increase in time spent with the non-preferred male in both the “live mating” condition and the “video mating” condition; whereas there was no change in the “video alone” condition. More interestingly, there was no difference between the results of the “live mating” and the “video mating” condition; suggesting the females perceived the mute TFT video sequences as live.

Other evidence that video displays can provide effective cues for training animals comes from studies of discrimination learning. Dittrich *et al.* (1998)

demonstrated that that pigeons can discriminate categories of biological movement using video displays. Finally, Mottley and Heyes (2003) demonstrated that budgerigars are capable of discriminating different videos of movements of their conspecifics. Budgerigars were shown video images of a conspecific opening a stopper for food by either pulling the stopper up, or pushing the stopper down. They subsequently displayed a tendency to perform the response they had observed over the one they had not observed.

## **1.5 Summary**

There is a small body of evidence to suggest that birds are capable of imitating the actions that are performed by conspecifics. Heyes and Ray (2000, see also, Heyes, 2001, 2005) have put forward an Associative Sequence Learning theory to explain how such imitation takes places. In essence, this theory assumes that animals are able to acquire representations of the actions they observe, and to associate these representations with response units responsible for generating an equivalent response in the observer. Although this model is able to account for successful demonstrations of imitation, it has been subjected to rather little critical scrutiny. For example, Heyes and Ray (2000) assume that the representation of the observed action consists of a succession of sensory units representing individual postures that are linked associatively in the order in which they occur. If this claim is correct then animals should be able to discriminate between different movements performed by a model, on the basis of dynamic cues created by the transition from one posture to another. There is currently no evidence showing that animals can solve a discrimination in this

way. Thus the purpose of the experiments to be reported was to assess whether birds can discriminate between different natural movements on the basis of dynamic, rather than static cues. A second concern of the reported experiments is to test the prediction of Associative Sequence Learning theory that imitation is an automatic reaction to observing a demonstrator, and will occur in any set of circumstances. The final section of the foregoing discussion suggests that it should be possible to conduct the experiments using television screens, particularly TFT screens, to display the relevant images to the experimental subjects.

## Chapter 2

The experiments in Chapters 2 and 3 were conducted in order to evaluate a fundamental assumption of the Associative Sequence Learning theory of Heyes (2001, 2005, see also Saggerson & Heyes, 2000). I argued in Chapter 1 that if this theory is correct then animals should be able to discriminate between different biological movements on the basis of information provided by the sequence of postures that is performed. In other words, they should be able to discriminate between different actions on the basis of information provided by dynamic cues. I further argued that there is no convincing evidence to show that animals are capable of making this type of discrimination. The three experiments that are described in Chapters 2 and 3 therefore examine whether birds are capable of discriminating between different movements on the basis of the dynamic cues they create. The two experiments in the present chapter used budgerigars, whereas the single experiment in Chapter 3 used pigeons.

In order to determine if the discrimination of natural movement can be based on dynamic cues, the following experiments adopted a rather different design to the studies just reviewed in Chapter 1. Subjects were shown a video clip of a model

walking forwards, and they were also shown the same video clip but modified so that it showed the model walking backwards. The actions depicted in the two video clips were therefore composed of the same frames, and hence depicted the same array of postures. However, the sequence in which these postures were presented varied between the video clips. Thus the discrimination could not be solved by referring to static cues based on individual postures. Instead, its solution might be based on dynamic cues created by the transitions from one posture to another, or from one frame to another. Although this rationale lies behind each of the reported experiments, it will become evident shortly that alternative explanations for the successful solution of this discrimination are possible, and that additional tests were needed to eliminate them.

## **2.1 Experiment 1**

For the first experiment, a group of budgerigars was shown on a computer monitor a video clip of a model walking forwards and the same clip played in reverse. Given the shortcomings of using cathode ray tube displays for presenting moving images to animals (D'Eath 1998; Mottley & Heyes 2003), we used thin film transistor

(TFT) liquid crystal displays. The experimental subjects were budgerigars because they can discriminate between different actions shown on TFT displays (Mottley & Heyes 2003). I originally intended to use a budgerigar as the model for walking, but my attempts to record one walking in a straight line were thwarted by their reluctance to engage in this activity for more than a few steps before changing to some other activity. Accordingly, it was decided to use a female human walking a dog on a leash as the models. The combination of the human and dog was intended to provide a richer source of movement cues than a human alone.

Initially, the budgerigars were shown two video clips: one of the person and dog walking forwards from left to right across the screen; the other of the person and dog walking backwards also from left to right across the screen. Examples of single frames from each of the clips can be seen in the left half of Figure 2.1. Responding in the presence of one of these clips (S+) resulted in the delivery of food whereas responding in the presence of the other clip (S-) never resulted in food. The assignment of the clips to S+ and S- was counterbalanced across subjects, and Figure 2.1 shows this assignment for the birds who were reinforced for responding during the clip of the models walking forwards.

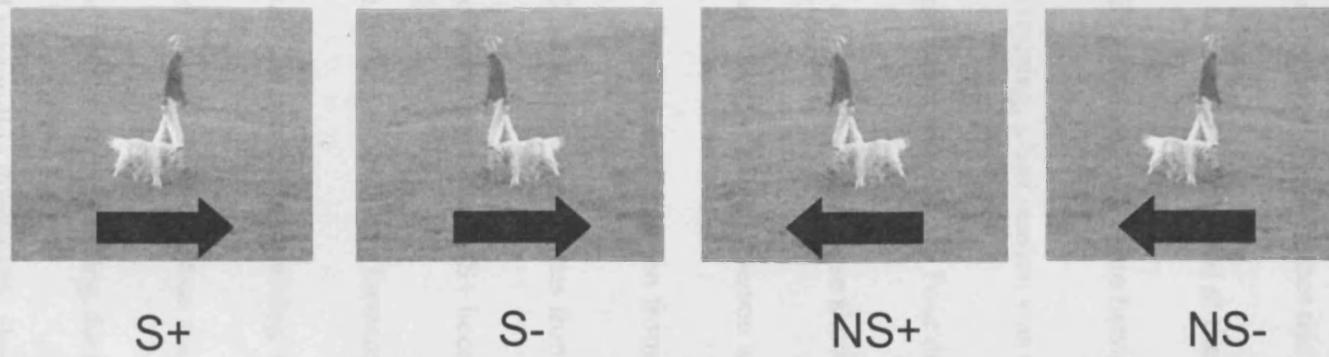


Figure 2.1. Frames selected from the four video clips that were shown in Experiment 1, 2 and 3. The arrows depict the direction in which the models were heading.

The solution of the discrimination between the two clips shown in the left half of Figure 2.1 would be of little theoretical interest because it could be solved on the basis of a static cue, for example, whether the person and dog were facing to the left or right. Even so, video clips were used at the outset of the experiment in order to confirm that the birds could discriminate between our training stimuli. After the completion of this training, a test session was conducted to identify the cues on which the original discrimination was based. Four different video clips were shown in the test session. Two of the clips were those shown during the initial training. The two new clips (NS+ and NS-) were of the person and dog walking either forwards or backwards and moving across the screen from right to left which was opposite to that shown in S+ and S-. Examples of frames from these clips can be seen in the right half of Figure 2.1. One frame is labelled NS+ because it is taken from the new clip of the models walking in the same direction (forwards) as shown in S+. The other frame is labelled NS- because the models are walking in the same direction (backwards) as shown in S-. If the original discrimination was based on whether the models were facing to the left or right, then responding during NS+ should be at a similar rate to that during S-, and responding during NS- should be similar to that during S+.

Another possibility is that during their original training the budgerigars discriminated between the two clips by using a dynamic cue consisting of the actions performed by the models – if they were walking forwards or backwards. On this basis, responding during NS+ should be similar to that recorded during S+, and responding during NS- should be similar to that during S-.

### **2.1.1 Method**

*Subjects.* The subjects were nine naïve male and female adult budgerigars (*Melopsittacus undulates*) of unknown age, but they were at least 9 months old at the start of the experiment. Their weights ranged from 33 to 50 g. They were housed together in a cage (88.0 x 40.0 x 30.0 cm; height x width x depth) in a holding room with a 12:12 hr light-dark cycle and a temperature of  $19 \pm 2^{\circ}\text{C}$ . The birds had free access to water, cuttlebone, grit and water baths. During the experiment they were weighed daily and maintained at 85% of their free-feeding weights by being fed a restricted amount of food after each experimental session. The food was “Budgie Mix” (H. G. Gladwell & Sons, Ltd, Ipswich, UK) which is a mixture of canary seed and white and red millet.

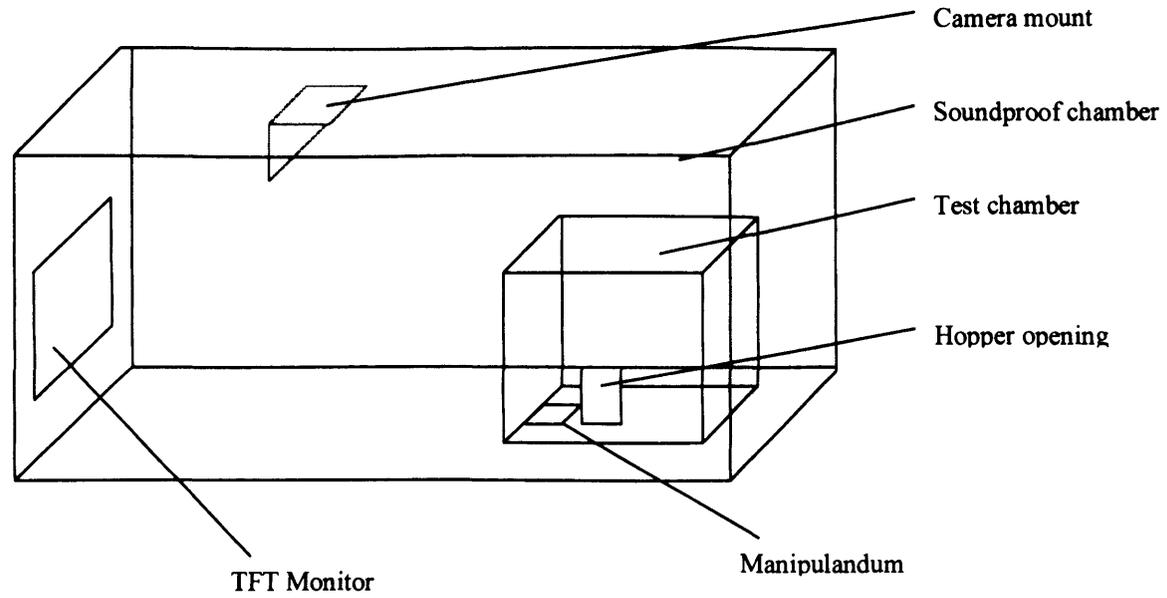


Figure 2.2. The apparatus used for Experiments 1, 2, 6 and 7.

On days when the experiment was not performed, subjects were given a free supply of food which was removed 16 hours before testing resumed.

*Apparatus.* Four conditioning chambers (25.0 x 25.0 x 25.0 cm) were housed in separate light- and sound-attenuating chests (78.0 x 46.0 x 44.0 cm). A sketch of the apparatus can be seen in Figure 2.2. A colour TFT monitor (ViewSonic, VS10057) with a screen that was 27 cm high and 34 cm wide was attached to the left-hand side wall of each chest. The midpoint of the screen was 20 cm above the floor, 20 cm from the rear wall, and 8.5 cm from the left-hand side wall of the chest. The walls of the conditioning chambers were made from clear Perspex. The wall of each chamber that was nearest to the TFT screen was hinged at the bottom to serve as a door. This door was parallel to the TFT screen and 40 cm from it. The floor of each chamber was 6 cm above the floor of the chest. During the experiment Budgie Mix was made available by a grain dispenser (Colbourn Instruments, Lehigh Valley, PA) that was attached to the wall to the left of the door of the conditioning chamber. The grain feeder had an opening that was 5.0 x 6.0 cm. The midpoint of the opening was 3.5 cm above the floor of the chamber, and 7 cm from the door. A square Perspex response box with sides of 6 cm, and with a lid on top, was located on the floor of the

conditioning chamber. The top of the lid was 0.5 cm above the floor of the chamber and its midpoint was 4 cm from the door, and 12 cm from the wall containing the grain feeder. The sides of the response box were red, and the lid was blue. A microswitch operated whenever a force of greater than 6 gm was applied to the lid. A closure of this switch for more than 10 ms was recorded as a response. The floor of each conditioning chamber, except for the response box, was covered with cage-lining paper. Illumination in the conditioning chambers was provided by the events on the TFT screen, and by a bulb in the grain feeder that was turned on whenever grain was made available. The presentation of stimuli on the TFT screens, the recording of responses and the operation of the grain feeder was controlled by a PC computer (Research Machines, Abingdon, UK) running Windows XP. The computer was programmed in VisualBasic and the interface with the experimental apparatus was controlled by Whisker software (Campden Instruments Ltd, Loughborough, UK).

*Video Stimuli.* The video clips shown in the experiment were all based on a recording made in colour by a digital video camera (Sony Handycam DCR-HC30E) of an adult female person leading a golden retriever dog at the end of a 1-m leash. The camera was stationary during recording so that the video clip consisted of the models

walking from left to right against a static background which was grass on the bank of a steep hill. When this clip was played on the TFT screen, an interval of 4 s elapsed between the time that the models appeared on one side of the screen and disappeared from the other side. The height of the person on the screen was 9 cm, and her feet were 13 cm above the bottom of the screen.

The original clip was edited using Adobe Premiere Pro 1.5 to create four clips: the original clip of the models walking forwards from left to right, a horizontal flip of the original to show the models walking forwards from right to left, a reverse of the original to show the models walking backwards from right to left, and a reverse of the original clip that was flipped horizontally to show the models walking backwards from left to right. Each clip was repeated 30 times to create a looped display that lasted for 120 s.

*Procedure.* Subjects were introduced individually to the test chamber with the hopper jammed open and food (white millet) scattered on the floor. Birds were left inside the chamber for no longer than 30 min per session. The amount of food scattered on the floor was decreased gradually until there was only food outside the open hopper. It took between 20-28 days for the subjects to learn to eat from the open

hopper. After the birds were reliably eating from the open hopper, they were then trained to eat from the whenever it was raised. The hopper was lowered while the birds were eating from it, and raised when they returned to look in it. This training continued for between 21 to 35 days until the birds consistently approached the hopper whenever it was raised.

After the birds were magazine trained, they were then trained to step on the manipulandum to trigger the hopper. For one session, the hopper was operated for 5 s whenever the bird stepped on the manipulandum. Thereafter reward was made available according to a variable interval (VI) schedule. The mean interval for this schedule was 1 s for 2 days, which was gradually increased through values of 5 s, 10 s, 15 s, 25 s, and finally 30 s. Birds progressed to the next value of the schedule if the rate of responding for a given value was faster on one session than the during the one before it. It took a total of 27 days until all the birds were trained with the VI 30-s schedule.

The experiment itself was conducted over 46 sessions, which took place at the same time each day, five days a week. During each session, the clips of the models walking either forwards or backwards from left to right across the screen were each presented seven times, for 2 min at a time, in a random sequence with the constraint

that the same clip was not shown more than twice in succession. There was an interval of 20 s before the first video clip was shown, and there was an interval of 10 s between successive clips. The TFT screens were entirely white during these intervals. Food was made available for stepping on the box according to a VI 30-s schedule during the clip of the models walking forwards for four budgerigars, and during the clip of the models walking backwards for the remaining five budgerigars. A new value for the VI schedule was selected at the start of every trial. The same VI schedule was in operation during the trials with the other video clip, but food was never presented on these trials. The number of responses made during the first interval selected from the VI schedule was recorded on every trial. These numbers were then used to calculate individual mean rates of responding for all the reinforced and all the nonreinforced trials of every session. Note that these response rates reflect the influence of the video clips on responding uncontaminated by the conditioned and unconditioned effects that would result from the delivery of food during a clip.

The training that has just been described was continued for a test session of the experiment but in this test session there were four extra trials with clips, for the first time, of the models walking from right to left across the screen. For two of these trials the models were walking forwards and for the other two they were walking

backwards. The trials were presented at randomly selected points among the original training trials in an alternating sequence. Food was not presented during the trials with the two new video clips.

A type-1 error rate of  $p < .05$  was adopted for all statistical tests in the thesis.

### **2.1.2 Results**

The left-hand panel of Figure 2.3 shows the group mean rates of responding, in two-session blocks, during presentations of the video clip that signalled food was available, S+, and during the clip that signalled food was not available, S-. The rate of responding was soon faster during S+ than S- trials. A two-way analysis of variance (ANOVA) of individual mean response rates for each two-session block revealed a significant effect of stimulus (S+ or S-),  $F(1, 8) = 9.04$ , of two-session block,  $F(22,176) = 2.62$ , and a significant interaction,  $F(22,176) = 2.68$ . Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S- trials for Session Block 9 and 10, and from Session Block 12 onwards,  $F_s(1, 184) > 4.77$ .

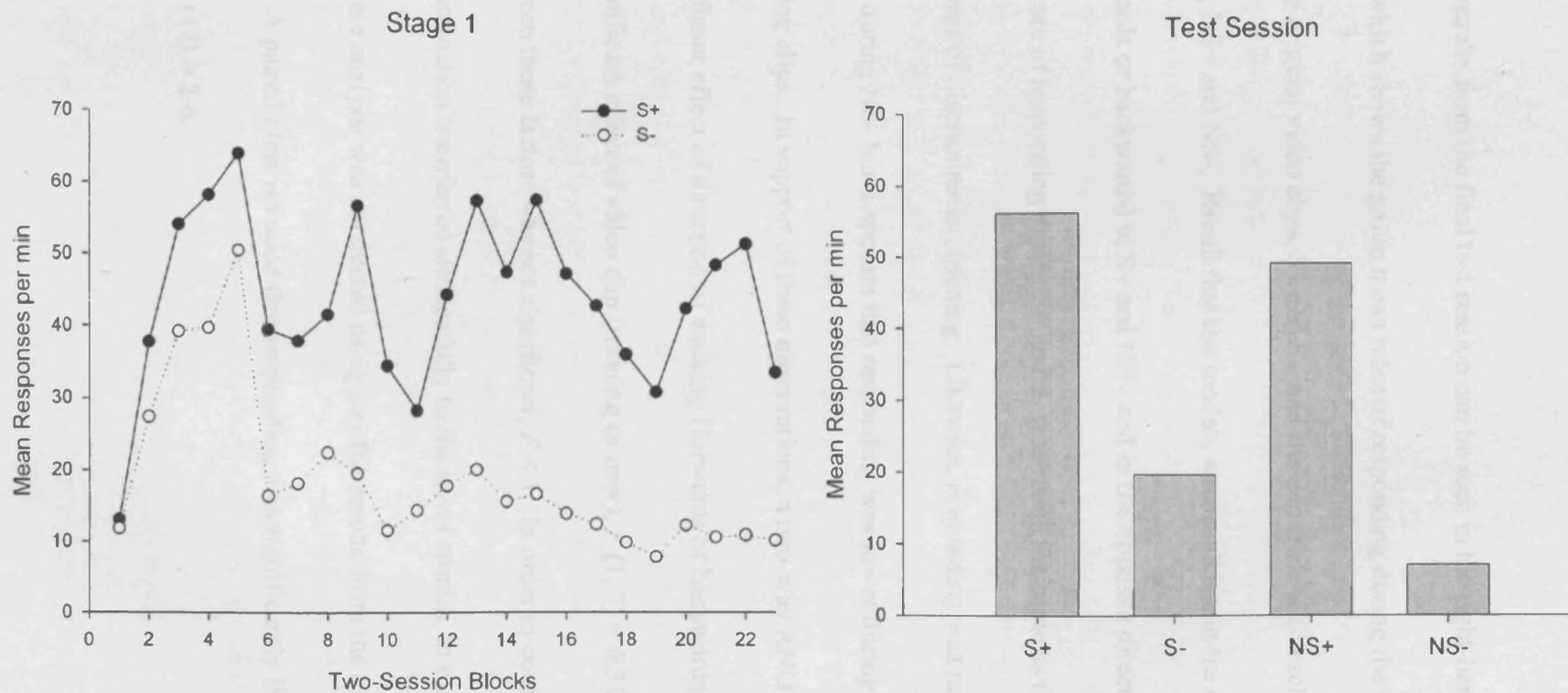


Figure 2.3. The mean rates of responding during the video clips that served as the reinforced, S+, and nonreinforced, S-, stimuli for the training session of Experiment 1 (left-hand panel) and the mean rates of responding in the test session during the trials with the same video clips and with two new clips (right-hand panel). NS+ and NS- refer to new clips that showed the same direction of walking (forwards or backwards) as S+ and S-, respectively.

The results from the final test session can be seen in the right-hand panel of Figure 2.3, which shows the group mean rates of responding during the seven trials with each of the original video clips, S+ and S-, and the two trials with each of the test video clips, NS+ and NS-. Recall that the models were walking in the same direction (either forwards or backwards) in S+ and NS+ and in the opposite direction in S- and NS-. The rate of responding during S+ and S- was much the same as that during the final sessions of discrimination training. Likewise, responding was rapid during NS+ and slow during NS- but it appears that responding was lower during the test clips than the training clips. In support of these observations, a two-way ANOVA revealed a significant effect of direction of walking (forwards or backwards),  $F(1, 7) = 8.0$ , and a significant effect of video clip (training or new),  $F(1, 7) = 6.31$ . The interaction between these factors was not significant,  $F < 1$ . In order to confirm that the discrimination transferred successfully to the novel stimuli, in the test session, a separate analysis was conducted using just the results from the trials with NS+ and NS-. A paired  $t$  test revealed that responding was significantly faster during NS+ than NS-,  $t(7) = 2.6$ .

### **2.1.3 Discussion**

A clear conclusion to be drawn from these results is that the discrimination between the training patterns was not solved on the basis of the direction in which the models were facing. During the two video clips shown throughout the training stage, the models were facing in one direction during S+ trials, and in the opposite direction during S- trials. If subjects had relied on this difference between the clips to solve the discrimination, then they should have responded rapidly during the NS- video clip in which the models were facing in the same direction as during the S+ trials.

Responding was slow on these test trials. Conversely, they should have responded slowly during the NS+ video clip in which the models were facing in the same direction as for the S- trials. Responding was fast on these test trials.

Although the results are consistent with the claim that the discrimination between S+ and S- was based on the dynamic cue of whether the models were walking forwards or backwards, an alternative, static-cue explanation can be developed for the findings of the experiment. During their initial training subjects may have paid no attention to the sequence of postures exhibited by the models, rather they may have focused on the relationship between the direction in which the models

faced and the direction in which they moved. When walking forwards, a model would be moving in the direction they were facing, whereas when walking backwards they would be moving away from the direction they were facing. If subjects detected this relationship, then not only would they solve the original discrimination, but they would also respond correctly during the test video clips. Experiment 2 was conducted in order to test this account for the results that have just been described.

## **2.2 Experiment 2**

The birds that were used in Experiment 1 were also used in Experiment 2, and they were trained with stimuli based on those shown in Figure 2.1. The principal difference between the experiments is that instead of the walking across the screen, the models were shown walking on the spot, as if they were on a treadmill, in the middle of the screen. For the first stage of the experiment, the models were walking forwards facing to the right, and walking backwards facing to the left (see two left-hand panels of Figure 2.1). If subjects solved the discrimination in Experiment 1 by focussing on the relationship between the directions in which the models were facing and moving, then once the models were stationary it should no longer be possible to

solve the discrimination. As for the previous experiment, the successful solution of this discrimination would not necessarily imply that subjects were discriminating between the two video clips on the basis of the dynamic cues relating to the movements of the models. The direction they were facing by itself would provide a sufficient static cue for distinguishing between the two video clips. However, we decided to train the birds initially with these two clips in order to provide them with a relatively simple problem before they were exposed to test trials designed to identify the cues that were used to solve the discrimination.

After 30 sessions of the training, the group showed no indication of having solved the discrimination. One possible explanation for this failure is that the models occupied a relatively small region of the screen and it may have been difficult for the birds to perceive the movements they made. Accordingly, the video clips were modified by increasing the size of the models. This change was followed by the development of a successful discrimination between the two video clips during a subsequent 20 sessions of training.

Upon the completion of the training, the group received a single test session which was conducted in much the same way as the test session of Experiment 1, except that the models remained stationary in the middle of the TFT screen. There

were four video clips shown in the test session, two that were used for the initial training, S+ and S-, and two new ones, NS+ and NS-. The new clips were of the models walking either forwards facing to the left or walking backwards facing to the right (see the two right-hand panels of Figure 2.1). If the original discrimination was based on the dynamic cues of walking forwards or backwards, then during the test trials with the new patterns, the strength of responding would be determined by the direction of walking. On the other hand, if the original discrimination was based on the direction that the models were facing, then this factor should determine responding during the two new video clips.

### **2.2.1 Method**

*Subjects, apparatus and stimuli.* The subjects and apparatus were the same as for Experiment 1. The original video clip that was used for Experiment 1 was edited to create a video clip of the person and dog walking, without moving, in the centre of the TFT screen. To create this clip, the torso of the woman was used as the central point of each frame, and the remaining objects were moved relative to this reference point. The edited clip was modified further to create three additional clips: the models

walking backwards facing to the left, the models walking backwards facing to the right, and the models walking forwards facing to the right. The height of the person on the screen was originally 9 cm, but this was increased to 22 cm. Each video clip lasted for 2 min.

*Procedure.* Experiment 2 commenced 19 days after the completion of Experiment 1. For each of the first 50 sessions of the experiment, there were seven trials with the video clip of the models walking forwards and facing to the right, and seven trials with the models walking backwards facing to the left. The height of the person in the video clips was 9 cm for the first 30 sessions, and 22 cm for the remainder of the experiment. Stepping on the response box was rewarded with access to grain according to a VI 30-s schedule during the video clip of the models walking forward for the four budgerigars for whom S+ in the previous experiment had also been of the models walking forwards. The video clip of the models walking backwards served as S-. This relationship between the video clips and the availability of food was reversed for the remaining birds.

After the discrimination training, there were seven trials with each of S+ and S-, plus two trials with each of the remaining two video clips, NS+ and NS-. Procedural details that have been omitted were the same as for the previous Experiment 1.

### **2.2.2 Results**

The mean rates of responding during the two types of trial for the 50 sessions of discrimination training, in two-session blocks, are shown in Figure 2.4. The group failed to discriminate between S+ and S- during the first 30 sessions, but when the image of the models was increased in size for the remaining 20 sessions then a faster rate of responding during S+ than S- became evident. A two-way ANOVA of individual mean response rates for the final 10, two-session blocks revealed a significant effect of session block,  $F(9, 63) = 3.25$ , and a significant Session Block x Stimulus interaction,  $F(6, 63) = 2.85$ . Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S- for the final four two-session blocks,  $F_s(9, 63) > 5.00$ .

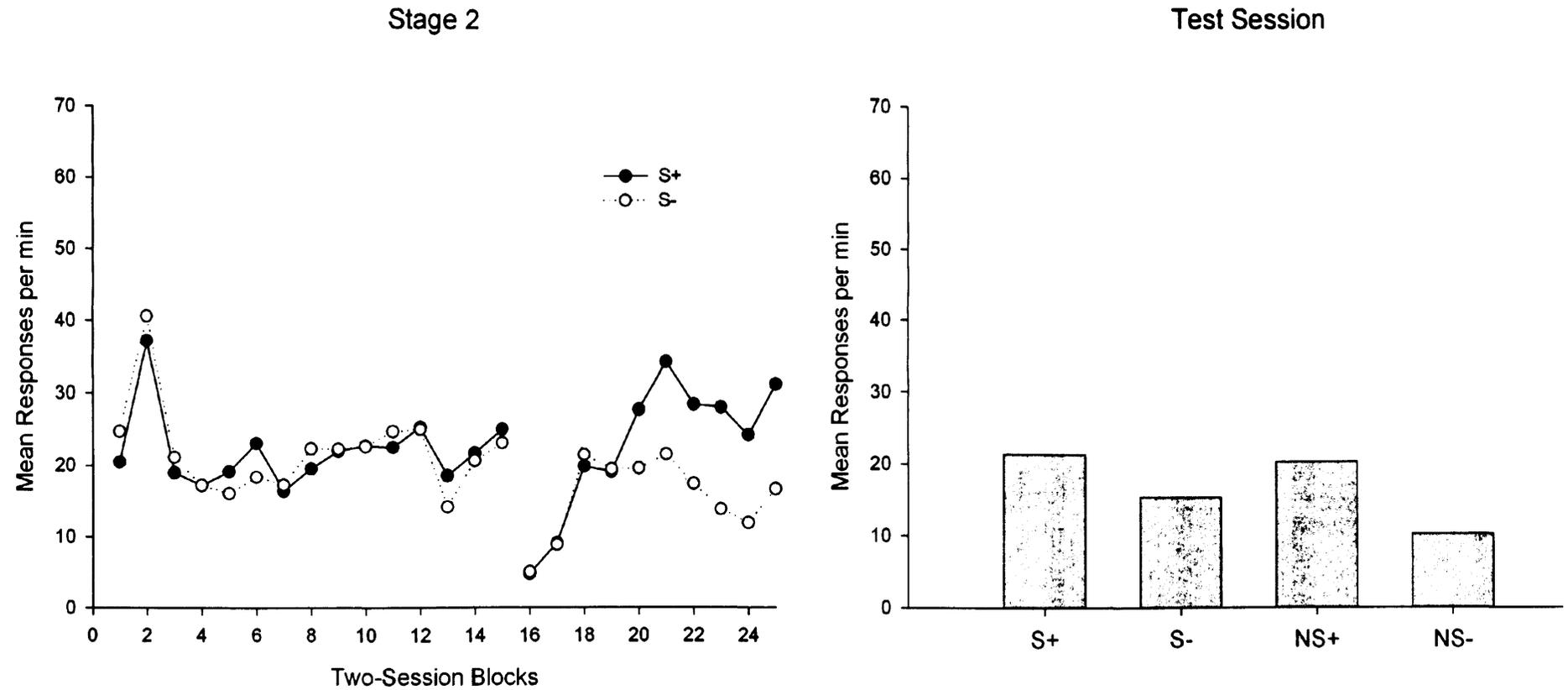


Figure 2.4. The mean rates of responding during the reinforced (S+) and nonreinforced (S-) video clips for the training sessions of Experiment 2 (left-hand panel), and the mean rates of responding in the test session during the trials with the same video clips and with two new clips (right-hand panel). NS+ and NS- refer to new clips that showed the same direction of walking (forwards or backwards) as S+ and S-, respectively.

The histograms in the right-hand panel of Figure 2.4 show the results from the test session. In keeping with the results from the final session of training, responding was more vigorous during S+ than S-. In addition, responding during the new clips was faster during NS+, for which the direction of walking (forwards or backwards) was the same as during S+, than during NS-, for which the direction of walking was the same as during S-.

A two-way ANOVA of individual mean response rates during the four video clips shown in the test session revealed a significant effect of the direction of walking,  $F(1, 7) = 14.14$ , but the effect of whether the clips were original (having been shown throughout training) or novel (introduced for the test session) was not significant,  $F < 1$ , and the interaction was not significant,  $F < 1$ . In order to confirm that subjects did indeed discriminate successfully between NS+ and NS-, a separate analysis was conducted using the results from just these trials. The analysis confirmed that the rate of responding during NS+ was significantly faster than during NS-,  $t(7) = 3.7$ .

### **2.2.3 Discussion**

The successful discrimination between the two video clips used for the training trials could have been based on a dynamic cue, that is whether the model was walking forwards or backwards. Alternatively, the discrimination could have been based on a static cue, that is the direction that the models were facing. The results from the two new video clips introduced in the final test session revealed support for the first of these interpretations, but not the second. Moreover, because the same video footage was used to create the four video clips, it was not possible to discriminate between them in terms of the postures shown by individual frames. The experiment thus provides a clear demonstration that one species of bird, the budgerigar, is able to discriminate between two different natural movements using information provided by the transitions from one posture to another during the course of these movements.

The experiments in this chapter have revealed that budgerigars are able to discriminate between two movements that consist of the same postures performed in different sequences. It has been argued that this discrimination is controlled by dynamic rather than static cues based on the sequence of postures executed by the models.

## Chapter 3

The results from the previous chapter demonstrate that budgerigars are able to discriminate between different sequences of natural movement on the basis of dynamic cues. The results thus provide a novel source of support to the Associative Sequence Learning theory of Heyes and Ray (2000, see also Heyes 2005). Given the theoretical importance of these results, a further experiment was conducted with pigeons in order to determine the reliability and generality of the results that have just been described.

### 3.1 Experiment 3

A single group of pigeons received four stages of training, with a number of sessions in each stage. During Stage 1 of Experiment 3, the birds were given the same discrimination that had been used for the training stage of Experiment 1 in Chapter 2 (see the left-hand half of Figure 2.1). That is, they were required to discriminate between video clips of the models walking, either forwards or backwards, from left to right across the screen. The group was then shown, for Stage 2, the four clips that had been used for the test session of Experiment 1 in Chapter 2. However, rather than repeat the test session of that experiment, the four clips were used for a new discrimination in which the two clips of the models walking forwards signalled one outcome, and the two clips of the models walking backwards signalled the other outcome.

After the completion of Stage 2, the birds progressed to Stage 3, in which the two video clips of the models walking as if on a treadmill that had been used for the training stage 1 of Experiment 2 were used for discrimination training. For the fourth training stage of the experiment, the four clips shown in the test session of Experiment 2 were used for a number of sessions of discrimination training. Throughout the experiment, responding was reinforced according to whether the models were walking forwards or backwards.

The results from the test trials of Experiment 1 and, particularly, Experiment 2, have been regarded as being of some theoretical importance. However, the critical results from the tests were obtained from only two presentations of the video clips that were introduced in the test sessions. There was a concern, therefore, that the discrimination between these new clips might not be particularly robust. It was in order to explore this possibility that instead of including test sessions in this chapter, I used the four clips for a number of sessions of discrimination training. If the capacity to tell the difference between walking forwards and backwards is robust, then the discrimination between the video clips introduced in Stage 2 of Experiment 1 and 2 will be acquired rapidly and sustained with little difficulty.

### **3.1.1 Method**

*Subjects.* Sixteen adult experimentally naïve male and female pigeons (*Columba livia*) were used for the experiment. They were housed in pairs in a vivarium that had a 12-

hr light-dark cycle and were maintained at  $19 \pm 2^{\circ}\text{C}$ . There was free access to water and to grit in the home cages throughout the experiment. The birds were maintained at 80% of their free-feeding weights by being fed a restricted amount of food after each experimental session.

*Apparatus.* The apparatus was based on that used for Chapter 2 but it was larger and contained a different manipulandum. The dimensions of the soundproof chamber (see Figure 2.2) were 78 cm  $\times$  46 cm  $\times$  44 cm (width  $\times$  depth  $\times$  height). The dimensions of the clear Perspex conditioning chambers were 34 cm  $\times$  30.5 cm  $\times$  33 cm. The positioning of each conditioning chamber with respect to the TFT screen was similar to that in Experiments 1 and 2, but the distance between the wall of the chamber nearest to the screen and the screen was 35 cm. A Colbourn Instruments (Lehigh Valley, PA) grain feeder was attached to the wall of the conditioning chamber that was nearest to the door of the soundproof chamber. The centre of the opening of the grain feeder was 12.5 cm above the floor of the conditioning chamber and 6.5 cm from the left-hand wall. The wall of the conditioning chamber that was nearest to the TFT screen was hinged at the bottom to serve as a door. The centre of a Campden Instruments (Loughborough, United Kingdom) 1-cm circular pigeon response key was located 13.5 cm above the middle of the opening of the grain feeder. The key could be illuminated with white light. Pecks at the response key were detected by the closure of a reed relay. The remaining details of the apparatus were the same as for Chapter 2. The video clips for the experiment were the same as those used in Chapter 2.

*Procedure.* All subjects first received seven habituation sessions. They were introduced to the test chamber individually, and remained inside the test chamber for one hour every day. Magazine training session started after the habituation phase. For the first six magazine training sessions, all the twenty subjects were introduced individually to the testing chamber with the hopper jammed open and food scattered on the floor. Birds were left inside the chamber for 50 min in each session. The amount of food scattered on the floor decreased gradually until there was food only in the open hopper. Then the subjects were given fourteen sessions of feeding from the open hopper. After they were eating reliably from the hopper whenever it was permanently raised, the birds were then trained to eat from the hopper whenever it was operated, starting from session 22. Throughout Session 22, the hopper was raised for 5 s, and then lowered for 25 s for 50 min. The period for which the hopper was lowered was the gradually increased to 55 s by Session 28. The hopper light was turned on whenever the hopper was operated.

After the magazine training, the birds were then trained to peck on the response key to operate the hopper. For the five days of response shaping, the response key light was turned on white until the pigeon peck on it. Pecks were reinforced according to a continuous reinforcement schedule. For the next five days subjects were reinforced according to a VI schedule which was increased gradually from 5 to 30 s.

Before entering Stage 1 of the experiment, the subjects were given eight sessions of red-green discrimination training. The subjects were evenly divided into two groups. The first group was given food reward according to a VI 30-s schedule for pecking at the response key when the entire TFT screen was illuminated red and the second group was

rewarded for pecking during the presence of a green screen. Pecks during the presence of the other screen colour were not reinforced. The subjects were trained with the red-green discrimination task for 8 sessions.

Two days after the completion of the red-green discrimination training, the pigeons received eight sessions of Stage-1 training. In each session, eight of the birds were shown the video clip of the models walking forwards from left to right across the screen as S+, and the video clip of the models walking backwards from left to right as S-. The opposite assignment of the video clips to S+ and S- was used for the remaining birds. The duration of each trial was 60 s. There was an interval of 10 s between each trial, during which the TFT screen was entirely white. No more than two trials of the same type occurred in succession, and there were 40 trials in a session (20 with S+ and 20 with S-). Pecking on the response key during S+ but not S- was reinforced according to a VI 30-s schedule.

Training continued in the manner just described with S+ and S- for the six sessions of Stage 2, but there were additional trials with the two video clips of the models walking from right to left across the screen. Food was made available for responding during the new clip NS+ if the models were walking in the same direction (either forwards or backwards) as for S+. Food was not made available during the other new clip (NS-) if the models were walking in the same direction as for S-. The four clips were each shown ten times in each session. Other procedural details were the same as for Stage 1.

Stages 3 and 4 of the experiment were conducted in the same manner as Stages 1 and 2, respectively, except that instead of the models moving across the TFT screen, the video clips showed them in the middle, walking as if on a treadmill. There were 10 sessions in Stage 3, with two clips based on those used in Stage 1 that are again referred to as S+ and S-; and 12 sessions in Stage 4, with four clips based on those shown in Stage 2 that we refer to as S+, S-, NS+, and NS-. The height of the person on the screen was 22 cm throughout Stages 3 and 4. The remaining procedural details were the same as for Experiments 1 and 2. Throughout the experiment, the method for measuring the rate of key pecking during each trial was the same as for Experiment 1. Thus, the response rates that are reported were obtained during a period commencing at the start of each trial, the duration of which was determined by the VI schedule.

### **3.1.2 Results**

The results from the first two stages of the experiment are presented in the left-hand panel of Figure 3.1. The left half of the panel shows the group mean response rates during S+ and S- that were shown during Stage 1. The right half of the panel shows the equivalent results for the four video clips that were shown during Stage 2. The discrimination was acquired without much difficulty in Stage 1, and it was sustained throughout Stage 2. Moreover, the discrimination transferred immediately, and with only a moderate disruption, to NS+ and NS- when they were introduced at the start of Stage 2.

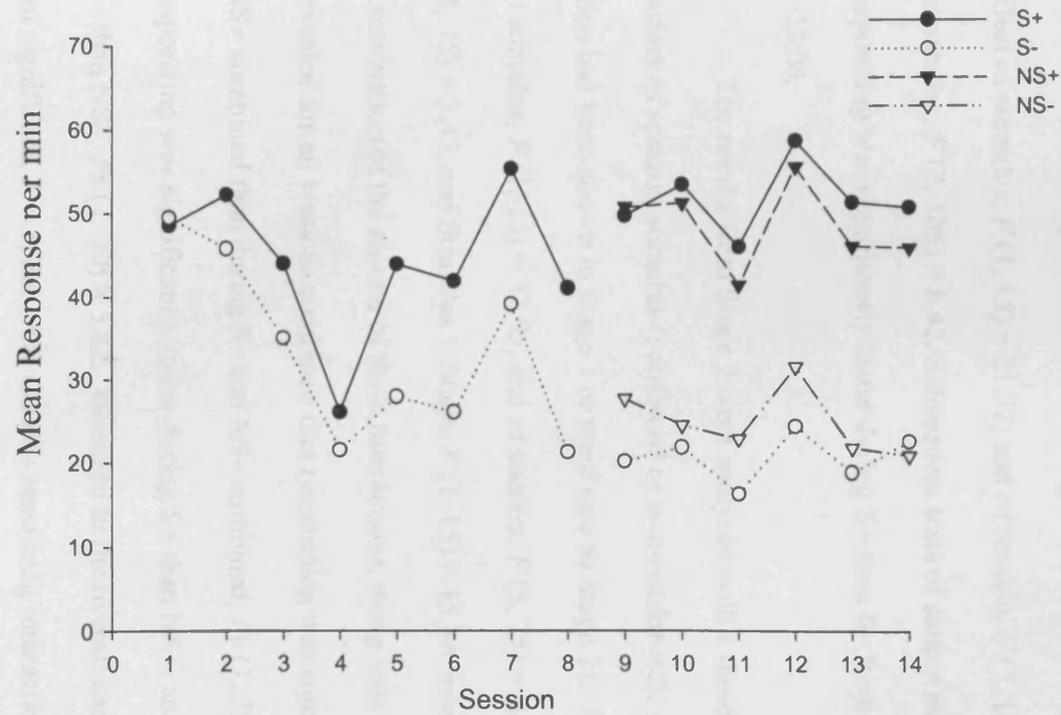


Figure 3.1. The mean rates of responding for Experiment 3 during the reinforced (S+) and nonreinforced video clips (S-) in Stage 1 (left-half of the figure), and during reinforced (S+, NS+) and nonreinforced (S-, NS-) video clips in Stage 2 (right-half of figure). NS+ and NS- refer to new clips that showed the same direction of walking (forwards or backwards) as S+ and S-, respectively.

The foregoing observations were supported statistically. A two-way ANOVA of individual mean response rates for the eight sessions of Stage 1 revealed a significant effect of stimulus,  $F(1, 15) = 21.72$ ; and of session,  $F(7, 105) = 7.72$ ; and a significant interaction,  $F(7, 105) = 8.42$ . Subsequent tests of simple main effects revealed that responding was significantly faster during S+ than S- from Session 5 onward,  $F_s(1, 120) > 23.06$ .

The results from Stage 2 were analyzed with a three-way ANOVA with the factors of session, stimulus (reinforced or non-reinforced), and stage (whether the video clips had been shown in Stage 1 or were new to Stage 2). There was a significant effect of stimulus,  $F(1, 15) = 27.95$ ; and of session,  $F(5, 75) = 3.66$ ; and the Session  $\times$  Stage,  $F(5, 75) = 3.47$ , and Stimulus  $\times$  Stage,  $F(1, 15) = 15.86$ , interactions were also significant. Examination of the second of these interactions, using tests of simple main effects, revealed for all sessions combined that responding was significantly faster during S+ and NS+ combined than during S- and NS- combined,  $F_s(1, 30) > 20.27$ . In addition, responding was significantly faster during S+ than NS+, and significantly slower during S- than NS-,  $F_s(1, 30) > 5.82$ . To return to the overall analysis, the effect of stage was not significant,  $F < 1$ , nor were the two remaining interactions,  $F_s < 1$ .

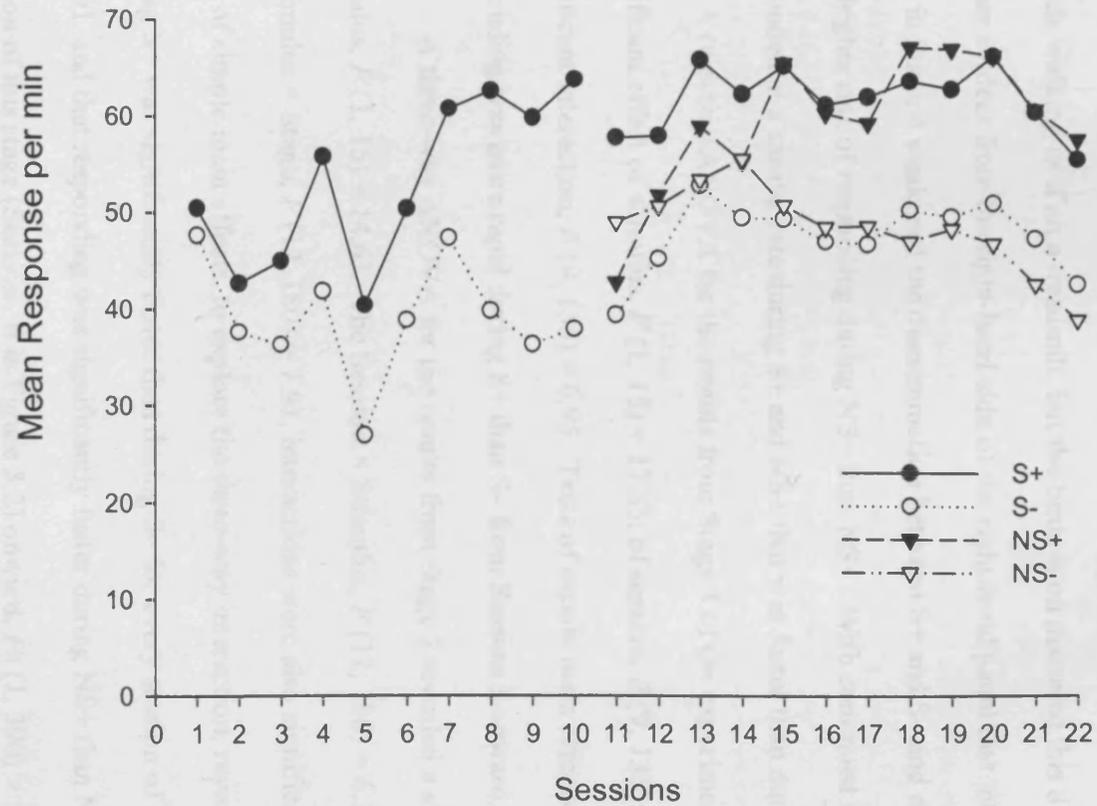


Figure 3.2. The mean rates of responding during the reinforced (S+) and nonreinforced (S-) video clips in Stage 3 of Experiment 3 (left-half of figure) and during the reinforced (S+, NS+), and nonreinforced (S-, NS-) in Stage 4 of Experiment 3 (right-half figure). NS+ and NS- refer to new clips that showed the same direction of walking (forwards or backwards) as S+ and S-, respectively.

The findings from the final two stages of the experiment can be seen in the right-hand panel of Figure 3.2. It is evident from the left side of this panel that the discrimination between S+ and S- from the previous stage was disrupted by showing the models walking as if on a treadmill, but the birds soon mastered this discrimination. It is further evident from the right-hand side of the right-hand panel that introducing NS+ and NS- in Stage 4 weakened the discrimination between S+ and S- and resulted temporarily in a higher rate of responding during NS- than NS+. With continued training, the birds responded at a similar rate during S+ and NS+ that was faster than during S- and NS-.

A two-way ANOVA for the results from Stage 1 of the experiment revealed a significant effect of stimulus,  $F(1, 15) = 17.83$ ; of session,  $F(9, 135) = 3.95$ ; and a significant interaction,  $F(9, 135) = 6.95$ . Tests of simple main effects then revealed that responding was more rapid during S+ than S- from Session 3 onward,  $F_s(1, 150) > 4.00$ .

A three-way ANOVA for the results from Stage 2 revealed a significant effect of stimulus,  $F(1, 15) = 14.63$ . The Session  $\times$  Stimulus,  $F(12, 180) = 6.30$ , and the Session  $\times$  Stimulus  $\times$  Stage,  $F(12, 180) = 7.91$ , interactions were also significant. Subsequent tests of simple main effects, to explore the three-way interaction, revealed that responding during S+ was significantly faster than during S- for every session of Stage 2,  $F_s(1, 390) > 8.01$ , and that responding was significantly faster during NS+ than NS- from the sixth session of this stage (Session 16 in Figure 3.2) onward,  $F_s(1, 390) > 5.39$ . In addition, responding during NS+ was slower than during NS- for the first session of Stage 4,  $F(1, 390) = 8.74$ . The remaining effects and interactions from the overall ANOVA were not

significant: stimulus,  $F(12, 180) = 1.48$ ; stage,  $F(1, 15) = 1.47$ ; Session  $\times$  Stimulus,  $F(12, 180) = 1.10$ ; and Stimulus  $\times$  Stage,  $F(1, 15) = 3.61$ .

### **3.1.3 Discussion**

The results show that pigeons are able to discriminate between the natural movements of walking forwards and backwards. Moreover, on the basis of the results from Stage 4 of the experiment, it is reasonable to conclude that the success of this discrimination depends upon an ability to perceive dynamic cues created as a model changes from one posture to another.

## **3.2 General Discussion**

The results from the present experiment largely replicated the findings from Experiments 1 and 2. It thus appears that pigeons share with budgerigars an ability to discriminate between different natural movements. Having drawn this conclusion, we should acknowledge that the results revealed one difference between the performances of these species. Pigeons and budgerigars were both able to discriminate between the two video clips they were originally shown of the models walking forwards or backwards as if on a treadmill facing to the left. Their performance when they were introduced to new video clips of these actions, but with the models facing to the right (NS+ and NS-),

suggests, however, that they solved the original discrimination between the two clips of these actions in different ways. On first being exposed to the new clips, budgerigars in Experiment 2 immediately responded more rapidly to NS+ than NS-, which implies the original discrimination was based on the direction in which the models were walking. In contrast, when the pigeons were first exposed to these clips in Stage 4 of their experiment they initially responded more rapidly to NS- than NS+. This result suggests that the pigeons solved the discrimination in Stage 3 by referring to the direction in which the models were facing, rather than whether they were walking forwards or backwards. The remaining results from Stage 4 demonstrate that pigeons were able to tell the difference between the directions in which the models were walking, but they appeared to be more reluctant than budgerigars to make use of this information. It is not clear on the basis of the available evidence how this difference between the two species can best be explained.

Despite the slight differences between the two experiments, their findings both point forcefully to the conclusion that birds are able to discriminate between natural movements on the basis of dynamic cues. One purpose of the next chapter will be to explore the implications of this conclusion for the Associative Sequence Learning theory of Heyes and Ray, 2000, and Heyes, 2005.

## Chapter 4

The previous experiments have shown that pigeons and budgerigars are able to discriminate between the actions of walking forwards and backwards on the basis of cues provided by the transition from one posture to another. One interpretation of these findings, which is compatible with the model proposed by Heyes (2001, 2005), is that while observing a model perform a particular action, the observer acquires a series of snapshots of postures that contribute to the action, and then forms associations between successive postures (see also Giese & Poggio, 2003). This associative sequence could then, in its entirety be associated with the presence or absence of food. By comparing an associatively activated sequence of postures, with the action that is currently being performed, the observer should then be able to classify the observed action as one that signals the presence or absence of food.

An important component of the above explanation is the assumption that birds form snapshots, or templates, of postures from the actions they observe. To my knowledge there is no evidence to support this claim with dynamic stimuli, but an experiment by Haselgrove, George and Pearce (2005) lends support to the claim that birds form snapshots or templates of the visual stimuli that are used for a discrimination. In brief, they trained pigeons to discriminate between patterns composed of adjacent coloured rectangles. For example, red to the left of green might have signalled food, and green to the left of red might have signalled no food. The patterns were then distorted by

separating the rectangles. This manipulation disrupted responding. However, the degree of disruption was closely related to the extent to which the test pattern overlapped with a presumed template of the training pattern. Haselgrove *et al.* (2005) therefore concluded that the representations of the stimuli used for training can be likened to a direct copy of the stimuli themselves. When a pattern is subsequently presented for a test trial, the stored template is then moved over the test pattern until the closest fit is determined, and the degree of this fit then governs the response to the test pattern (see also Blough, 1985). It is not implausible to suppose that a similar process is responsible for the discrimination of natural movement. The two experiments in the present chapter were designed as rather simple tests of this account for how animals are able to tell the difference between different natural movements.

#### **4.1 Experiment 4**

The first experiment made use of the pigeons from Experiment 3. Immediately after the completion of Stage 4 of the previous experiment, the birds were exposed to the video clips of the models walking on the spot, either forwards or backwards, and facing to the left, that were used in Stage 3. However, for the present experiment the video clips were inverted so that the models appeared to be walking upside down. There is good evidence that after pigeons have been trained to discriminate between different geometric patterns, their performance is not affected at all, if the patterns are presented in a novel orientation, even upside down (Hollard & Delius, 1982). If the discrimination of biological

movement is based on a memory for templates of individual postures, then inverting the video clips of the models should also reveal a similar rotational invariance. The experiment revealed a remarkably good transfer of the discrimination to the inverted video clips. Accordingly, a further stage was included in order to determine if rotational invariance would also be found with the four clips that were used for Stage 4 of Experiment 3. Finally, subjects were trained with the same four clips, but in their normal orientation, in order to determine if this change should result in an improvement of the discrimination.

#### **4.1.1 Method**

*Subjects, apparatus, and video stimuli.* The subjects were the sixteen pigeons used for the previous experiment. The apparatus was the same as that used for the previous experiment. The video clips were based on those used in Stages 3 and 4 of Experiment 3, and consisted of a human and a dog (see Figure 2.1) walking on the spot. These clips were inverted using Adobe Premiere Pro 1.5 software. As a consequence, the inverted clip of the human and dog walking forwards, and facing to the left, resulted in the models performing same action and facing in the same direction, but upside down.

*Procedure.* Testing commenced on the day following the completion of Experiment 3. For Test 1, each subject was trained with the same two video clips, and the same reinforcement contingencies as for Stage 3 of Experiment 3, except that each clip

was inverted. Thus if a pigeon received reward in Stage 3 of Experiment 3 for responding in the presence of the models walking forwards on the spot facing to the left, then it was rewarded for responding in the presence of the upside down models walking forwards and facing to the left. This bird would also not receive reward during the other clip which would be of the upside down models facing to the left and walking backwards. There were three sessions in Test 1, which were conducted in exactly the same manner as for Stage 3 of Experiment 3.

The two sessions of Test 2 were conducted in exactly the same manner as for Stage 4 of Experiment 3, except that the four video clips were all inverted. To continue with the example of the bird considered in the previous paragraph, in addition to the training just described, this bird would also receive clips of the models upside down and facing to the right, with responding being rewarded when the models were walking forwards, but not backwards

The final two sessions of the experiments, Test 3, were conducted in an identical fashion to Stage 4 of Experiment 3. Thus the four clips were presented in their normal orientation, and the bird described above would receive food if the models were walking forwards on the spot, facing either to the left or right, but not if they were walking backwards. The method for recording the results was the same as for Experiment 3.

### **4.1.2 Results**

For purposes of comparison, the left-hand panel of Figure 4.1 portrays the mean rates of responding during four clips that were shown to the pigeons for the final stage of Experiment 3. The left-hand set of three points in the right-hand panel of Figure 4.1 portrays the mean rates of responding during Test 1 which involved the inverted video clips of the models facing to the left and walking on the spot. From the outset of this test, birds showed a clear discrimination between the reinforced and nonreinforced clips, and the magnitude of this discrimination was no different to that seen with the same video clips in their correct orientation at the end of Experiment 3. This discrimination was sustained in Test 2, the results of which are portrayed in the middle of the right-hand panel of the figure. In addition, the discrimination transferred without disruption to the two video clips of the inverted models facing to the right that were introduced for this stage. The remaining points in the figure show the results for the test trials that were conducted with the video clips shown in Test 2, but in their normal orientation. It is evident that restoring the video clips to their normal orientation had rather little impact on the discrimination.

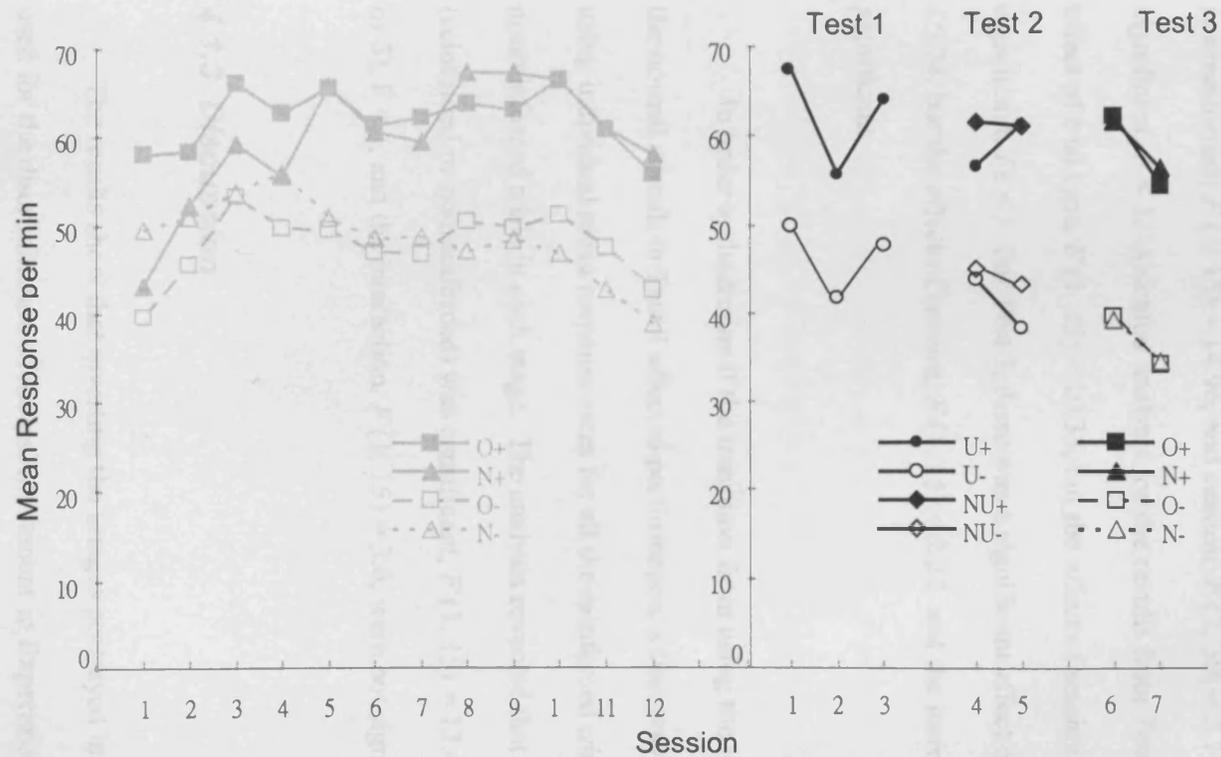


Figure 4.1. The mean rate of responding by the single group of pigeons during the 12 sessions of Stage 4 of Experiment 3 (left-hand panel), and during the three test stages of Experiment 4 (right-hand panel). O+ = the reinforced video clips, and O- = the nonreinforced video clips of the models facing to the left in their normal orientation. N+ = reinforced video clips and N- = the nonreinforced video clips of the models facing to the right in their normal orientation. U+ and U- are equivalent to O+ and O-, except that the video clips were inverted. NU+ and NU- are equivalent to N+ and N-, except that the video clips were inverted.

The foregoing observations were supported by statistical analyses. A two-way ANOVA for the results of Test 1 revealed a significant effect of trial type (reinforced or nonreinforced)  $F(1, 15) = 14.96$ , and session,  $F(2, 30) = 5.77$ , but the interaction was not significant,  $F < 1$ . A similar analysis for the results from Test 2 revealed a significant effect of trial type,  $F(1, 15) = 10.33$ , but the effect of session and the interaction were not significant,  $F_s < 1$ . For Test 3, there was a significant effect of trial type,  $F(1, 15) = 15.74$ , but the effect of session,  $F(1, 15) = 2.22$ , and the interaction,  $F < 1$ , were not significant.

In order to determine if the transition from using the inverted stimuli in Test 2 to the normal stimuli in Test 3 affected performance, a two-way ANOVA was conducted using individual mean response rates for all the reinforced trials in each stage, and all the nonreinforced trials in each stage. The analysis revealed that the effect of stimulus (reinforced or nonreinforced) was significant,  $F(1, 15) = 13.46$ , but the effect of Test (2 or 3),  $F < 1$ , and the interaction,  $F(1, 15) = 3.6$ , were not significant.

#### **4.1.3 Discussion**

The results show that inverting the images portrayed in the video clips that were used for the discrimination of natural movement in Experiment 3 had no impact on performance on this task. As soon as birds were exposed to the inverted stimuli they continued to respond as if they were in their normal orientation. This outcome was true

when either two or four of the original video clips were shown in their inverted form. Moreover, when the original clips were shown in their normal orientation, there was no apparent improvement in performance. This pattern of results is entirely in keeping with findings reported by Hollard and Delius (1982) and demonstrates for the first time rotational invariance in animals using dynamic rather than static stimuli. It may be worth noting that informal observation of the stimuli by humans indicated that it was rather difficult to judge whether the inverted clips of the models were walking forwards or backwards. If this observation can be confirmed empirically, then it would be in keeping with the claim by Hollard and Delius (1982) that pigeons and people differ in the way in which they respond to inverted stimuli. From the point of view of the present theoretical concern, the results are of interest because they are consistent with the claim that pigeons represent biological movement as an associatively linked sequence of templates.

## 4.2 Experiment 5

Experiment 5 was conducted in order to explore further the claim that representations of individual postures, stored as templates or mental snapshots, underlie the ability of pigeons to discriminate between different natural movements. Humans, of course, are capable of discriminating between natural movements, and one technique that has proved valuable for investigating this ability is based on point-light displays. The first experiment using point-light displays was by Johansson (1973). He presented humans with animation sequences consisting of a few dots strategically placed on the joints of humans filmed in various activities. The participants promptly recognized the biological object depicted by the displays and could even identify his or her action, confirming the contribution of motion cues to the identification of biological objects (Parron, Deruelle & Fagot, 2007). Still pictures of the point-light stimuli are unrecognizable as objects, but when seen in movement they are easily recognized by human observers. Point-light displays were then widely used in human vision experiments. From point-light displays, human subjects can recognize the identity of a friend, the nature of the action, the gender of the person, the weight of an object being lifted and the emotion being expressed (see Dittrich *et al.* 1998 for review).

All these findings are of interest because they would not be expected from the account that has been developed thus far of how animals discriminate between different natural movements. According to this account, the discrimination is based on a stored representation of individual postures created by the model. Moreover, this representation

is regarded as being a reasonably faithful copy of the model's posture. There is a considerable difference between the image of a model in a single posture, and the point-light display created from that posture. Any template-matching account of discrimination learning will thus be led to predict that a discrimination based on natural movement will transfer poorly to a point-light representation of that movement. Perhaps, therefore, the account being proposed for how animals discriminate between different natural movements, does not apply to humans. Likewise, with animals as subjects, if good transfer can be shown between point-light displays and the video clips on which the point-light stimuli are based, then it would have to be accepted that the account developed above does not apply very well to animals. A number of experiments have studied how animals discriminate between point-light displays of natural movements. Their findings, however, do not allow clear conclusions to be drawn about the degree to which training with one class of stimuli, say point-light displays, transfers to the full displays on which the point-light patterns were based, as the following review shows.

Blake (1993) performed the first animal, biological motion, point-light display study using cats. He trained two cats to discriminate between point-light displays depicting biological movement (a cat walking as if on a treadmill facing right), against a series of point-light displays of non-biological movements (random motion, Brownian motion, positionally scrambled motion and phase-scrambled motion). After training, one of the two cats eventually showed good transfer to the same point-light display of the cat walking facing left, and to a novel animation of a cat running rather than walking.

Following Blake, several studies with pigeons (Dittrich *et al* 1998; Omori 1998; Omori &

Watanabe 1996); chicks (Regolin, Tommasi, & Vallortigara 2000; Vallortigara, Regolin, & Marconato 2005), quail (Yamaguchi & Fujita 1999), chimpanzees (Tomonaga 2001), and bottlenosed dolphins (Herman *et al.* 1990) confirmed that animals can discriminate biological movement point-light displays from non-biological ones (Parron *et al.*, 2007).

Although these findings indicate that animals can discriminate between point-light displays of different natural movements, as noted in Chapter 1, it is not clear that this ability depends upon the detection of dynamic cues. Instead, it could be based on static cues created by configurations of the points of light creating the display. Particularly telling evidence in support of this claim can be found in a study by Parron *et al.* (2007) who trained baboons to discriminate between a point-light display of a model (either human or baboon) performing an action, such as walking, from a scrambled version of the same display. The baboons mastered this task, but only after many trials, which would not be expected if the discrimination of natural movement from point-light displays was spontaneous. Moreover, when the baboons were shown a point-light display of the natural movement, but with the upper and lower halves transposed, they continued to perform as if it was the original clip. Thus the subjects appeared to be more sensitive to local configuration of the light points, than the movement they created.

Turning to pigeons there is again rather little evidence that they can discriminate between different natural movements depicted by point-light displays. The most thorough study to address this issue was by Dittrich, Kea, Barrett and Gurr (1998). In their Experiment 2, the Dittrich group first trained pigeons to discriminate between video clips of two different natural movements (conspecific walking versus conspecific

pecking), and then discriminate between point-light displays representing the same two movement categories in the second stage. The results were not encouraging. Only 3 out of the 8 birds were able to solve the first discrimination and were thus tested with the point-light displays in the second stage. However, performance on the transfer trials was substantially worse than on trials with the original stimuli, and barely above that expected on the basis of chance.

In Experiment 3, Dittrich *et al.*, (1998) further trained another eight pigeons to discriminate point-light displays of the pecking movements from the point-light displays of the walking movements. Following similar procedure as in Experiment 2, birds that successfully solved the discrimination in stage one were then given transfer tests but this time with the video clips on which the point-light displays were based. For stage one, half of the subjects (four out of eight) learnt to solve the point-light movement category discrimination. When these four birds were tested in Stage 2, there was very little evidence of transfer from the point-light to the full-detail stimuli.

There are several concerns regarding Dittrich *et al.*'s (1998) experiment. First, only a few subjects were successfully trained to discriminate the stimuli. In Experiment 2, only 3 pigeons made it through to the second stage; and in Experiment 3, only 4 birds entered the second stage of training. Second, the effects of learning shown by the results were very weak even in subjects claimed to be successfully trained. Actually in the second stage of the Experiment 2, only one pigeon obtained over 80% correct responses with the stimuli that were shown in Stage 1. The correct response rates for the remaining

three birds were all below 70%. Similar results were obtained in Experiment 3 of the study.

The experiment to be described next was intended to examine further whether pigeons trained to discriminate between point-light displays of different natural movements can show spontaneous transfer to the displays on which the point-light stimuli were based. There were two groups of pigeons: a full-display group and a point-light group. The full-display group was trained with the complete video images on which the point-light displays were based. In this way, the motion pathway of the points and their representing figures were identical in both groups.

In keeping with the previous experiments in this thesis, the stimuli used for discrimination training were video clips of a human and a dog walking either forwards or backwards (see Figure 2.1). The experiment in Chapter 3 demonstrated that pigeons are able to discriminate between these clips. The first question that Experiment 5 was designed to address is whether pigeons can solve equally well a discrimination based on point-light versions of these stimuli.

For the full-display group, the subjects first received training to discriminate between a normal video clip of the person and dog walking forwards from the left, versus the two models walking backwards from the left. The point-light group received discrimination training with point-light versions of the same videos. After 16 sessions of training, the full-display group successfully solved the discrimination, which was consistent with the results in Chapter 3. The point-light group, however, failed to learn the discrimination. In view of this failure there was little point in continuing to the next

phase of the experiment in which transfer to the original video clips was to be assessed. Nonetheless, as shown in the discussion that follows the experiment, the failure to solve the discrimination with the point-light stimuli is of some theoretical interest and it is for this reason that the experiment is reported.

#### **4.2.1 Method**

*Subjects.* Twenty adult experimentally naïve pigeons (*Columba livia*) of both sexes were used for the experiment. The method of housing and food deprivation was the same as for Experiment 3. At the start of the experiment the birds were assigned at random to two groups of equal size.

*Apparatus.* The apparatus was the same as that used for Experiment 3.

*Video stimuli.* The video stimuli for the full-display group were the same as those used for Stage 1 of Experiment 3. One video clip showed a human and a dog walking forwards from left to right, and the other showed these models walking backwards from left to right. The height of the human was 9 cm and her feet were 13 cm above the bottom of the screen. These two clips were used to create the point-light video clips, using Go Dotty on an Apple computer. Red dots were marked on certain reference points of the model in each frame to create a smooth moving point-light figure against the same green grass background as the full-display video clip. A total of 24 points were used: one

on middle of the female's head, one on the middle of her neck, one on each of her shoulders, one on each of her elbows, one on each of her wrists, one in the middle of her waist, one on each of her knees, and one on each of her ankles; one on the dog's eye, one on the dog's shoulder, one on the dog's haunch, one on the dog's tail, one on each of the four ankles of the dog, and one on each of the dog's four feet. Each of the four clips (Full-Display Forwards, Full-Display Backwards, Point-Light Forwards and Point-Light Backwards) was repeated 30 times to create a looped display that lasted for 120 seconds.

*Procedure.* Preliminary training was the same as for Experiment 3, and included the red-green discrimination that was conducted in that study. Upon the completion of this discrimination, the two groups received 16 sessions of Stage-1 training with their respective video clips. The duration of each session was 43 min 40 s. For the full-display group, in each session there were ten presentations of the 2-min video clip of the model walking forwards from left to right, and ten presentations of the 2-min video clip of the model walking backwards from left to right. For the point-light group, each of the 2-min point-light versions of the forwards and backwards clips was shown.

Food was made available according to a VI 15-s schedule for pecking on the response key during clips of the models walking forwards in both group but not when they were walking backwards. The video clips were each presented ten times in a random sequence with the constraint that no more than two clips of the same type could occur in succession. Each clip was separated by an interval of 10 s, and there was an interval of

20 s after the computer program was started before the first trial commenced. During these intervals the screens of the TFT monitors were completely black.

In order to measure the rate of responding during reinforced, S+, and non-reinforced, S-, trials, a value from the VI schedule was selected by the computer at start of both types of trials. The number of responses was then recorded until this value had elapsed. The rates of responding during these intervals were used to calculate the overall rate of responding on both types of trial in each session.

#### **4.2.2 Results**

Figure 4.2 shows the mean rates of pecking by the two groups for each of the 16 sessions of discrimination training. The discrimination was acquired by the full-display group, but not by the point-light group. A three-way ANOVA with the factors of session, group, and trial (reinforced or nonreinforced) revealed a significant effect of trial,  $F(1, 18) = 11.01$ , but the effect of session,  $F(15, 270) = 1.02$ , and group,  $F < 1$  was not significant. There was a significant interaction of Group x Trial,  $F(1, 18) = 4.39$ , Session x Trial,  $F(15, 270) = 3.14$ , and Group x Session x Trial,  $F(15, 270) = 1.83$ , but, the interaction of Group x Session,  $F < 1$ , was not significant. A simple main effects analysis was carried out to explore the interaction of Group x Session x Stimulus, the effect of stimulus in the full-display group was significant,  $F(15, 270) = 4.06$ , whereas the effect of stimulus in the point-light group was not,  $F < 1$ . The effect of Group x Stimulus was significant on day 10 to 14, and 16,  $F_s(1, 288) > 4.00$ . The effect of stimulus was

significant for the full-display group on days 9 to 16,  $F_s(1, 288) > 4.48$ , but not significant on any days in the point-light group,  $F_s(1, 288) < 3.53$ .

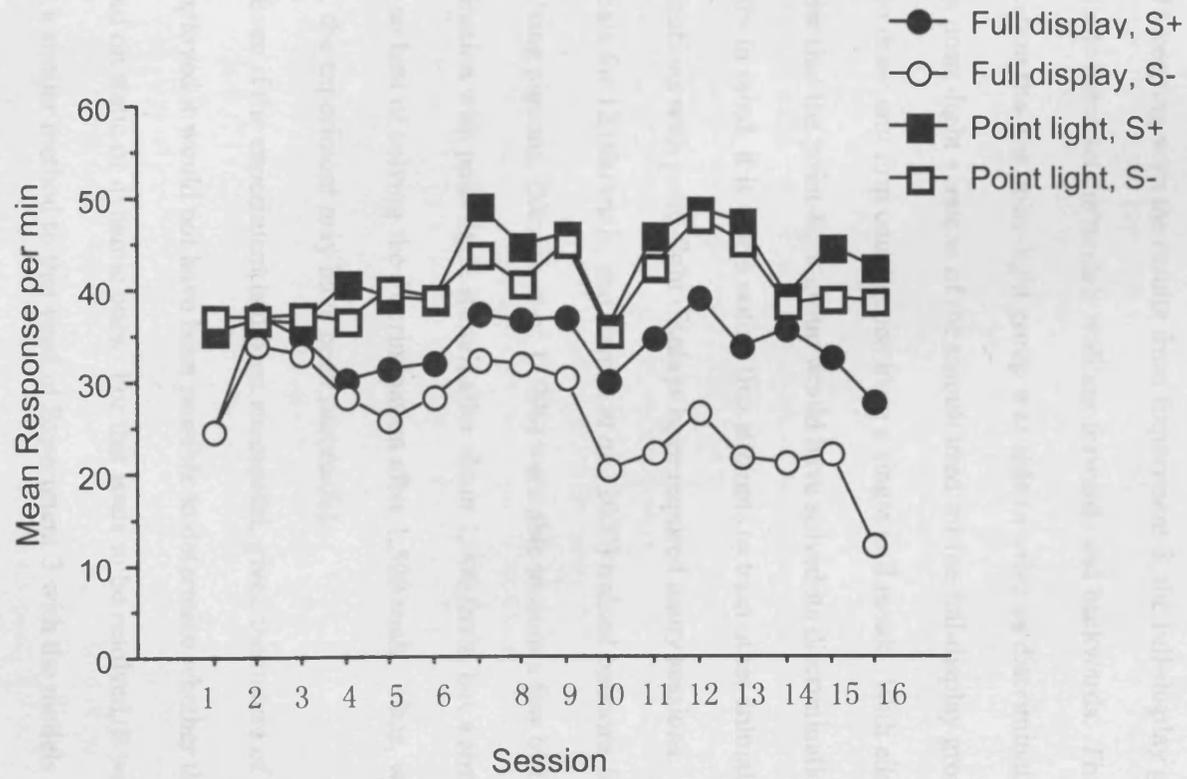


Figure 4.2. The mean rates of responding by the full-display and the point-light groups of Experiment 5 during the reinforced (S+) and the nonreinforced (S-) video clips.

### **4.2.3 Discussion**

In keeping with the results from Experiment 3, the full-display group was able to discriminate between the models walking forwards and backwards. There was, however, no indication that the point-light group was able to solve its discrimination, which was based on point-light versions of the stimuli used for the full-display group. It would be foolish to draw any firm conclusions from a single null result. With additional training, it is possible that the point-light group would have solved its discrimination. With this possibility in mind, it is worth noting that attempts to train other animals to solve discriminations with point-light displays have required many sessions. Blake (1993) trained cats for 12,000 trials, and Parron *et al.* (2007) trained baboons for over 8,000 trials. Using pigeons, Dittrich *et al.* (1998) were able to train a few birds on a discrimination with point-light stimuli after about 1,000 trials, but a similar number showed no hint of solving the discrimination after 1,500 trials. Thus, with extended training, the experiment may have been successful.

Even if the experiment had been successful, given the nature of the stimuli that were employed it would not have been possible to determine whether the discrimination was based on static or dynamic cues. For this issue to be resolved, it would be necessary to adopt a similar method to that used in Experiment 3 with the models facing to the left and right, walking as if on a treadmill forwards and backwards. In view of the present results, the chances of birds solving such a complex discrimination appear slender.

The present experiment was unusual in using a human walking a dog on a leash as the model on which the point-light display was based. When my point-light display was shown to naïve human observers they were able to identify the movements involved almost as readily as if they were shown the original video clips. On this basis, it would seem that despite its unusual nature, there was nothing fundamentally wrong with my point-light display which made it unsuitable for the experiment.

As noted in the introduction to this experiment, the failure of the pigeons to solve the discrimination with the point-light displays is entirely consistent with predictions that can be derived from one version of the Associative Sequence Learning account of how animal's represent biological movement (Heyes & Ray, 2000; Heyes, 2005). According to this version, the components of the associative sequence are templates that correspond reasonably closely to individual postures from the action being represented. On this basis, there is no reason to suppose that just because an animal can discriminate between movements portrayed by a video film of the model, that it will also be able to discriminate between point-light representations based on the film. Indeed, one would expect there to be rather little generalization from one mode of portraying the action to another. Although the present experiment did not specifically evaluate this prediction, tests for evidence of transfer from a realistic model to a point-light model, or vice versa have met with rather little success (see Parron *et al.*, 2007, for a review).

Two experiments have been described in this chapter. Experiment 4 demonstrated for the first time that pigeons are readily able to discriminate spontaneously between inverted video clips of models walking either forwards or backwards, after they have been

trained to discriminate between these actions with normal video clips. Experiment 5 has shown that pigeons are unable to discriminate between point-light displays of models walking forwards or backwards. Collectively the results are consistent with an Associative Sequence Learning account for the discrimination of biological motion.

## Chapter 5

The results from the previous experiments lend support to the principles on which the Associative Sequence Learning theory of Heyes and Ray (2000; see also Heyes, 2001, 2005) is based. This theory, however, was not developed to account for how animals discriminate between different natural movements, and it was not developed to explain how animals solve discriminations based on inverted stimuli or point light displays. Instead, the theory was developed in order to provide an account of how one animal is able to imitate the actions of another.

Chapter 1 describes a number of experimental findings which show that birds are capable of imitation. The methods that were adopted, however, were rather complicated. For instance, Dorrance and Zentall (2002) first trained pigeons to peck a treadle for food in the presence of a white light, and to step on the treadle in the presence of a green light. They were then required to reverse this discrimination. Prior to each session of reversal training, a consistent group observed a demonstrator performing the new discrimination, and an inconsistent group observed a demonstrator perform the original discrimination. The reversal was acquired more readily by the consistent than inconsistent group, which presumably reflects the impact of the observers imitating the demonstrators. Given the complexity of this experiment, one might ask why Dorrance and Zentall (2002) did not adopt a simpler design and omit the initial discrimination training for the two groups of observers. In other words, why did they not simply look at the influence of the demonstrators on the acquisition of a discrimination, rather than the reversal of a

discrimination? In fact, Dorrance and Zentall (2002) employed this simpler methodology and failed to find an effect of imitation (see also Saggerson *et al.* 2005). In terms of Associative Sequence Learning theory, this finding is puzzling because there is no obvious reason why imitation should facilitate the reversal but not the acquisition of a discrimination (but see Sa Saggerson *et al.* 2005).

In light of this puzzle, the purpose of the experiments in the present chapter is to determine whether it is indeed possible for imitation to influence the acquisition of a discrimination. If the experiments should fail to find any evidence of imitation then they will pose a serious problem to Associative Sequence Learning theory.

## 5.1 Experiment 6

During the first stage of this experiment two groups of budgerigars were shown video clips of a budgerigar either stepping on the top of a box (step video), or pecking at the top of a box (peck video). The compatible group was reinforced with food for stepping on the box when shown the step video, but not when shown the peck video. The incompatible group was required to step on the box for food during the peck but not the step video. If budgerigars imitate the actions they observe performed by conspecifics, then they should be encouraged to step on the box in the presence of the step video. Such a tendency will then facilitate the acquisition of the discrimination between the two video

clips in the compatible group, and hinder it in the incompatible group. In fact, the results failed to reveal a difference between the groups. One explanation for the failure to reveal an influence of imitation is that both groups might have paid rather little attention to the actions performed by the different demonstrators, choosing instead to base the discrimination on the differences between their physical characteristics. In view of this possibility, a further stage of training was conducted in which the same budgerigar demonstrated both stepping and pecking. Budgerigars were chosen for these studies because their propensity to mimic vocally suggests they may be unusually well disposed towards imitating the actions of other budgerigars.

### **5.1.1 Method**

*Subjects and apparatus.* The subjects were eleven naïve male and female adult budgerigars (*Melopsittacus undulates*) of unknown age, but they were at least 9 months old at the start of the experiment. Their weights ranged from 33 to 50 g. Another two adult budgerigars of similar weight that were not tested experimentally were used as demonstrators. All birds were obtained from a commercial supplier and allowed to habituate to the laboratory environment for at least one week prior to the experiment. All the observers and demonstrators were housed together in a single cage (88.0 x 40.0 x 30.0 cm). The manner in which the birds were housed and deprived of food was the same as for Experiment 1. The apparatus was the same as for Experiment 1.

*Video stimuli.* Seeds were initially attached to the square key on the box that was used for detecting response with clear tape in order to obtain footage of a demonstrator pecking. The number of seeds taped to the key was gradually reduced and pecks on it were recorded. Once Demonstrator A was reliably pecking the manipulandum a video recording was made of its activity in a 30-min session. A similar recording was also made of Demonstrator B who had received no prior training.

The video clips were recorded with a digital video camera (Sony Handycam DCR-HC30E), and edited using Adobe Premiere Pro 1.5. The footage was filmed so that the images played on the TFT screen were life size. The camera was placed outside the testing chamber, between the monitor screen and the front wall of the testing chamber. The camera was fitted on a tripod, facing towards the chamber, where from the camera's perspective, the hopper was on the right. For the purposes of creating the video clip of the response of stepping, one instance in which the foot was lifted from the floor of the chamber and placed on the response box was selected for each demonstrator from the 30-min recordings made in the single recording session. During video editing, the original instance of the selected response was played forward and then in reverse to create a smooth single step on the box. The speeds of the clip, which consisted of the foregoing sequence repeated twice, were adjusted to make it last for a total of 3 s. The 3-s clip was then looped 40 times to make 80 steps in the 2-minute video (Step video). Thus, the step video showed a bird standing upright, which then placed its right foot on the box with its body shifted a little, and then drew its foot back to the original position with the body also

shifted back. A similar method to that just described was adopted in order to create a 2-min loop of Demonstrator A pecking the box (Peck video).

*Procedure.* Magazine training and response shaping was the same as for Experiment 1. Both groups then received 12, 30-min sessions of discrimination training in Stage 1. In each session there were seven presentations of the 2-min video clip of a budgerigar pecking at the box, and seven presentations of the 2-min video clip of another budgerigar stepping on the response box. Food was made available according to a VI 30-s schedule for stepping on the box. This response occasionally resulted in the delivery of food during the clip of the demonstrator stepping for the consistent group, and during the clip of the demonstrator pecking for the inconsistent group. A new value from the VI schedule was selected randomly at the start of every reinforced trial. Responses during the other video clip did not result in the delivery of food. The video clips were presented in a random sequence with the constraint that no more than two clips of the same type could occur in succession. Each clip was separated by an interval of 10 s, and there was an interval of 20 s after the computer program was started before the first trial commenced. During these intervals the screens of the TFT monitors were completely white.

After twelve sessions of training in Stage 1, subjects were given different video stimuli in Stage 2. Instead of video clips of different demonstrators pecking and stepping, Stage 2 used a pecking and a stepping video clip of the same demonstrator. Subjects were trained in Stage 2 for 16 sessions.

In order to measure the rate of responding during reinforced, S+, and nonreinforced, S-, trials a value from the VI schedule was selected by the computer at the start of both types of trial. The number of responses was then recorded until this value had elapsed. The rates of responding during these intervals were used to calculate the overall rate of responding on both types of trial in each session. A response was recorded as the closure of a microswitch which took place whenever the square response key on top of the box was depressed by a force of 6 g or more. Remaining procedural details that have been omitted were the same as for Experiment 1.

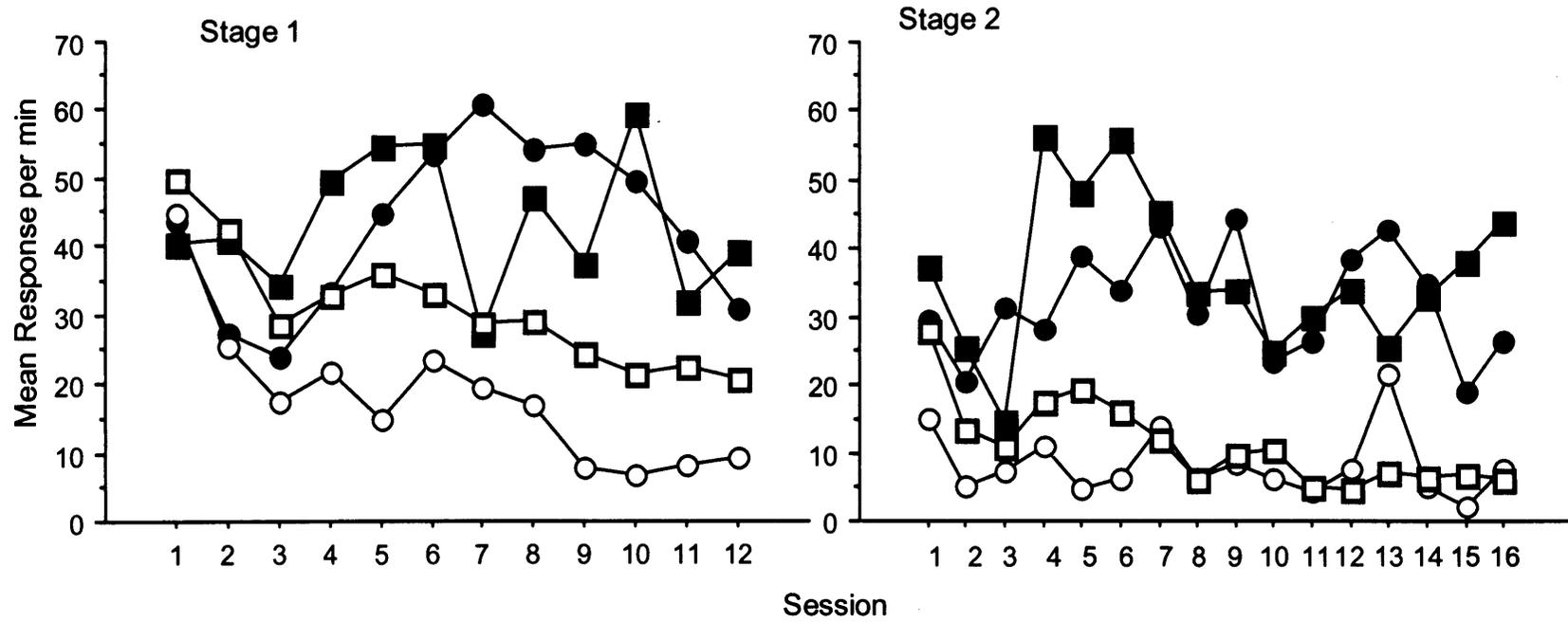


Figure 5.1. The mean rates of responding during the reinforced (+) and nonreinforced (-) video clips for the two groups during Stage 1 (left-hand panel) and Stage 2 (right-hand panel) of Experiment 5.

### 5.1.2 Results

The left-hand panel of Figure 5.1 shows the mean response rates of responding by the two groups during the first stage of the experiment when actions of stepping and pecking were demonstrated by different birds on the TFT screen. The right-hand panel shows the equivalent results for Stage 2 when the same bird was used to demonstrate both actions. Both groups solved the discrimination in Stage 1 by eventually responding more rapidly during the reinforced than the nonreinforced video clip. There is a hint that the magnitude of the discrimination was more marked in the inconsistent than the consistent group. The discrimination transferred readily to Stage 2. There was very little difference between the results of the two groups during the second stage.

The results for the two groups during Stage 1 were analysed with a three-way ANOVA of individual response rates, for each session, for the reinforced and the non-reinforced trials. There was a significant effect of stimulus,  $F(1, 7) = 12.47$ , but the effects of group and session,  $F_s < 1$ , were not significant. The Stimulus x Session interaction was significant,  $F(11, 77) = 2.36$ , but none of the remaining interactions was significant,  $F_s < 1$ . The tests of simple main effects show that responding was significantly faster during S+ than S- on Sessions 5 to 12,  $F_s(1, 84) > 1.93$ .

A similar ANOVA for the results from Stage 2 revealed a significant effect of stimulus,  $F(1, 7) = 15.26$ , and session,  $F(15, 105) = 1.93$ , but the effect of group,  $F < 1$  was not significant. Significance was found in the interaction of Session x Stimulus,  $F$

(15, 105) = 1.83, but not the interaction of Group x Session,  $F(15, 105) = 1.60$ , and the interaction of Group x Stimulus,  $F < 1$ . Tests of simple main effects were conducted to further explore the Stimulus x Session interaction. These tests show that responding was significantly faster during S+ than S- on Sessions 4 to 9, and 11 to 16,  $F_s(1, 154) > 5.90$ . The interaction of Group x Session x Stimulus,  $F(15, 105) = 1.08$ , was not significant.

### **5.1.3 Discussion**

Two groups of budgerigars were required to step on a box in order to gain food. For one group this response was rewarded in the presence of a video clip of a budgerigar stepping on the same box but not during a clip of a budgerigar pecking the box. If budgerigars imitate the actions of the conspecifics that they observe on a video monitor, then the tendency to imitate the action of stepping during the reinforced trials would be expected to facilitate the acquisition of the discrimination. The second group was required to step on the box during the video clip of the demonstrator pecking and to withhold this response during the clip of the demonstrator stepping. On this occasion, any tendency to imitate the actions of the demonstrator would disrupt the acquisition of the discrimination. In contrast to these predictions, there was no difference between the performances of the two groups, which implies that they did not imitate the actions that they observed.

One explanation for the failure to find any effect of imitation in Stage 1 of the experiment is that the subjects solved the discrimination by focusing on the appearance of

the different demonstrator in the two video clips, rather than on the response they performed. However, the discrimination was only slightly disrupted with the introduction of Stage 2, when the same demonstrator was used in both video clips. This finding suggests that the discrimination in Stage 1 was indeed based on the two responses. Moreover, during Stage 2, the only cues on which the discrimination could be based were provided by the responses of pecking and stepping, and there was no hint of an influence of imitation during this phase of the experiment. Overall, therefore, the results from this experiment imply that budgerigars do not imitate the actions of conspecifics that are displayed on a TFT screen. Of course, it is possible that the method for detecting imitation in this experiment was not sufficiently sensitive. In view of this possibility, the next experiment adopts a rather different test of imitation in budgerigars.

## **5.2 Experiment 7**

A possible reason for the failure of the previous experiment to reveal an influence of imitation is that the discrimination might have been too simple. If both groups found it easy to tell the difference between the two actions, the discrimination might then have been solved so rapidly that it was not possible for a more subtle influence of imitation to influence the outcome of the experiment. The next experiment was designed with this possibility in mind. Two groups of budgerigars observed, on video, a conspecific demonstrator pecking at (peck video), or stepping on (step video), a response key. The

pecking and stepping stimuli were each presented briefly and in an unpredictable sequence. To obtain food reward, the birds in the compatible group were required to peck during the peck video and to step during the step video, whereas the birds in the incompatible group were required to step during the peck video, and to peck during the step video. Under these conditions, imitation would be consistent with correct (rewarded) responding in the compatible group, and inconsistent with correct responding in the incompatible group. Therefore, if imitation in birds can interfere with efficient performance of an ongoing task, then the Incompatible group should make fewer rewarded responses than the compatible group. Moreover, given the complexity of this task, it is likely that even a subtle influence of imitation will influence the acquisition of the discrimination.

Thus far in my thesis, subjects have been required to perform only a single response to gain food, either stepping on a manipulandum such as a box, or pecking a response key. In order to monitor these responses, the number of times that a microswitch was activated was recorded. Such a measure is inadequate for the proposed experiment where it is necessary to differentiate between the action of stepping and pecking. Rather than make this judgment by observing the animals, I decided to adopt a technique developed by Saggerson *et al.* (2005). They required pigeons either to step on or peck at a panel in order to gain food, and discovered that the duration of contact with the panel, and hence the duration for which a microswitch was closed, was shorter when the birds pecked the panel than when they stepped on it. Closures of the microswitch for less than 150 ms were treated as pecks, and closures for longer than 150 ms were treated



as steps. Observation of the birds on selected sessions, indicated that this was a highly accurate method for separating pecks from steps. In adopting this methodology for my experiment, it was necessary to identify for budgerigars, and for the manipulandum, the appropriate duration for distinguishing between pecks and steps.

### **5.2.1 Method**

*Subjects.* The subjects were 22 naïve adult budgerigars. Their weights ranged from 33 to 60 g. The method of housing and food deprivation was the same as that described for Experiment 1.

*Apparatus.* The apparatus used was the same as for the previous experiment, except that the response key was modified to allow detection of two different responses. The response key consisted of a round Perspex box with a diameter of 3 cm, which was located on the floor of the conditioning chamber. The top of the lid was 0.5 cm above the floor of the chamber and its midpoint was 3 cm from the door, and 12 cm from the wall containing the grain feeder. The round lid was surrounded by a metal rim with a diameter of 3.2 cm. The lid was semi-transparent. A microswitch operated whenever a force of greater than 6 g was applied to the lid.

*Video stimuli.* Two video clips were used—one showing a budgerigar pecking the response key and another showing the same bird stepping on the key. Details of the method of recording were the same as for Experiment 6. For the purposes of creating the

video clip of stepping, one instance in which the foot was lifted from the floor of the chamber and placed on the response key was selected from a 30 min recording. During video editing, the original instance of the selected response was played forward and then in reverse to create a smooth single step on the response key. The speed of the clip, which consisted of the foregoing sequence repeated twice, was adjusted to make it last for a total of 2.14 s. The clip was then looped 56 times to make 112 steps in the 2 min video (step video). Thus, the step video showed a bird standing upright, which then placed its right foot on the response key with its body shifted a little, and then drew its foot back to the original position with the body also shifted back. A method similar to that just described was adopted in order to create a 2 min (112 pecks) video of the demonstrator pecking the response key (peck video).

*Procedure.* Throughout the experiment, every time that the microswitch on the response key was operated, a record was taken of the duration for which it was closed. A peck was deemed to have been responsible for this closure if the duration of closure was less than 0.10 s. If this duration was greater than 0.10 s then the response was classified as a step. These values were selected on the basis of pilot work with three budgerigars that were hand shaped to both peck and step on the response key to gain food. For two birds, pecks were rewarded when the entire television screen was red, and steps were rewarded when the entire television screen was green. For the remaining bird, pecks were rewarded during the green light, and steps during the red light. This training continued until more than 90 per cent of the responses made during each stimulus were correct. I

then recorded during a 1-min presentation of each stimulus, the duration of each response. During the stimulus that signalled the availability of food for pecking, the three birds made a total of 67 responses. If one outlier response was removed (0.31 s), the mean duration of the remaining responses was 0.038 s (range: 0.008–0.102) and the standard deviation was 0.020. During the stimulus that signalled the availability of food for stepping, 89 responses were recorded. If one outlier response was removed (2.03 s), the mean duration of the remaining responses was 0.259 s (range: 0.090–0.879 s) and the standard deviation was 0.144. There were two responses during the stimulus in which pecking was rewarded which were longer than the 0.10 s criterion, and three responses during the stimulus in which steps were rewarded which were shorter than 0.10 s.

After being trained to feed from the food hopper in the manner described for Experiment 6 (21–35 days), the birds were trained to peck and step on the response key to operate the hopper. Both responses were then reinforced on a continuous schedule for 2 days, and then on a gradually increasing VI schedule until, after 20 days, the birds were performing reliably on a VI 15 s schedule.

To familiarize the birds with the procedure to be used in the peck–step discrimination task, and to make sure that the birds assigned to the compatible and incompatible groups did not differ in their discrimination learning ability, all the birds were given red–green discrimination training. In each session there were nine trials in which the screen was illuminated green for 1 min, and nine trials where it was illuminated with red. The sequence of the illumination was randomized. The screen was dark for an interval of 10 s between each trial. Eleven subjects (six in the compatible group and five

in the incompatible group) were trained to peck in order to gain food delivered according to a VI 15-s schedule when the TFT screen was green and to step for food when it was red. Pecks during red and steps during green were without programmed consequences. The remaining 11 subjects were trained in a manner opposite to that just described.

Two days after the completion of red–green discrimination training, the birds received 13 sessions of peck–step discrimination training. The observers were divided equally into two groups (compatible group and incompatible group). Subjects in the compatible group were rewarded with food on a VI 15-s schedule when they performed the same response as the demonstrator (peck when the video of pecking was presented; step when the video of stepping was presented). For subjects in the incompatible group, performing the response opposite to that being demonstrated was reinforced, also according to VI 15 s schedule. That is, food was presented when subjects pecked at the response key during the stepping video, and stepped on the key during the pecking video. In each trial, the total number of correct and of incorrect responses that were made was recorded. Correct responses were those that could potentially result in the delivery of food, whereas incorrect responses were those that could not result in the delivery of food.

In each session, the peck and step videos were each presented seven times, 2 min at a time, in a random sequence with the constraint that the same clip was not shown more than twice in succession. There was an interval of 20 s before the first video clip was shown and there was an interval of 10 s between successive clips. The TFT screens were entirely white during these intervals. Procedural details that have been omitted were the same as for Experiment 6.

### 5.2.2 Results

To compare the performance of the Compatible and Incompatible groups on the red–green discrimination, for each subject, the mean number of correct responses that were made during the red and green trials, and the mean number of incorrect responses were calculated for the final two sessions of red–green training. The group means were the following: compatible group, correct—137.56; compatible group, incorrect— 96.31; incompatible group, correct— 168.41; and incompatible group, incorrect— 104.27. Two-way analysis of variance (ANOVA) revealed a significant effect of response (correct or incorrect),  $F(1, 20) = 32.55$ , indicating that the birds acquired the discrimination. However, the effect of group,  $F(1, 20) = 2.06$ , and the Group x Response interaction,  $F < 1$ , were not significant, confirming that the Compatible and Incompatible groups did not differ in their red–green discrimination performance.

The results from the test phase of the experiment are shown in Figure 5.2, which portrays the mean number of responses made during each session in the presence of the reinforced and non-reinforced video clips for the two groups. The data from the first three sessions are not included because they were lost due to an error in the computer program that recorded responses. Figure 5.2a shows the mean rates at which the correct and incorrect responses were performed by the compatible group. Figure 5.2b shows the equivalent results for the incompatible group. From these graphs, it is evident that the compatible group made more correct responses than incorrect responses throughout the

10-sessions of testing for which data were recorded. By contrast, the incompatible group made the same number of correct and incorrect responses during the first few sessions of training, and only gradually developed some tendency to make more correct responses than incorrect ones. Thus, the discrimination performance of the incompatible group was substantially weaker than that of the compatible group.

These impressions were confirmed by ANOVA in which response type (correct or incorrect), stimulus video (peck or step) and session (1–10) were within-subjects factors, and group (compatible or incompatible) was the between-subjects factor. This revealed a significant main effect of response type,  $F(1, 20) = 12.26$ , indicating that there were more correct responses than incorrect responses. It also yielded a significant main effect of session,  $F(9, 180) = 3.53$ , and a significant Response Type x Session interaction,  $F(9, 180) = 2.93$ , showing that the number of responses per session increased over sessions, and that this trend was more pronounced for correct responses than for incorrect ones. Of principal interest, the analysis revealed a significant Response Type x Group interaction,  $F(1, 20) = 7.53$ , confirming that the discrimination performance of the incompatible group was inferior to that of the compatible group. No other main effects or interactions (two-, three- or four- way) were significant.

In spite of their weaker performance, the incompatible group did eventually acquire the peck–step discrimination; across the last three sessions of testing, they made more correct responses than incorrect responses,  $F(1, 10) = 17.36$ .

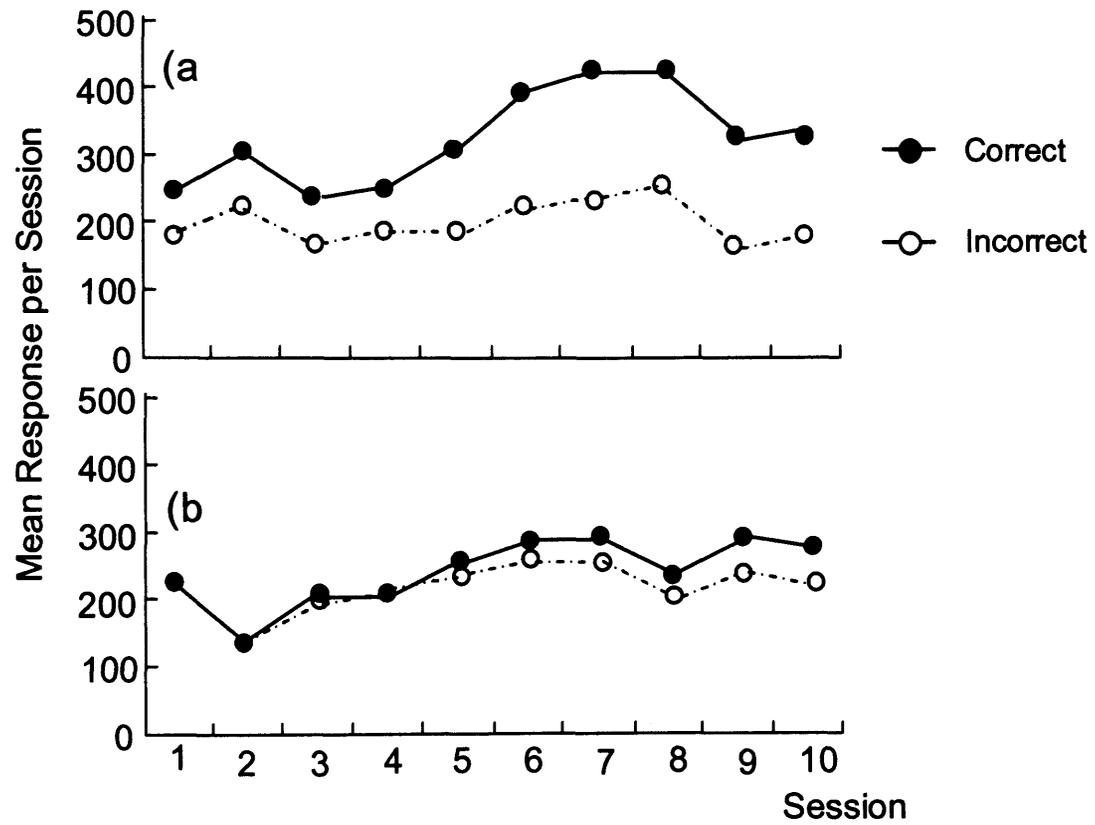


Figure 5.2. Mean number of correct (filled circles) and incorrect (open circles) response by birds in each session in the (a) compatible and (b) incompatible groups during the test sessions of Experiment 6.

### **5.2.3 Discussion**

A group of budgerigars that was required to gain food by pecking on a response key when it observed a demonstrator pecking at the key, and to step on the key when it saw a demonstrator performing the same response, solved this discrimination more readily than a group trained with the opposite contingencies. A straightforward explanation for this outcome can be developed if it is accepted that the experimental subjects imitated the actions they observed on the TFT screen. Imitating these actions would facilitate the acquisition of the discrimination in the compatible group, and interfere with it in the incompatible group.

It is worth remarking that the present experiment provides a particularly convincing demonstration of imitation. Since both stepping and pecking resulted in the response key being depressed, the results are difficult to explain in terms of emulation learning. Moreover, since both responses were directed to the same object it is not easy to see how the results could be explained in terms of local enhancement or stimulus enhancement. By default, therefore, the results appear to be a consequence of the observers copying the actions of the demonstrators (see also Dorrance & Zentall, 2001).

The analysis of the data from the current experiment did not reveal an asymmetry between automatic imitation of pecking and stepping; the ANOVA did not yield a significant main effect of stimulus (pecking versus stepping), or any significant interactions involving this variable. However, visual inspection of the data suggested that

the tendency to imitate pecking was stronger than the tendency to imitate stepping, and this pattern is consistent with the results of a recent study that has found reliable imitation of pecking, but not of stepping, in budgerigars (Heyes, personal communication).

As far as we are aware, the present study is the first to use a fully automated procedure to investigate imitation in nonhuman animals. Some previous studies of imitation in birds have used computer-controlled video stimuli (Heyes, personal communication), or computer-recorded measures of response type (Saggerson *et al.* 2005), but they have not combined these techniques. A fully automated procedure allows both precise stimulus control and reliable, impartial response measurement.

### 5.3 General Discussion

Imitation was successfully demonstrated in Experiment 7, but not Experiment 6. Although it is not possible to provide with complete confidence an explanation for the discrepancy between the outcomes of the two experiments, it is likely that the different discriminations used for the two experiments played an important role. Bearing in mind that the results from the first three sessions of Experiment 7 were lost, a comparison of Figures 5.1 and 5.2 indicates that the test discrimination was acquired more readily in Experiment 6 than Experiment 7. As noted in the introduction to the second of these experiments, if the effects of imitation on behaviour are slight then it is possible they will be evident only when a discrimination develops slowly. The results reported in this chapter are certainly consistent with the conclusion.

Whatever the reason for the failure to detect an influence of imitation in Experiment 6, the most important point to draw from this chapter that evidence of imitation was revealed in Experiment 7. A failure to find imitation in this study would have posed a problem for Associative Sequence Learning theory because it predicts that imitation should have occurred with the methodology I adopted.

## Chapter 6

The experiments described in this thesis have revealed a number of novel findings. Experiments 1, 2 and 3 have shown that birds are able to discriminate between different natural movements on the basis of dynamic cues. That is they can tell the difference between a model walking forwards and backwards on the basis of information provided successive changes in the model's posture. Experiment 4 revealed that once a pigeon has been trained to discriminate between two natural movements shown in normal orientation, the discrimination is unaffected if the video clips of the movements are inverted. Experiment 7 revealed that an influence of imitation is able to disrupt the acquisition of a discrimination. I now consider the theoretical significance of these findings.

### 6.1 The discrimination of natural movement

Two different types of cues can be used by an animal when it discriminates between the actions of another animal. I have referred to one type as a static cue because it can be derived from individual postures selected from the overall sequence of the behavior. The other type of cue has been referred to as dynamic because, to be perceived, it is necessary for the model to change from one posture to another. Experiments 1 and 2 were conducted in order to discover whether animals make use of dynamic cues when solving discriminations based on the natural movements of another animal. The most

convincing evidence for the use of these cues was provided by the test trials in Experiment 2 and 3. In the latter case, for example, pigeons were able to discriminate between stationary models walking forwards, facing either to the left or right, from the same models walking backwards, facing either to the left or right. The video clips of the models walking forwards were composed of the same frames as the clips of the models walking backwards, which means that by referring to individual postures from the two actions it would be impossible to solve the discrimination. Instead, it must have been solved on the basis of different dynamic cues arising from walking forwards and backwards.

Having established that animals are sensitive to dynamic cues, it then becomes important to identify these cues. According to Giese and Poggio (2003), two different types of dynamic cues provide information about biological movement, at least for mammals. One type is the optic flow emanating from the movement of images across the retina. Giese and Poggio argued that information about optic flow is processed by the dorsal stream. Neurons at the lower levels of this pathway are said to be sensitive to the local motion created by small components of the moving body. Neurons at higher levels are meant to be sensitive to the optic flow of the entire body as it changes from one posture to another. Ultimately, in the dorsal stream, there are predicted to be neurons that are sensitive to the optic flow created by an entire movement such as walking.

Experiments have revealed that neurons in the pigeon brain may be sensitive to optic flow (e.g., Wang & Frost 1992; Wylie, Bischof, & Frost 1998). It may not, however, be easy to determine whether the optic flow created by the models in Experiments 1, 2, and 3 was

responsible for the ability of our subjects to discriminate between them walking forwards and backwards. The problem is that the moving images shown to the birds were complex, which makes it extremely difficult to analyze the contribution made by optic flow to birds' performance.

The other type of dynamic cue is based on form and was said by Giese and Poggio (2003) to be processed by the ventral stream. At the lowest level of this pathway are neurons that are sensitive to lines at particular orientations. Higher up the pathway are neurons that are sensitive to snapshots of particular postures, and if these neurons are excited in a particular sequence then they will excite motion pattern neurons that will fire when one type of movement is observed. Thus, seeing a given sequence of snapshots might excite a motion pattern neuron for walking forwards, whereas observing the reverse of this sequence might excite a motion pattern neuron for walking backwards. These proposals have much in common with the ideas expressed by Heyes and Ray (2000) concerning the manner in which the movement by a live model is represented.

Perhaps, therefore, the subjects in our experiments discriminated between the two types of walking by taking note of the order in which the various postures were performed. A possible problem with this proposal is the finding that after subjects had been trained with the models walking forwards, say, from left to right, the discrimination transferred immediately to trials in which the models were walking forwards from right to left. This outcome was observed in the test trials of Experiments 2 and 3. If, as Giese and Poggio (2003) suggested, the postures in a currently observed action must correspond with snapshots of previous exemplars of this activity for the activity to be recognized,

then it does not necessarily follow that recognition will be possible when the mirror image of the action is viewed. Indeed, Giese and Poggio suggested that recognition of movement, based on changes in posture, will be very difficult when the mirror image of an action is viewed for the first time. The implication of our results is that this type of recognition is less viewpoint dependent, at least for certain birds, than Giese and Poggio assumed. Support for this claim can be found in the results of Experiment 4 where the discrimination of movement transferred without disruption to inverted video clips of the same movements.

## **6.2 Theories of discrimination learning**

My results have implications not only for theories concerning the perception of natural movement, but also for theories of discrimination learning. George, Ward-Robinson, and Pearce (2001) argued that according to most of these theories (e.g., Pearce 1987, 1994; Rescorla & Wagner 1972), a discrimination between two patterns of stimulation will be possible only if the patterns are composed of different features. If two patterns consist of different arrangements of the same components, then, according to these theories, information about the structure of the patterns is ignored and the discrimination will be impossible to solve. If it is accepted that the discrimination of natural movement is based on an appreciation of the order in which a sequence of postures is executed, then the present results pose a similar problem for theories of

discrimination learning because the theories do not explain how the order in which stimuli occur is encoded. As we have just seen, the theories of Giese and Poggio (2003), and Heyes and Ray (2000) provides one solution to this problem by proposing that unidirectional associations develop between neurons, or sensory units, that are successively activated as a sequence of postures from a given action is observed. Provided this sequence is activated in the correct order, a motion pattern neuron will be activated that will then effectively represent the action concerned

### **6.3 Implications for imitation**

Humans are known to be subject to ‘automatic imitation’; the sight of another person’s action tends to elicit the same action from the observer, even when this imitative tendency interferes with efficient performance of an ongoing task. For example, if a person is instructed to open his/her hand as fast as possible whenever he/she sees a hand movement, responses are slower when the stimulus hand closes than when it opens (Heyes, Johnson & Haggard 2005). According to Associative Sequence Learning theory automatic imitation is an inevitable consequence of any experience that results in associations being formed between internal units responsible for the perception of an action and those responsible for the performance of an action. For movements of the human hand, this kind of experience—in which action execution is predictive of, and

temporally contiguous with, observation of the same action—can be obtained by watching one's own movements.

A broad range of vertebrate and invertebrate species are capable of associative learning (Pearce 2008), and many non-human animals are likely to receive, through self observation or by other means, correlated experience of observing and executing at least some of their behaviours. Therefore, if the Associative Sequence Learning theory is correct, one would expect to find automatic imitation in non-human species.

Recent work on the 'pecking–stepping imitation effect' suggests, but does not show conclusively, that birds are subject to automatic imitation. When one group of birds has observed a conspecific pecking an object, and a second group has observed a conspecific stepping on the object, the members of both groups typically direct both pecks and steps to the object. However, the proportion of pecking to stepping responses is biased towards pecking in the birds that observed pecking, and towards stepping in the birds that observed stepping (e.g. budgerigars: Dawson & Foss 1965; pigeons: Zentall *et al.* 1996; Nyuyen *et al.* 2005, Saggerson *et al.* 2005, McGregor *et al.* 2006; quail: Akins & Zentall 1996; Dorrance & Zentall 2001).

In all of these studies reporting a pecking–stepping imitation effect, the tested birds are likely to have had experience of feeding in groups. In birds, social foraging provides correlated experience of observing and executing pecking behaviour. Therefore, it is plausible that, as the Associative Sequence Learning model suggests, the birds' imitative behaviour in these experiments was due to prior associative learning. However, in all of these studies, the observer birds were rewarded with food for both pecking and

stepping, or for neither response, and under these conditions the occurrence of imitation had no impact on reinforcement rate; on the efficiency with which the bird discharged its task of obtaining food. Therefore, previous studies leave open the question of whether, like automatic imitation in humans, the tendency of birds to imitate pecking is so strong that it will interfere with efficient performance of an ongoing task.

Experiment 7, however, can be said to have tested for automatic imitation. In that study budgerigars were required to step on a manipulandum in the presence of video clip A, and peck at the manipulandum during clip B. This discrimination was acquired more readily by the compatible group, for which clip A was of a bird stepping and clip B was of a bird pecking, than by the incompatible group for which assignment of the video clips to A and B was reversed. For subjects in the inconsistent group any tendency to imitate would be against the subjects' best interests and interfere with the performance of a response that would lead to food. The poor discrimination that was observed in the inconsistent group might thus be regarded as evidence of an influence of automatic imitation. In the absence of a suitable control group, however, the possibility remains that the difference between the two groups was entirely due to the impact of imitation on the performance of the consistent group.

In the majority of previous studies of imitative pecking and stepping, observer birds saw rewarded pecking or rewarded stepping, and were themselves rewarded with equal frequency for pecking and stepping (e.g. Dawson & Foss 1965; Akins & Zentall 1996; Zentall *et al.* 1996). These studies were important in establishing that a pecking–stepping imitation effect can be reliably detected in a variety of bird species, but they did not

address the question of whether imitation in birds is goal directed. More specifically, they did not investigate whether imitation in birds depends on action–outcome learning by observation (e.g. learning that pecking is followed by the delivery of food), and whether imitative responses are made in the expectation that they will be rewarded (but see Dorrance & Zentall 2001; Saggerson *et al.* 2005). One previous study (McGregor *et al.* 2006) found a pecking–stepping imitation effect in pigeons when neither the observers nor the demonstrators were rewarded for pecking or for stepping. This suggested that imitative behaviour in birds is not goal directed; that they will imitate in the absence of any extrinsic reward for imitation, and when they have not seen the demonstrator’s responses being rewarded. However, unlike the present study, McGregor *et al.* did not show that birds will imitate even when imitation is costly, when it reduces the rate at which they can obtain food. The birds in the incompatible group were tested under these conditions, and yet, when contrasted with the birds in the compatible group, they continued to provide evidence of imitation throughout the experiment. This suggests that, at least in the context of the pecking–stepping imitation effect, imitation in birds is automatic or involuntary and that it cannot be inhibited by mechanisms that are sensitive to behavioural outcomes.

## 6.4 Concluding comments

The overall concern of my thesis has been to evaluate the Associative Sequence Learning theory proposed by Heyes and Ray (2000). The theory predicts that animals will

be able to discriminate between different natural movements on the basis of dynamic cues, and my experiments have confirmed this prediction. My experiments have also provided a novel demonstration of imitation. This demonstration lends support to the theory because it predicts that imitation should be found whenever one animal observes the actions of another, provided the observer has acquired the necessary associations between the appropriate sensory input units and response output units.

The foregoing proviso leads the theory to make a number of interesting predictions. For example, it follows that animals should be unable to imitate a response they have never seen before. In contradiction to this prediction, experiments by Moore (1992) with a parrot, and Custance, Whiten and Bard (1995) with a chimpanzee, have shown that at least some animals are capable of imitating actions they observe for the first time. It is not at all clear how the theory of Heyes and Ray (2000) can explain these findings. Another prediction is that imitation should only be possible with responses that the animal has previously performed while watching another animal make the same response. It follows, therefore, that if birds could be prevented from gaining this experience with regard to stepping and pecking then they would fail to reveal evidence of imitation. To my knowledge, this important prediction has yet to be tested.

There are, therefore, some experimental findings that do not sit comfortably with Associative Sequence Learning theory. Indeed, Heyes and Ray (2000) anticipated that the theory may have its shortcomings when they said “we would be very surprised if it turned out to provide a fully accurate account of imitation” (p. 222). Nonetheless, because of the precise manner in which the theory is specified it has the merit of being able to generate

testable predictions. For this reason, together with its success thus far, the theory merits further scrutiny.

Finally, the experiments described in this thesis have been possible because of the use of automated techniques for displaying the experimental stimuli, and for recording responses. The experiments have revealed the great advantage of using these techniques (see also Saggerson *et al.*, 2005), which should be of considerable benefit for future investigations into both imitation and the perception of natural movement.

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