This is to certify that the

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INVESTIGATING AN IMAGERY PROCESS IN PIGEONS

By

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ABSTRACT

INVESTIGATING AN IMAGERY PROCESS IN PIGEONS

By

Julie Janelle Neiworth

The structural and functional qualities of an imagery process were investigated in a memory task with pigeons (Columba livia). The goal of the investigation was, first, to determine whether imagery was a memory process used by a nonhuman species, and, second, to define the characteristics of a representation of movement in such a species. A movement estimation task involving a rotating clock hand stimulus was employed. Subjects were required to discriminate constant velocity from aberrations from constant velocity (i.e., acceleration and deceleration) by a choice response. The memory component of the task was that , on some trials, subjects had to extrapolate stimulus movement after the stimulus disappeared in order to judge its final location. In a previous set of studies, this task successfully uncovered a cognitive estimation strategy in pigeons that supported some of the characteristics of an imagery process.

Experiment 1 presented various delays to determine to what extent the physical characteristic of time was represented when movement was represented. Although fairly accurate in their response to novel delays, pigeons' process for estimating movement did not always support subtle changes in the delay. Further analyses of subjects' patterns of errors indicated that fast accelerations overwhelmed the subjects' range of estimation and forced a shift of strategies from movement estimation to S-R associations. Within a particular low range of accelerations and decelerations, subjects accurately estimated stimulus movement, but demonstrated a tendency to confuse acceleration with constant velocity. A phenomenon like "mental rotation" was observed, in that subjects made more errors as the distance of extrapolation increased.

In Experiment 2, the speed of visible stimulus movement was increased or decreased in two test conditions. Resulting performance to these speed changes was accurate, indicating that subjects could utilize the information about rate presented in the stimulus display to estimate the location of the moving stimulus. A timing strategy was refuted, and an imagery process was supported.

The stimulus display of movement was removed in Experiment 3 and its effect on performance was monitored. The result was a complete shift of strategies from estimation to S-R associations again. This result further supported the hypothesis that imagery was used, for an imagery process requires a perceptual display for proper representation of movement.

The investigation provided strong support that pigeons use an imagery process to represent a stimulus as it moves and disappears. The set of studies also revealed some constraints of representing movement in pigeons.

To Mark,

To Marie,

To my family,

And to Emma .

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INTRODUCTION

How the results of experience are maintained or "represented" so as to affect later behavior has long been of concern to animal learning theorists (Cole, 1907; Thorndike, 1938; Skinner, 1984) . The popular contention has been that there is a mapping relation between the features of a "representation" and the features of a stimulus such that the study of the representation is not necessary because the two worlds (real and representational) are equivalent (Skinner, 1984; Schwartz, 1984; Carter & Werner, 1978; Zentall, Edwards, Moore & Hogan, 1981). Only recently, with the advent of the study of cognitive abilities in animals has the question of the form of representation in animals arisen (Roitblat, 1982). Imagery is the most frequently chosen answer to this question (Griffin, 1981; Jerison, 1973; Terrace, 1985). However the answer is formulated from the thinking of Darwin, Wundt, and others who argued that images are omnipresent, or are "the mothers of all internal representations" (Wundt, 1894; Kosslyn, 1980). While it has been theorized that animals' (i.e., monkeys', pigeons' and rats') representations of real-world events contain perceptual characteristics of those events and are thus image-like (see Roitblat, 1982 for a review), there has been no systematic investigation of the possible identification and use of an imagery process in the cognitive system of any one of these species.

The function of an image is to maintain perceptual characteristics of stimuli in memory. Imagery is a cognitive process to which neural activity responsible for perception must be channeled and maintained. The neural mechanisms involved in basic perceptual processes have been traced in many species, with a special emphasis on avians, cats and monkeys. The goal of the present investigation is the identification of an imagery process in a nonhuman species for which biochemical and neural investigations are possible. Because of its ties with perception, the study of imagery seems best-suited for an investigation of cognitive and brain function. The aim is to eventually develop an animal model of perceptual/cognitive processing that can yield descriptions of mind-brain function which can be used to tailor information processing models. In developing an animal model of such function, it is not assumed that the neural systems of humans and of nonhuman species are of near-equivalence, nor that their cognitive systems are identical. It is assumed that some basic similarities exist (i.e., homologous visual pathways and some basic cognitive processes) that make the systems compatible. Of central importance is the assumption that an animal model of mind-brain processing is at least as veridical as is a computer model of such processing. While computer and communications models have been very useful in describing humans' mental or "mind" functions, it is clear that the neural processing that accompanies such mental functioning is much different than the programmed binary interactions that occur in a simulated computer-run mental operation (Posner, Pea & Volpe, 1982) or that occur in a serial process developed from communications models (Lachman, Lachman & Butterfield, 1979). The neural processing that occurs with cognitive processing in various species draws a more realistic picture of processing characteristics because the basic structure of activation and feedback is maintained and the neural medium through which activity occurs is similar.

In selecting an animal model for cognitive study, two factors are of importance: 1)whether the animal shares the same phylogeny with the species for which the process under study is to be generalized, and 2)if the animal's cognitive processing and perceptual processing warrant such study. The goal at present is to find a simple organism in which neural and cogntive processing may be studied simultaneously. Therefore the simpler one-celled organisms used to investigate the chemical and neural correlates of learning (Kandel, 1971; Thompson, 1986) are not the proper species in which to study higher level cognitive and perceptual processing. While rats have been the simpler mammalian family of interest in neural investigation, they do not exhibit well-developed abilities in visual information processing. In fact, it is suggested that for cognitive processing and visual information processing, the pigeon's system may be more similar to higher mammals' system (i.e., to humans) than to the lower mammals' systems (i.e., rats and dogs). While the pigeons hold a position on a different phylogenic tree than do humans, their visual system seems functionally and structurally equivalent to that of monkeys (Maxwell & Granda, 1979). In addition, they are very responsive to visual stimuli, and their overt behaviors to them are clearly noted in the animal learning literature. An argument can be made here for parallel evolution, for even though humans and avians occupy different branches of the evolutionary tree, their visual systems seem to have evolved structurally and functionally as similar. While pigeons are the species of interest in these studies, it is probably prudent that other types of mammals, specifically cats and monkeys, are studied in this way. There are certainly some qualitative differences between mammals and avians that warrant cross-species considerations.

A Theoretical Description and an Operational Definition of an Image

Imagery has been defined generally as the processing of visual information not currently before the organism (Pinker, 1984). The structure of an image remains unclear: some have said that images are mental "pictures" that are stored (Plato, Bugelski, 1970), or that images are memories that activate the same neural mechanisms as do percepts (Hebb, 1968; Woodworth & Schlosberg, 1954), or that images are simply "picture-like", with details of their structure left open-ended (Kosslyn, 1980). From the many studies of the structure and function of images, it seems clear that visual perception and imagery are related. Specifically, it seems that perceptual detail, or the <u>structure</u> of an object, is maintained in an image as it is perceived. Moreover, it is clear that in imaging it is possible to transform or change a representation of an object. In fact this is described as the active "use" or <u>function</u> of an image, insofar as it is easier to transform a perceptual-like display(as in an image) than it is to contrive calculations and change descriptors (as in abstract codes). And finally it has been demonstrated that perception actually can <u>interact</u> with an ongoing imagery process in positive or negative ways, i.e., percepts can facilitate imaging or they can interfere with imaging. Because of the structure, function and interactive nature of imagery, many researchers believe that imagery is a separate and distinct memory process that can be identified from a converging set of evidence which supports each of these three qualities. Operationally, imagery can be identified if it is demonstrated that perceptual characteristics are maintained in the representational process (the structural assumption), that stimulus transformations are made possible by the process (the functional assumption), and that perception itself interferes with or facilitates the representational process (the interactive assumption).

An organism must maintain a representation of a stimulus after the stimulus has been presented and before a test is given. An operant task employed to test imagery must require perceptual information to be maintained and transformations to occur during a delay interval between the stimulus presentation and the test. The organism's accuracy to respond after the delay interval can reflect its ability to maintain perceptual information and to employ mental transformations if proper tests are administered.

The Identification of Some of the Characteristics of Imagery:

A Brief Review of Previous Research

Previous research has tested to some extent two of the three characteristics that describe an image (Neiworth & Rilling, 1987). The task employed was a conditional discrimination involving movement estimation. In it pigeons were required to discriminate a clock hand that rotated in a continuous fashion from one that did not. Figure 1 presents the various trial types used in training and testing.

There were three trial types presented in training: a perceptual type, an imagery type and a violation type. On perceptual trials, the rotating clock hand moved at a rate of 90° per s along an arc from a 12:00 presentation, or a 0° orientation, to a final location. Imagery and violation trials were similar to perceptual trials, except that the rotating clock hand disappeared at a 90° orientation, and some time later, reappeared at the final location. On imagery trials, tł duration of the delay corresponded with the time it would take for the stimulus to be rotated from 90°, its point of disappearance, to its point of reappearance. On violation trials, the duration of the delay did not correspond with continuous stimulus movement. For example, in the 135° violation trial (top panel of Figure 1), the stimulus disappeared at a 90° orientation an was absent for 1.0 s, or the time it would take it to be rotated to 180°, and then it reappeared at 135°. Perceptual and imagery trials were reinforced with 3-s access to grain for left key responses. A left key response indicated that the stimulus moved continuously even if it did disappear for some time. Pigeons were reinforced for right key responses on violation trials. The rationale for this methodology was to force the use of an imagery process by requiring subjects to remember a moving stimulus and to transform it through space in its absence. It should be noted that strategies other than imagery could be used to accomplish the task: Specifically, subjects could memorize a series of rules associating delay and location with a choice response, or subjects could simply count or time the stimulus presentation and respond appropriately with little need for a visual image. An attempt to test these alternatives was made, and is pursued further in the dissertation experiments.

Experiment One

Five subjects were first trained with 135° trials (top panel, Figure 1) until criterion performance of 80 percent correct was met, and then they were exposed to 180° training trials (middle panel, Figure 1) until criterion was met, and then to 135° and 180° training trials presented in alternating sessions to criterion. There were two reasons for this approach: first, a pilot study revealed that pigeons could not learn to respond to all the trial types presented in the figure in training simultaneously; and second, a goal of the experiment was to determine what kind of strategy pigeons were using at each step of acquisition of the cognitive process of estimating the location of the rotating stimulus.

The test given to determine the strategy pigeons were using is described in the bottom panel of Figure 1. Novel perceptual, imagery and violation trials were presented at 158° twice each within 135° and 180° training sessions. The amount of transfer, or the accuracy of

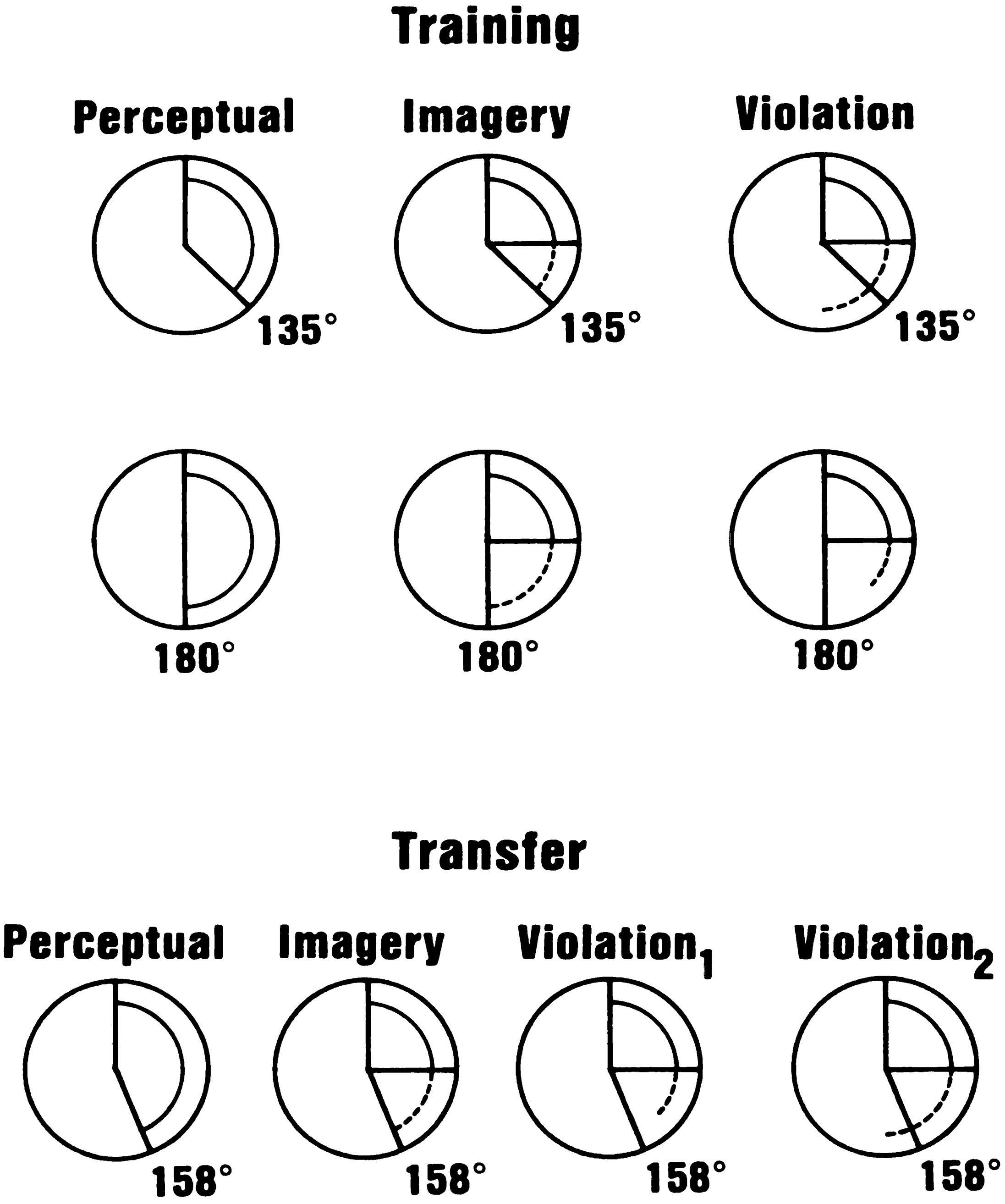


Figure 1. Trial types for 135° and 180° training, and for the test of transfer at 158°.

response to these novel trials, was observed for 12 sessions. The first important feature to notice about the test trials is that a 158° orientation was a novel location never before presented but located halfway between the two trained orientations (135° and 180°). According to Shepard and Cooper (1982), imagery is an analog process. If the subjects' representations are in analog form, then they most likely transform a representation of the clock hand from 90° to 135° and to 180°, and thus the intermediate location of 158° should also be represented. The result of the use of an analog imagery process in this task, then, would be immediate and positive transfer to the intermediate location.

The second feature to note in the test trials is that the 158° imagery trial introduced a novel delay (0.75 s) for which the subjects could have no prior associations. A rule-based strategy predicts chance performance to first presentations of the 158° position. According to a rule-based strategy, some practice with these trials is necessary for learning new delay - location rules. However, an imagery strategy predicts immediate positive transfer, because this strategy is based on the assumption of continuous rotation applied to a novel example.

Two tests of transfer were conducted in Experiment 1, one test series after 135° training, and one after 135° and 180° training. The top panel of Figure 2 shows transfer to 158° trials after 135° training. Transfer was not complete. The strategy indicated by this pattern of results was that pigeons were following a simple timing rule: If there was no delay or if there was a short delay, subjects pecked the left key ; but if there was a long delay, subjects pecked the right key.

The bottom panel of Figure 2 shows mean percent correct scores to 158° trials after 135 and 180° training. The result was positive and complete transfer. The rule-based strategy adopted after 135° training was not used here. If it had been used, subjects would have applied conflicting rules for responses associated with the trained delays and would have responded at chance levels to these delays in the 158° test condition (i.e., to the violation trials). In addition, there was no prior stimulus-response rule for the delay and location presented in the 158° imagery trials, and chance responding should have been observed to those trials. The

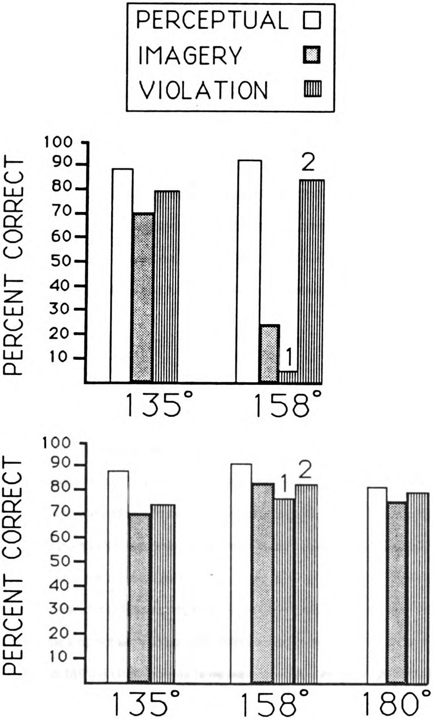


Figure 2. Mean percent correct scores from the 158° test after 135° training (top panel) and after 135°-180° training (bottom panel).

fact that subjects responded accurately to these trials suggested that they used some strategy of estimating the stimulus location during the delay. Imagery is a likely candidate here, but a timing strategy would also result in accurate estimation. In such a timing strategy, left key responses would be associated with 0-s delays or short delays, and right key responses would be associated with longer delays within each location condition. Such a strategy requires memorized associations between delays, locations and responses. It does not require an updated memory of stimulus movement.

Nevertheless, this experiment supported the notion that pigeons were retaining accurate perceptual characteristics of movement during stimulus absence, and that their representations for movement could be transformed or changed to accommodate a novel example. The structural and functional characteristics of imagery are supported in part by this result.

Experiment Two

Next, three naive pigeons were trained with 135° trials, then with 180° trials, and finally with alternating sessions of 135° and 180° trials until criterion performance was met. Only one test of transfer at 158° was given in this experiment to put to a test the argument that the subjects showed positive transfer in Experiment 1 because of the practice they obtained with the novel trials in the two tests of transfer. Figure 3 shows mean percent correct scores obtained from the three subjects to 158° trials after 135° and 180° training. Positive and complete transfer to these completely novel 158° trials was obtained. Thus practice with the novel trials was not likely to be responsible for the positive transfer. Exposure to two exemplars (135° and 180°) in training was necessary for subjects to use an estimation process.

Experiment Three

All subjects (i.e., the five subjects from Experiment 1 and the three from Experiment 2) were retrained to accurately respond to 135° and 180° alternating training sessions , and then

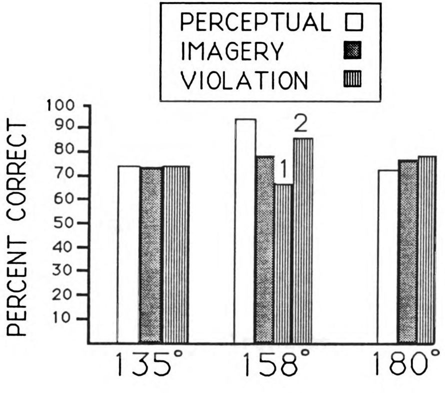


Figure 3. Mean percent correct scores from the 158° test after 135° and 180° training (Preliminary Experiment 2).

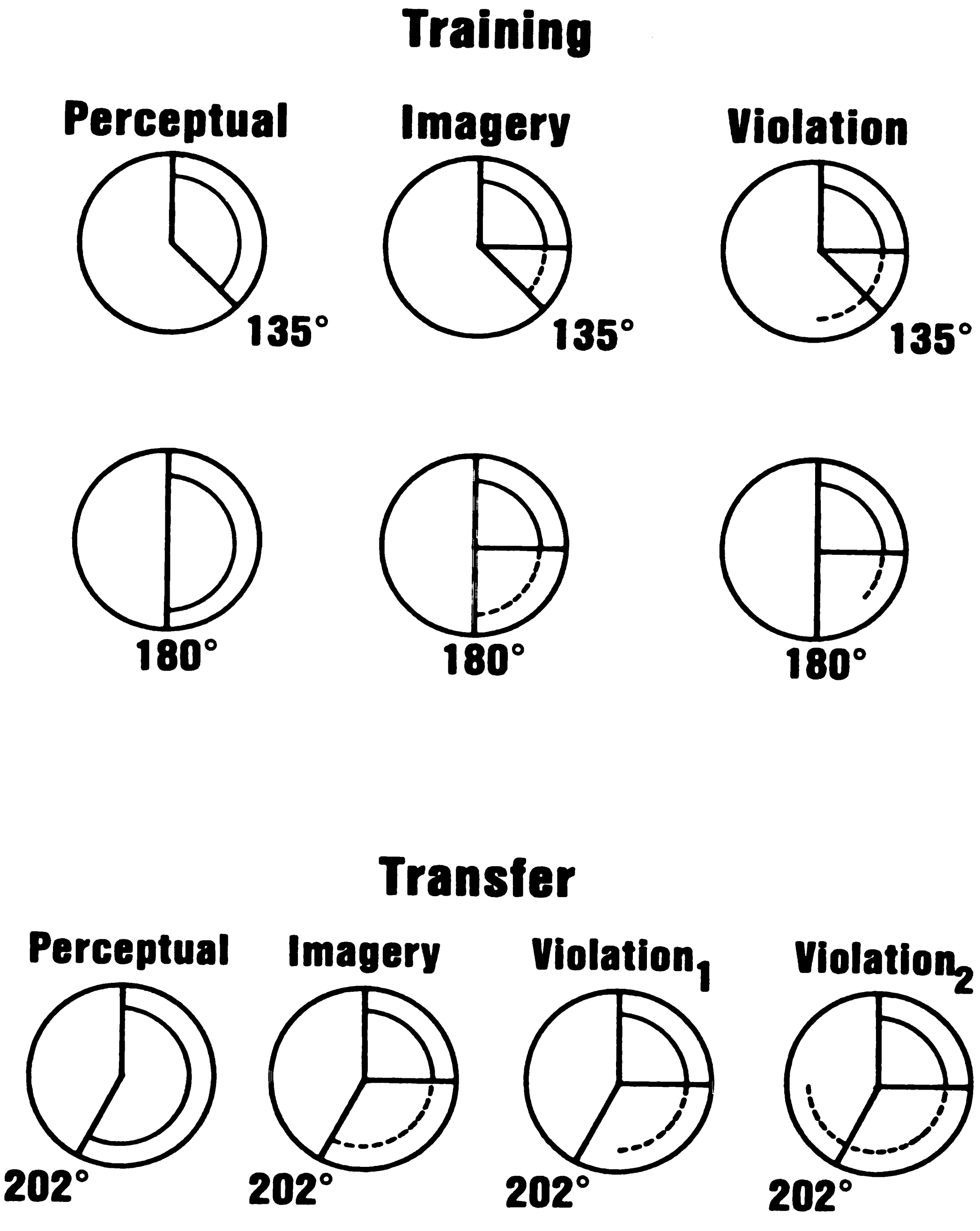


Figure 4. Trial types for 135° and 180° training and for the test of transfer at 202°.

the amount of transfer to a location outside the boundaries of training which was completely novel was tested. Figure 4 shows 135° and 180° training trials, and 202° transfer trials. The same testing procedure was used here as was used in 158° testing (i.e., each of the four 202° trials was presented twice within single sessions of 135° and 180° training and this procedure was followed for 12 sessions). Figure 5 shows mean percent correct scores for the 8 subjects from 202° testing within 135° and 180° training sessions. Positive and complete transfer was obtained again. Together with the results from Experiments 1 and 2, these results show that pigeons can accurately represent rotation when the moving stimulus is absent, and that they can estimate stimulus movement sufficiently to determine whether novel test locations are appropriate, even when those locations lie outside training conditions. These results indicate that the strategy pigeons are using is not based on S-R rules, practice, or exposure to test locations. The results support the structural assumption of imagery, that the process maintains perceptual characteristics, and the functional assumption, that the representations are transformable.

Note that the interactive quality of imagery, that perception can interact and interfere with an imagery process, was not tested in this set of experiments, and thus a critical quality that defines an image was not investigated. Further, a timing strategy cannot be ruled out as an alternative to imagery, for it can support the results of Experiments 1 and 2 easily, and the results of Experiment 3, although less strongly. A more detailed description of such a timing strategy is provided in the next section.

Problems with Identifying an Imagery Process in the Pigeon
And a Solution: Quantifying the Representation

It is clear from the work described above that pigeons in these experiments are employing some cognitive process to accurately estimate the location of an object that moves

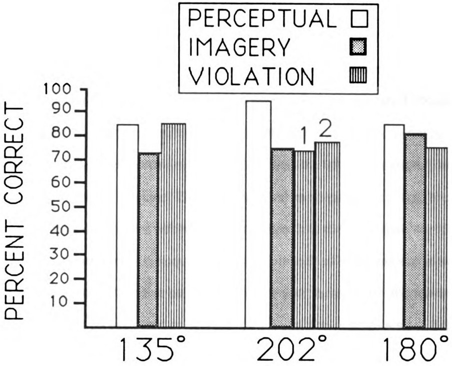


Figure 5. Mean percent correct scores from the 202° test after 135°-180° training.

and disappears. It is also evident that certain characteristics of an imagery process are present in this cognitive process. However, there is not enough detail about the representation that is quantified to conclude that imagery is at work. For instance, the structural and functional characteristics of a moving stimulus can be maintained by calculations or by a timing strategy, and not necessarily by the use of a transformable image.

A timing/counting strategy accounts for the previously collected data as follows: First, subjects determine a time or a terminal count for the perceptual trial in which movement is displayed to each location. Then subjects compare these times with a terminal count to the test location in imagery and violation trials. If the times match, the left key is selected, and if the times mismatch, the right key is selected. This strategy could be acquired in training, and applied easily to novel locations that fall within the training trials (i.e., 158°) because the 158° perceptua trials in which a terminal count is acquired is already embedded in the perceptual training trials. The timing strategy would have to be stretched to the 202° location, for the terminal count/time for this location must be estimated or generalized from training examples since it does not lie within training examples. Still, it does not seem that unlikely that subjects could apply a timing rule to a location 20° beyond the location trained, and the transfer to 202° was a bit weaker (as evidenced by less accurate responding than to 158° transfer) which could indicate an application of a learned strategy to a novel example. This strategy can account for all of the positive results of the previous set of experiments. The timing strategy represents an alternative to the imagery hypothesis, despite the results of the previous set of experiments.

A critical difference between a timing strategy and an imagery process is that timing is tied to a single dimension of time with paired associations for location, while imagery uses both space and time actively. Thus, a timing strategy does not require a display of movement, but imagery does. As long as the speed of movement remains constant, only the start location and the final location are necessary for the timing strategy, and a count can be accurately made between the two. Then, too, a timing strategy requires much practice along the dimension of time if the speed of movement is changed. Many trials would be required for the subject to learn the new terminal counts which would have to be formulated for the test locations based on a new speed.

The imagery process applies perceptual information about a stimulus in the stimulus' absence in order to estimate its location. In this case, then, a perceptual display of movement would facilitate mental transformations of the stimulus. Application of an imagery process should produce less accurate results if the perceptual display were removed, or if only the start location and the final location were presented.

However, the imagery process could accommodate changes in speeds of movement readily, as long as those speed changes were presented perceptually. The task of the imagery process is to use information about the stimulus that is presented and then to transform the stimulus in accordance with these perceptual characteristics. The application of this process to changes in the speed of movement should yield positive results with little need for training.

The Quantification of the Representation Apart From Verification of Imagery

The formulation of the characteristics of a timing strategy and an imagery process lead to experiments designed to determine if imagery is the representational process used. The specific manipulations which differentiate these two processes are: changing the speed of stimulus movement to be represented on probe trials, and removing the perceptual display for movement on probe trials. The results of these manipulations identify which strategy is most likely employed. They also test the functional assumption of imagery, that an image can be transformed in ways defined by the perceptual display, and also the interactive assumption of imagery, that the percept of movement influences the imagery process, for its removal is proposed to cause deleterious effects while its change (i.e., a change in the speed) is suggested to be incorporated in the image.

But another goal is realized in this research: The identification of the characteristics and/or the constraints of pigeons' representation of movement without regard for tests of imagery but with an aim to describe pigeons' "internal model" of movement. Much work has been accomplished in humans to investigate similarities and differences between mentally extrapolated motion (i.e., motion represented after a physical moving stimulus disappears) and the properties of actual physical motion. One finding is that cognitive processes resemble physical processes. An example of such a correspondence is that humans imagine or extrapolate the rotation of rigid objects in the way that objects actually rotate (Shepard & Cooper, 1982). Another example of correspondence is that humans represent momentum after moving objects stop (Freyd & Finke, 1984). These results suggest that humans' cognitive system has "internalized" many of the laws governing physical motion (Shepard, 1984).

Yet, some cognitive scientists have discovered a host of constraints and discrepancies in representing or "extrapolating" movement in humans. Specifically, after a stimulus moving at constant velocity disappears, humans tend to speed up or accelerate the representation of stimulus movement and, later, slow it to constant velocity again (Jagacinski, Johnson & Miller, 1983; Runeson, 1974). Humans exhibit a special problem with accelerating stimuli: They are unable to accurately predict paths of stimuli accelerating at speeds greater than 10° of visual angle/s^2 once the stimulus disappears (Gottsdanker, 1952; Rosenbaum,1975). The typical methodology for these studies is that subjects observe a stimulus moving and after it disappears, subjects press a response key to indicate when the stimulus that disappeared would have reached a fixed visible marker.

Other studies have shown that people demonstrate erroneous beliefs about motion when asked to predict the trajectories of objects (McCloskey & Kohl, 1983; Kaiser, Proffitt & Anderson, 1985). Specifically, people select as predictive of movement a trajectory that is inconsistent with the laws of classical physics (and also with natural observable laws of motion). Specifically, adults select a trajectory that implies continual movement along an object's initial motion path with gradual slowing to a stop. While their applied theory (the "impetus" theory) works for linearly moving objects, it is completely inadequate to predict paths of curvilinearly moving objects. There are debates concerning whether this nonpredictive strategy is "learned" because children express less of a tendency to follow it (Kaiser, Proffitt, & Anderson, 1985); however, these studies identify a nonveridical estimation of stimulus movement whose "impetus" is yet to be determined. A similar investigation of the "internal model" of movement in pigeons would add to the base of knowledge that describes movement representation and its constraints. As an avian species with a highly developed visual system, the investigation of movement representation in pigeons initiates an interface between studies of perception and studies of memory. For example, it provides a methodology for scientists to begin to label neural networks involved during movement perception and during movement representation. And it could identify deficits in pigeons' memory processing of movement which could be avoided in future examinations of movement representation. With regard to humans' abilities, it might be interesting to note whether a "simpler" nonverbal species represents movement more accurately than a more complex verbal species.

In sum, there are two issues under investigation in the present work. One is the imagery hypothesis, and the question of interest is: Does a nonhuman species (such as a pigeon) use imagery to remember objects and predict outcomes of change? To test for the existence of imagery, a movement task was selected so that subjects would be forced to maintain a perceptual-like representation of the stimulus to respond. But the use of a movement task brings forth a second issue to investigate: Do these subjects accurately represent movement? What are the limiting factors of movement representation in pigeons? Within what constraints does accurate representation of movement exist?

A theoretical description of an organism's cognitive system for extrapolating movement is limited by the measurement of the structure of the representation across space and time. While the set of experiments designed to test imagery also reveals some characteristics of the process for representing movement in pigeons, it is by no means definitive in describing the structure of cognitive extrapolation of movement in pigeons. However, the experiments test in a gross fashion specific variables which have constrained the process for representing movement in other species: Specifically, changes in velocity, acceleration and deceleration.

While both the issues of imagery and movement representation are investigated here , it should be made clear that one does not preclude or necessitate the other. Whether or not imagery is found to be the controlling memory process, movement must still be represented in order to estimate stimulus location in the task and its constraints within the task can be noted. And, if imagery is demonstrated to be the process in use, the constraints discovered of representations of movement may not bear directly on the imagery process, for they may have more to do with the subjects' ability to accurately perceive movement and to detect movement changes. For these reasons, the topics are investigated separately within these experiments.

Plan of Current Research

Three experiments were conducted to determine if imagery is the representational process used to estimate stimulus location, and also to reveal certain characteristics of the process of representing movement in pigeons. The first experiment identifies the nonveridical nature of representations of movement in the pigeon, and also helps to test the structural assumption of imagery: That a full perceptual description of the stimulus is maintained in memory if imagery is being used. The purpose of the experiment was to examine percent correct scores to violation trials in which novel delays are introduced. Positive transfer, or accurate performance across trained and test trials, indicates that imagery was used because it verifies that subtle changes in rate are noted in the representation of the stimulus. In addition, the pattern of errors obtained from different tests of violations in the movement estimation task indicate a constraint of representing movement. The error rates to these novel violation conditions reveal the degree to which space-time coordinates are updated during the process of representing stimulus movement. The results of this experiment help to draw a clearer picture of movement as it is represented and possibly "imaged" in the pigeon.

In the second experiment, the speed of initial rotation was manipulated within the same task. This experiment tests the amount of transfer of the representational process to novel movement conditions. In the description of this experiment, certain predictions are made concerning response accuracies to the novel speeds of movement if a timing strategy is used, or if an imagery process is used. The results of this experiment indicate which strategy is being used.

Finally, Experiment 3 examines the influence of the perceptual display of rotation from 0° to 90° on the cognitive process of representing movement. It identifies the triggering feature for representing movement as either the start location, or the start location and some display of movement. In this experiment, perceptual cues for movement are removed in test trials and only static stimulus displays separated by delays are provided. Movement is necessary for an imagery process, and so if imagery is employed, then removing the movement display should produce a decrement in response accuracy. Alternatively, if a timing strategy is employed successfully between 0° and 90°, then no decrement in performance should be obtained.

In sum, these three experiments help to determine if imagery is the process at work and quantify certain characteristics of the representational process: 1) its sensitivity to movement changes which occur in the stimulus' absence, 2) its responsiveness to changes in visible stimulus movement, and 3) its dependence on perceptual cues for movement.

Experiment One:

The Effects of Changes in Rate During the Delay

This experiment examines one quality of imagery, namely the amount of detail of timing and rate of a moving stimulus retained in memory . The previous set of experiments determined

whether the structure of the representation of the moving stimulus was accurate and flexible enough to accommodate novel locations. In this experiment, the duration of the delay is manipulated to determine how finely tuned the structure of the representation is to time. Accurate responding to novel delays further verifies that the structure of physical movement was aptly represented, and this result also indicates that imagery was used, in that another physical component of movement is transformed in the representation.

This experiment also identifies a constraint of the representational process by an analysis of patterns of errors to imagery and violation trials in which novel delays are presented. It was determined from the previous set of experiments (Neiworth & Rilling, 1987) that subjects made more errors to one type of violation trial than to any other violation trial or to any imagery trial. The specific increases in errors observed were not tied to a particular location or to a particular delay duration. Rather, a different view of these violation trials based on the type of stimulus movement that could occur during the delay to predict the location revealed a common element within each of these trials : momentum was represented in the image.

Figure 6 shows mean errors to the imagery trials (acceleration = 0) and to the violation trials (all others) in the test locations presented in the previous experiments (i.e., to 158° and 202°). The horizontal axis of this graph depicts the type of movement required of the stimulus, once it had disappeared, to reach its test location by the end of the delay. In imagery trials, the type of movement was continued constant velocity and so errors to imagery trials are plotted at the 0-point of the horizontal axis (meaning 0 acceleration during the delay). Those violation trials which presented a delay too short for constant velocity movement to the test location implied that the stimulus had to accelerate during the delay, hence errors to these violation trials are graphed on the positive side of the horizontal axis. Similarly, violation trials which presented a delay too long for the stimulus to move at constant velocity to reach the test location implied that deceleration occurred, and errors to these trials are plotted on the negative side.

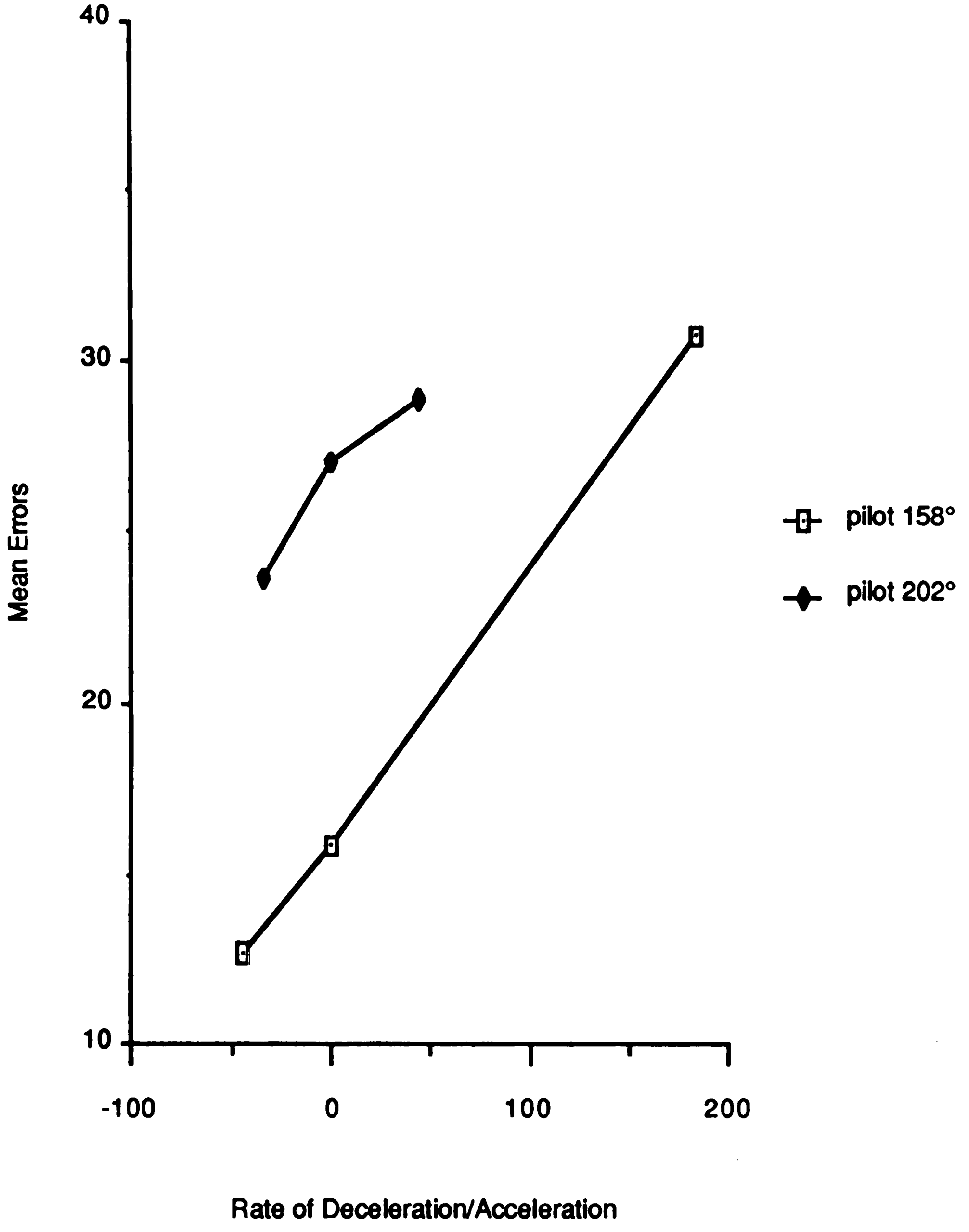


Figure 6. Mean errors plotted as a function of speeds tested in the imagery and violation trials in Preliminary Experiments 1,2, and 3.

Errors are a linear function of deceleration/acceleration in this graph. The linearity of the functions indicates that pigeons confuse acceleration with constant velocity. A strategy that would produce such a function is if subjects "speed up" their representation of movement once the stimulus disappears, thus stimuli that actually accelerate during the delay are more often confused with a stimulus supposedly moving at "constant velocity".

Note also that the functions are parallel. This indicates that errors may increase by some constant as the distance through which a representation must be rotated is increased (i.e., from 158° to 202°). This increase in errors is not due to the length of time in which the process is applied, for delay durations were counterbalanced across location conditions. Rather, errors increased as the stimulus required transformation through farther distances.

The functions in Figure 6 suggest two conclusions, the first, of concern to the imagery hypothesis, and the second, with regard to possible constraints of movement representation. The conclusion concerning imagery is that tests of certain delays (or of accelerating stimuli, in general) produce less transfer, and this implies that the timing and rate are <u>not</u> finely tuned in the representation or image. With respect to movement representation, the error patterns in the preliminary data reveal the "internal model" of a displayed movement trajectory that is constrained by certain characteristics of position as a function of time.

This experiment tests different points on these two functions and introduces a third function. The acceleration rates tested in the previous experiments were $44°/s^2$, $184°/s^2$, and $360°/s^2$. The only acceleration rate that did not produce increased errors was $360°/s^2$. This result may indicate that pigeons begin to clearly discern that a stimulus is accelerating in its absence when it accelerates at a rate of $360°/s^2$ or higher. Rates below this may be confused more often with constant velocity. Or the lack of errors to the $360°/s^2$ rate of acceleration may be a result of practice, since this trial was one of the original training trials and had been observed thousands of times by the subjects within the previous experiments.

A test of imagery in this experiment is a test of transfer (or a maintenance of accurate performance) across trained examples and examples with novel delays. In general, performance to perceptual, imagery and violation test trials should be similar to performance to trained perceptual, imagery and violation trials if imagery is used.

A test of the constraint of movement representation is a test of linear change of errors to each of the violation test trials. These two tests, the imagery test and the test of constraints, may seem opponent, since one is verified by similar performance across trials while the other is verified by differentiated performance across trials. However, the difference in the two tests is that in the first, similarity must exist between average training and test performance for it to be verified, while in the second, differences must exist between the various test trials for verification.

Method

Subjects

Eight White Carneaux pigeons served as subjects. The eight subjects participated in the three experiments reviewed in the introduction, and were trained to differentiate between constant velocity and violation conditions with a rotating bar stimulus. The subjects were maintained at 80 percent +/- 20 grams of their free-feeding weights. They were individually housed in a temperature-controlled, constantly illuminated colony room wherein water and grit was always available.

Apparatus

Two Life Sciences Associates secondary video monitors (CAT#509-MD1000-190) with 12 cm X 9.5 cm screens were fixed to the stimulus panels of two Lehigh Valley Electronics standard pigeon chambers. These chambers were used in the three experiments described in the introduction. Five of the eight subjects were tested in one chamber, and the other three were tested in the second chamber, complying with the previous experiments. A brief description of Chamber 1 follows, and then a description of the differences between it and Chamber 2 is provided.

Chamber 1. The secondary monitor was fixed to the stimulus panel so that it was positioned 6 cm from the top of the chamber and was centered from the sides. The secondary monitor was wired directly to the video display of a TRS-80 MIII microcomputer. The stimuli were constructed using computer graphics. Electromechanical equipment controlled the chamber operanda, and these devices were interfaced to the computer through an ALPHA 800 interface.

Three standard 2.54-cm diameter clear plastic keys were mounted in front of the video monitor so that they were 13 cm from the top of the chamber, 2 cm apart from each other, and 22 cm from the floor. The keys were connected to a sheet of plexiglass that covered the monitor. They required a force of 15 g. (0.15 N) to operate. A houselight (28V d.c., GE757) was placed at the top center of a wall adjacent to the stimulus panel. The grain magazine was 5 cm X 5 cm and was located 9 cm from the bottom of the chamber on the stimulus panel and directly below the middle response key. The chamber and monitor were housed in an insulated chamber equipped with a fan to provide ventilation and mask noise. The microcomputer collected trial-by-trial response data and averaged percent correct scores.

Chamber 2. This apparatus is almost identical to Chamber 1. The stimulus panel was slightly different: it contained an array of 7 keys. The middle three were used in this study, and the two on either side of these were taped and covered. The dimensions and placements of the keys, magazine and video monitor, and the size of the chamber and the stimulus were identical to those of Chamber 1.

Stimulus Parameters. The stimulus was a clock hand constructed of pixels, and it measured 4.5 cm X 1 cm. It was presented with these exact dimensions at a 0° position, a 90°

position and a 180° position. Seven positions, constructed at 13° increments, were presented between these 90° changes. The stimulus at these positions had "stair step" sides due to the low resolution of the computer graphics. The clock hand stimuli were presented statically for 70 ms, and were separated by 70 ms delays. By this method of presentation, the clock hand "rotated" about an axis at the center of the screen at a rate of 90° per s with the same kind of progressive change of movement used in Freyd and Finke's work (Freyd & Finke, 1984). Pigeons exhibit a wide range of perceived "apparent movement" from 2 cps to 64 cps when the object in question is apparently moving at a rate of 20 cm/s vertically, horizontally, and at angles (Siegel, 1970). They also exhibit this range of cps to rotary movement although the speed was not conveyed (Siegel, 1971). Still, 7 cps falls within the range of apparent movement by cycles described in the previous work. It should be noted here that humans who have perceived this movement describe it as "progressively moving" but not as "real".

With a completely black background, and strongly illuminated frequency gratings, pigeons' threshold for discriminating flicker is 150 cycles per s (Dodd & Wirth, 1953; Powell, 1967; Powell & Smith, 1968). Although the background was dimly illuminated in this experiment, the contrast of the stimuli was still high in the experimental chamber and the stimuli were presented at 7 cycles per second, so it is likely that the pigeons perceived these stimuli as separate flashes, not "fused" together. The test locations used in this experiment were 158°, 180°, and 202°.

Procedure

The procedure was a probe testing technique that tested specific acceleration and deceleration rates. Two questions were of interest: 1) whether positive transfer would be obtained to novel delay durations thereby verifying maintenance of the time-based characteristics of the image, and 2) whether there were patterns of errors that revealed certain characteristics of the internal model of representing movement. The specific patterns of interest were increased errors to increases in acceleration, and parallel error functions across location.

The specific deceleration/acceleration rates tested were: -30°/s^2, -10°/s^2, 44°/s^2, 80°/s^2, 184°/s^2, and 360°/s^2. The location conditions in which all of these rates were tested were: 158°, 180° and 202°. A 180° location was selected for probe testing because it was located between 158° and 202°, and so the error function to 180° would lie between the two functions shown in Figure 6 if there was a general effect of increased errors to increases in location. The rates of movement were selected so that specific areas of the functions were tested: A variety of points between 0 and 360°/s^2 to illuminate the acceleration problem and a few deceleration points to determine the shape of the functions there. Most of the rates suggested for testing had been probe-tested in the previous experiments in one of the three locations, and their points lie on one of the two functions drawn in Figure 6. The two deceleration rates were selected so that an area of the function very near constant velocity was tested. Increased error rates might be expected here since a slight deceleration is not that physically different from constant velocity. However, the preliminary error functions drawn in Figure 6 suggest that there is no confusion between constant velocity and deceleration, no matter how slight the deceleration. The only novel component of the probe trials was the delay durations, for new durations were presented in order to test the novel accelerations and decelerations during stimulus absence.

Experiment 1 consisted of training and testing phases. First, the eight subjects were trained to respond accurately to 135° and 180° training trials. Each session in training consiste of 64 trials of perceptual, imagery and violation trial types. In perceptual trials, the clock hand stimulus was present throughout the trial and could be observed as it rotated to its test location. In imagery trials, the clock hand rotated from a 0° position to a 90° position, and reappeared aft a delay at the position to which it would have rotated had it moved with constant velocity. There were two violation trials presented in training: 1) a 135° trial in which the stimulus decelerated a a rate of -90°/s^2 during the delay or was absent for 1.0 s, and 2) a 180° trial in which the stimulu accelerated 360°/s^2 during the delay, or was absent for 0.5 s. In both cases, the clock hand rotated at 90°/s from 0° to a 90° orientation, and then disappeared during a delay and reappeared at a location inconsistent with constant velocity rotation during the delay. Perceptual and imagery trials were reinforced with 3 s of access to mixed grain for left key responses indicating the stimulus moved at constant velocity, and violation trials were reinforced for right key responses indicating the stimulus did not move at constant velocity during the delay. Trial progression occurred as follows: the stimulus was presented statically at 0° for 5 seconds, then a VR-12 on the middle key of the three-key array initiated stimulus rotation, then the stimulus either rotated to the test location (perceptual trials) or rotated to a 90° orientation, disappeared for a certain delay interval, and reappeared at the test location (imagery and violation trials). Correct choice responses on the left or right key produced reinforcement, and incorrect responses were followed by a 15-s intertrial interval (ITI). After reinforcement, all trials terminated with a 15-s ITI. Only one location, either 135° or 180°, was presented per session. The training trials were displayed in Figure 1 of the introduction and are shown again here (Figure 7). Subjects remained in the training phase and alternated daily between 135° and 180° training until criterion performance, or 80 percent correct responding, was obtained for two consecutive days.

Next, probe trials at 158°, 180°, and 202° were presented infrequently within training sessions as a generalization test. Figure 8 identifies the various probe trials and the lengths of the delays presented.

Each testing session consisted of 72 trials, which included a random mix of 48 trials of 135° or 180° training and 24 trials of probes at a specific location (either 158°, 180°, or 202°). The probes consisted of six presentations each of two of the six violation trial types specified in Figure 8 for the test location, and six presentations each of the imagery and perceptual trial at that location. In other words, all the violation trial types for a specific location were not

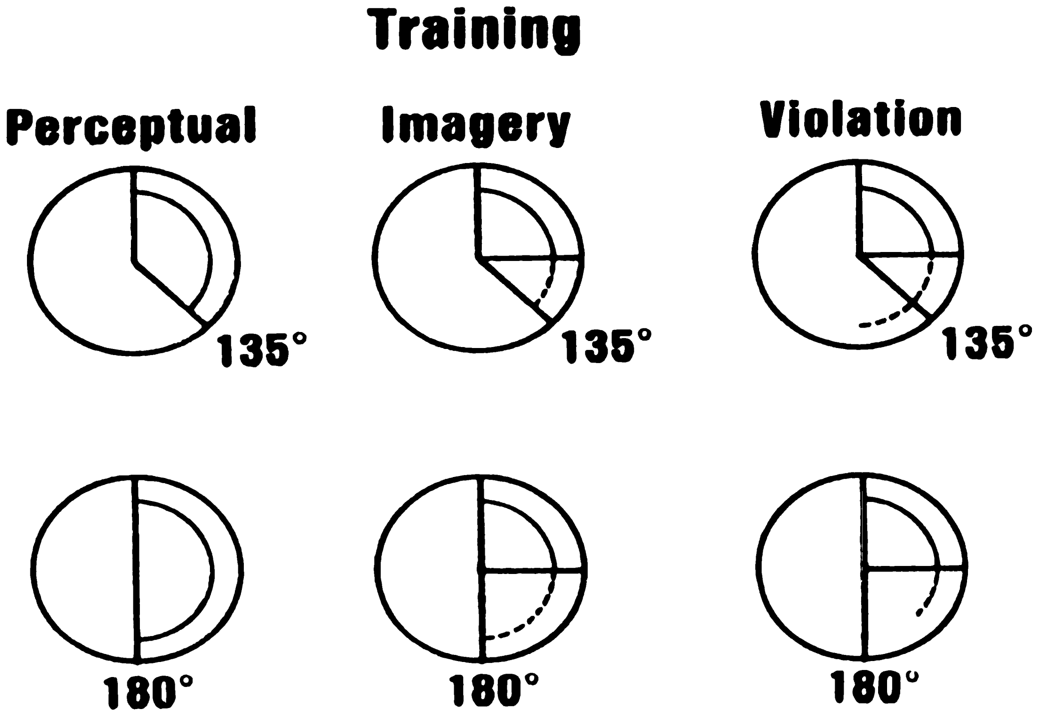


Figure 7. The training trials employed in Experiment 1. The dashed arcs indicate stimulus movement during stimulus absence. The solid arcs represent visible stimulus movement.

Locations and Delays of Imagery and Violation Trials in the Test

Test Location	Rate of Deceleration/Acceleration	Delay (in s.)
158°	$-30°/s^2$	0.89
158°	$-10°/s^2$	0.79
158°	$0°/s^2$	0.75
158°	$44°/s^2$	0.65
158°	$80°/s^2$	0.60
158°	$184°/s^2$	0.50
158°	$360°/s^2$	0.41
180°	$-30°/s^2$	1.27
180°	$-10°/s^2$	1.06
180°	$0°/s^2$	1.00
180°	$44°/s^2$	0.83
180°	$80°/s^2$	0.75
180°	$184°/s^2$	0.61
180°	$360°/s^2$	0.50
202°	$-30°/s^2$	1.76
202°	$-10°/s^2$	1.34
202°	$0°/s^2$	1.23
202°	$44°/s^2$	1.00
202°	$80°/s^2$	0.89
202°	$184°/s^2$	0.72
202°	$360°/s^2$	0.58

Figure 8. Speed changes and delay conditions of the novel violation trials.

TEST SERIES

Training Sessions	Probe Test	Violation Trials
135°	158°	-30°/s^2, 80°/s^2
180°	158°	44°/s^2, 184°/s^2
135°	158°	-10°/s^2, 44°/s^2
180°	158°	80°/s^2, 184°/s^2
135°	158°	-30°/s^2, 360°/s^2
180°	158°	-10°/s^2, 360°/s^2
135°	180°	80°/s^2, 184°/s^2
180°	180°	-30°/s^2, 80°/s^2
135°	180°	-30°/s^2, 360°/s^2
180°	180°	44°/s^2, 184°/s^2
135°	180°	-10°/s^2, 44°/s^2
180°	180°	-10°/s^2, 360°/s^2
135°	202°	44°/s^2, 184°/s^2
180°	202°	-30°/s^2, -10°/s^2
135°	202°	184°/s^2, 360°/s^2
180°	202°	44°/s^2, -30°/s^2
135°	202°	-10°/s^2, 80°/s^2
180°	202°	80°/s^2, 360°/s^2

Test Series Progression for each Subject

158, 180, 202 : # 25 & # 10
180, 202, 158 : # 2 & # 8
202, 158, 180 : # 4 & # 7
180, 158, 202 : # 9 & # 14

Figure 9. Order of testing of the violation trials.

probe-tested within a single session of training, rather only one-third of the violation trial types were tested per session. Reinforcement contingencies were the same in these trials as they were in training. Each location (158°, 180°, and 202°) was tested for six sessions. Each violatio type was presented a total of 12 times in testing. The exposure rate to violation trials was kept low to avoid any effects due to practice with these trials. Training trials were also presented within testing , and they consisted of 12 perceptual, 12 imagery, and 24 violation trials at either 135° or 180°. The sequence of testing days is outlined in Figure 9. By this plan, testing was accomplished in 18 sessions.

Results

Three hypotheses required testing: 1) whether positive transfer to the novel test trials was obtained, 2) whether errors to the test trials showed a systematic relationship with accelerations and decelerations, and 3) whether the errors to the test trials plotted for each location condition were parallel. An analysis of the shape of error functions (#2) reveals more about the acceleration biases inherent in movement representation in pigeons. Evidence of parallelism (#3) implies that "mental rotation" is involved, insofar as errors increase with increases in represented space through which transformations must occur. And, transfer (#1) is the more general result sought to determine if an imagery strategy is successfully applied to novel cases. Positive transfer is obtained if there are no differences between response accuracy to novel and to trained examples. No transfer is obtained if chance responding is observed to the novel examples.

Test of Transfer

A two-factor repeated measures analysis of variance (ANOVA) was conducted to compare percent correct scores across location (trained 135° and 180° trials, and test 158°, 180° and 202° trials) and across trial type (perceptual, imagery and violation trials). Data ente were mean percent correct scores for each subject collapsed across test sessions for perceptual, imagery and violation trials at each trained and test location. Scores to the various violation test trials were collapsed into one violation score for each subject at each test location. If the subjects responded to the novel violation trials introduced in this experiment with the same proficiency as they did the trained trials, then the prediction is a lack of significance to trial types and to location, as well as nonsignificant effects of their interactions. An imagery strategy predicts complete positive transfer, or consistently accurate responding, across familiar and novel examples.

Table 1 shows the results of the ANOVA. Significant differences in percent correct scores were obtained to location ($F_{4, 105} = 7.368$) and to trial type ($F_{2,105} = 117.5$) as well as to the interaction between the two ($F_{8, 105} = 3.405$). The significant trial type effect was a result of highly accurate performance to perceptual trials (mean = 93.97) as compared to imagery (mean = 71.156) and violation (mean = 62.372) trials. The difference between imagery and violation trials was not significant by a Tukey comparison (Q imagery-violation = 2.79, $p > 0.05$) but the difference between perceptual and imagery and violation trials was significant (Q perceptual-imagery = 7.25, $p < 0.05$; Q perceptual-violation = 10.051, $p < 0.05$). Since the significant effect was caused by more accurate responding, not less, it is not regarded as evidence against the imagery hypothesis. Average performance across all trial types was accurate. This is the relevant result, for if response accuracy to imagery and violation trials is still above chance, then the subjects have shown the minimum necessary performance to entertain the imagery hypothesis.

The significant difference found to location and to the interaction between location and trial type implies that transfer was not obtained from training to testing. However these difference results are not conclusive, for they could be a result of significant variation within the test locations and trial types or within the trained locations and trial types, and not between the two (i.e., between trained and test examples). To determine whether performance to test trials

Table 1. Analysis of Variance of Percent Correct Scores to Trained and Test Conditions.

SOURCE	DF	Sums of Squares	Mean Square	F-test	P value
Location	4	2330.304	582.576	7.368	0.0001
Trial Type	2	18589.801	9294.901	117.551	0.0001
L X TT	8	2154.069	269.259	3.405	0.0016
Error	105	8302.497	79.071		

Tukey Tests: Perceptual, Imagery and Violation Trained and Test Conditions

Trial Type	Comparison	Q value (=4.039,table)	Significance
Perceptual	180TR - 158	0.02767	not significant
	180TR - 180	0.02735	not significant
	180TR - 202	1.02134	not significant
	135TR - 158	-0.3403	not significant
	135TR - 180	-0.3406	not significant
	135TR - 202	0.653	not significant
Imagery	180TR - 158	3.516	not significant
	180TR - 180	0.865	not significant
	180TR - 202	2.3149	not significant
	135TR - 158	4.443	significant at $p < 0.05$
	135TR - 180	1.793	not significant
	135TR - 202	1.387	not significant
Violation	180TR - 158	2.6477	not significant
	180TR - 180	0.0229	not significant
	180TR - 202	2.543	not significant
	135TR - 158	1.454	not significant
	135TR - 180	3.124	not significant
	135TR - 202	6.645	significant at $p < 0.01$

was significantly lower than performance to training trials, a series of Tukey tests were conducted (bottom panel, Table 1). In these, comparisons were made between average percent correct scores to trained (135° and 180°) and test (158°, 180° and 202°) locations withi each trial type. For example, performance to trained 135° imagery trials was compared to performance to test imagery trials (i.e., 158°, 180° and 202° imagery trials). Altogether, 18 comparisons were necessary, and the results are displayed in Table 1.

There were no significant differences in response accuracy to trained and tested perceptual trials, as one would expect even without an imagery strategy in use. There was only one significant difference found in response accuracy between trained and tested imagery trials, but this difference indicated *more* accurate responding to the 158° imagery test trials than to trained trials, not less. In other words, positive and complete transfer was observed between trained and test perceptual and imagery trials. This is not surprising since these trials were tested before and positive transfer was obtained.

The critical test was whether response accuracy was significantly less to test violation trials (that introduced novel delays) than to trained violation trials. It is apparent that for the three locations tested, there was only one significant differences in response accuracy between trained and test violations. Average response accuracy to 202° violation trials was significantly less than that to 135° violation trials. However, positive transfer was evident to 202° violations well, as response accuracy to these was not distinguishable from response accuracy to trained 180° violations. Proof of transfer, that accuracy was maintained from training to testing, was t great degree obtained to the violation trials, since 5 of the 6 relevant comparisons produced nonsignificant differences.

An Examination of Error Patterns by ANOVA

Subjects demonstrated fairly accurate average response accuracy to the novel violation trials, and their estimation strategy could accommodate the new delays fairly well. However, specific test violation trials were met with increased errors, and a closer examination of these increases might reveal a quality of the representation of movement. Another ANOVA was conducted in which errors to imagery and violation test trials were compared directly, and as a function of location. The ANOVA was a three-way repeated measures ANOVA examining errors to each tested trial type (6 violations and 1 imagery),to the order of testing (n=4) and to each tested location (158°, 180° and 202°).

Table 2 presents the relevant statistics. Two main effects were statistically significant in the ANOVA: a significant difference between error scores to the various trial types tested ($F_{6,28} = 7.687$, $p < 0.0001$) and a significant difference between error scores to the three locations ($F_{2,56} = 9.035$, $p < 0.0004$). The order of testing effect, as well as all interactions between speed, order and location were not significant.

Figure 10 shows the error functions plotted for the imagery and violation trials at each location, and Table 3 presents the means and standard errors for each point. It seems apparent that the functions linearly increase as a function of increases in acceleration during the delay. And it is also suggested that the functions are parallel, both because they appear parallel in the graph and also because there was no interaction obtained between speed and location in the ANOVA. Certainly, a lack of interaction does not prove that the functions are parallel, but further regression analysies are employed to determine this.

The significant effects found in the ANOVA indicate that the tested aberrations in movement caused significant changes in the subjects' responding. Since it is clear that response accuracy was affected both by novel violation conditions as well as by the location of the test stimulus, a closer look at the shape and relationship of the error rates plotted as a function of these variables is necessary. Gained by this pursuit is a fuller description of the representation of movement as it changes over time and distance.

Linearity of Functions

A few characteristics are obvious from the graph of mean errors (collapsed across subjects) plotted in Figure 10: 1) the functions appear to be parallel with respect to location

Table 2. Three-Way Analysis of Variance with Repeated Measures
Trial Types (speed) X Order of Testing X Location Condition

Source	df:	Sum of Squares:	Mean Square:	F-test:	p-value:
Speed	6	34035.669	5672.612	7.687	0.0001*****
Order	3	1482.661	494.220	0.670	0.5778
Speed X Order	18	15911.061	883.948	1.198	0.3258
Subjects Within Groups	28	2662.187	737.935		
Location (repeated measure)	2	14095.342	7047.671	9.035	0.0004*****
Location X Speed	12	6312.846	526.070	0.674	0.7683
Location X Order	6	1915.538	319.256	0.409	0.8698
Location X Speed X Order	36	25713.200	714.256	0.916	0.6053
Location X Subjects W/in Groups	56	43683.909	780.070		
Total	Σ=167 (n-1)				

Calculated Degrees of Freedom:

Speed: 6 violations + 1 imagery = 7 (n-1 = 6)
Order: 4 orders (n-1 = 3)
Speed X Order: 6*3 = 18
Subjects Within (7 speeds * 4 orders = 28)
Location : 3 locations (n-1 = 2)
Location X Speed: 6 * 2 = 12
Location X Order: 3 * 2 = 6
Location X Speed X Order: 6 * 3 * 2 = 36
Subjects Within : 8 subjects * 7 speeds * 3 locations = 168.
For repeated measures, divide Within by repeated measure: 168 / 3 = 56.

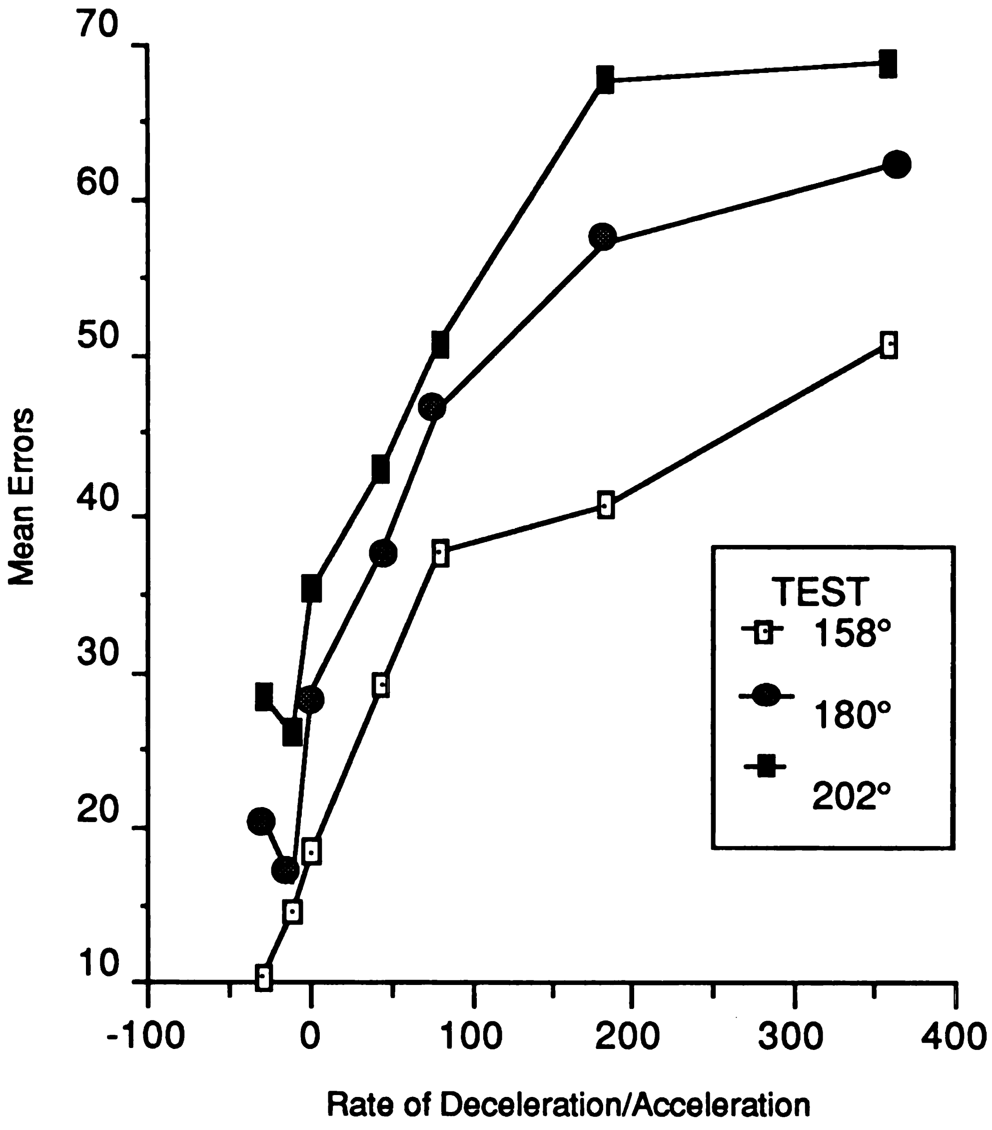


Figure 10. Mean errors plotted for imagery trials (acceleration = 0) and for violation trials (all others) for each location tested.

Table 3. Mean Errors and Standard Deviations to Speed Conditions at Each Location

Location	Speed	Count:	Mean:	Standard Deviation	Standard Error
158°	-30	16	10.416	13.437	3.359
	-10	16	14.583	21.837	5.459
	0	48	18.403	16.213	2.34
	44	16	29.167	23.96	5.99
	80	16	37.5	16.667	4.167
	184	16	40.625	27.195	6.799
	360	16	51.042	22.335	5.584
180°	-30	16	20.833	22.361	5.59
	-10	16	16.667	13.608	3.402
	0	48	28.819	19.369	2.796
	44	16	37.5	14.272	3.568
	80	16	46.875	16.351	4.088
	184	16	57.292	17.18	4.295
	360	16	62.222	36.983	9.549
202°	-30	16	28.125	18.972	4.743
	-10	16	26.042	17.18	4.295
	0	48	35.069	16.574	2.392
	44	16	42.708	21.055	5.264
	80	16	51.042	16.632	4.158
	184	16	67.708	23.936	5.984
	360	16	68.75	29.737	7.434

condition with the farthest orientation (202°) producing the greatest amount of errors, and 2) each function seems to increase as a function of increases in acceleration, with a flattening of each function occurring at higher rates of acceleration. These error functions were tested for linearity and curvilinearity by simple and polynomial regression analyses, and then for parallelism by a multiple regression analysis.

Figures 11a, 11b, and 11c display the best-fitting regression lines for each location tested, as well as the polynomial equations and correlations. Quadratic functions best fit the data for all three location conditions, even though the data for the 180° and 202° conditions appear in Figure 10 to be cubic (i.e., because of the curves at both ends of the functions).

Table 4 reveals the statistics of the trend analysis from which quadratic equations were selected as best-fitting. The test of each location condition spanned simple regression ($y=a+ßx$) to third-order or cubic regression ($y=a+ßx + ß_1x^2 + ß_2x^3$). The correlations of each function (r) are 0.55, 0.585, and 0.602, respectively. The R^2 terms which indicate the amount of variance accounted for by the functions remain between 30 and 36 percent. Although this is acceptable for regression analysis, it should be noted here that the R^2 terms are being held artificially low because both within- and between-subject variances were combined as error variance in these analyses. (The alternative was to enter means for each subject for each violation condition, but then within-subject variance would be completely ignored by this analysis.)

There was an insignificant increase of less than 1 percent of the variance gained from quadratic to cubic functions (which is probably due to the change of the statistics alone), but there was a gain of as much as 5 percent of the variance from linear to quadratic, indicating that quadratic functions might better fit the data. In addition, partial-F tests which examine the independent effects of the coefficients of "x" in the equations indicated that quadratic functions best fit the data, for the partial-F scores in the quadratic equations were highly significant while they were not for cubic equations (see Table 5). Statistical evaluation of the R^2

Figures 11 (a - c). Mean errors plotted for imagery and violation trials for each location condition, and the best-fitting regression line for each.

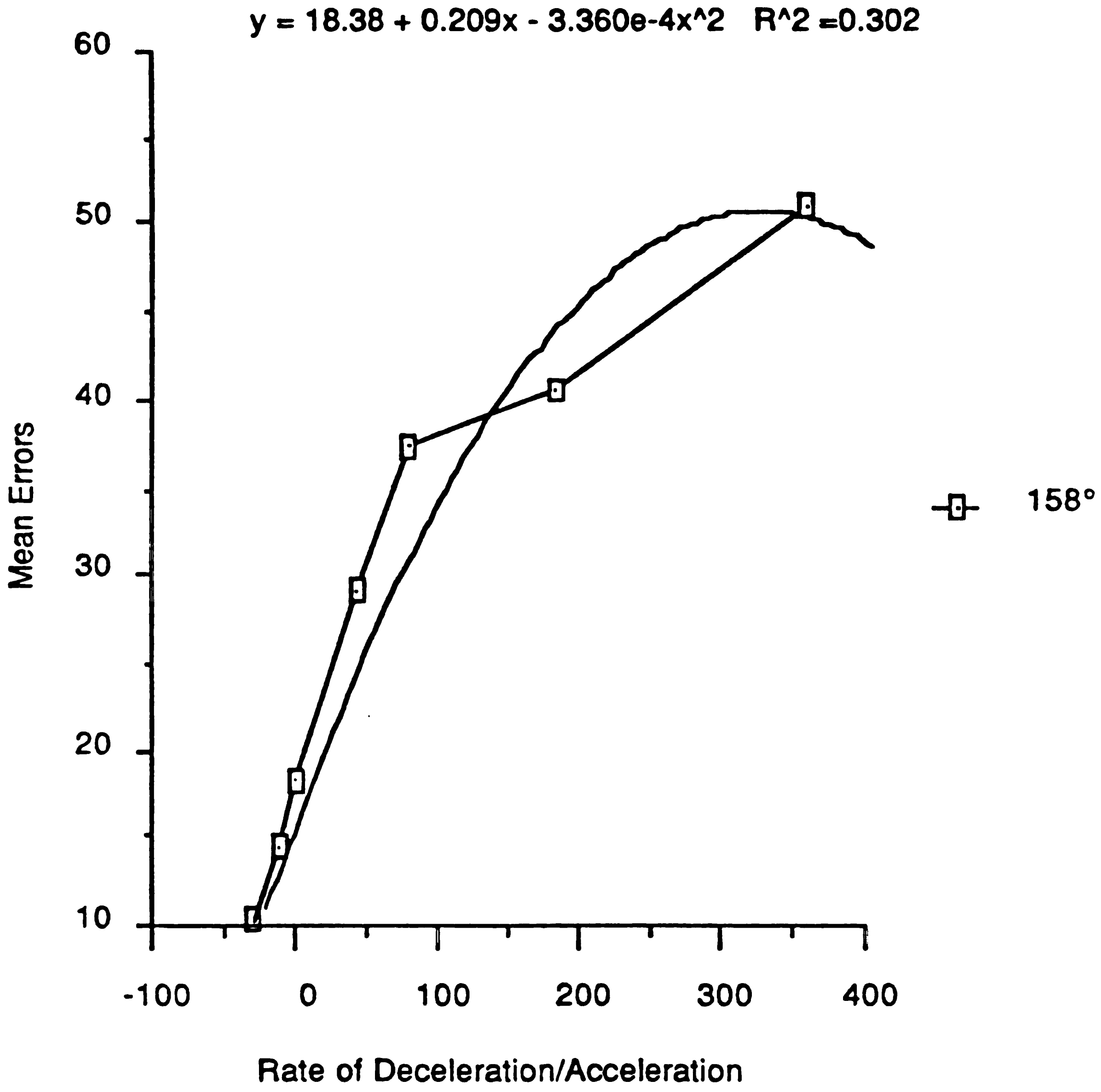


Figure 11a. Mean errors and the best-fitting regression line for the 158° test.

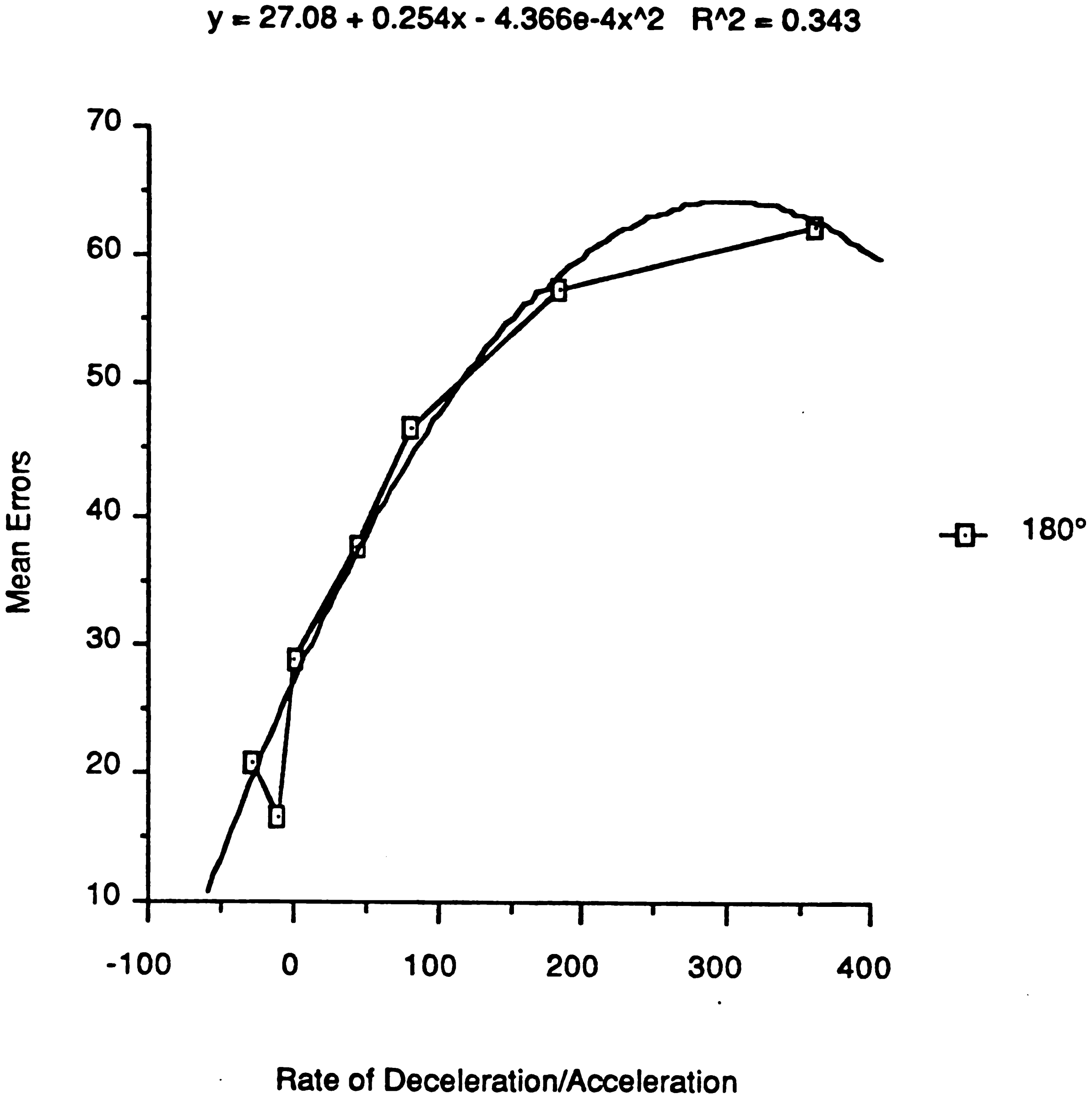


Figure 11b. Mean errors and the best-fitting regression line for the 180° test.

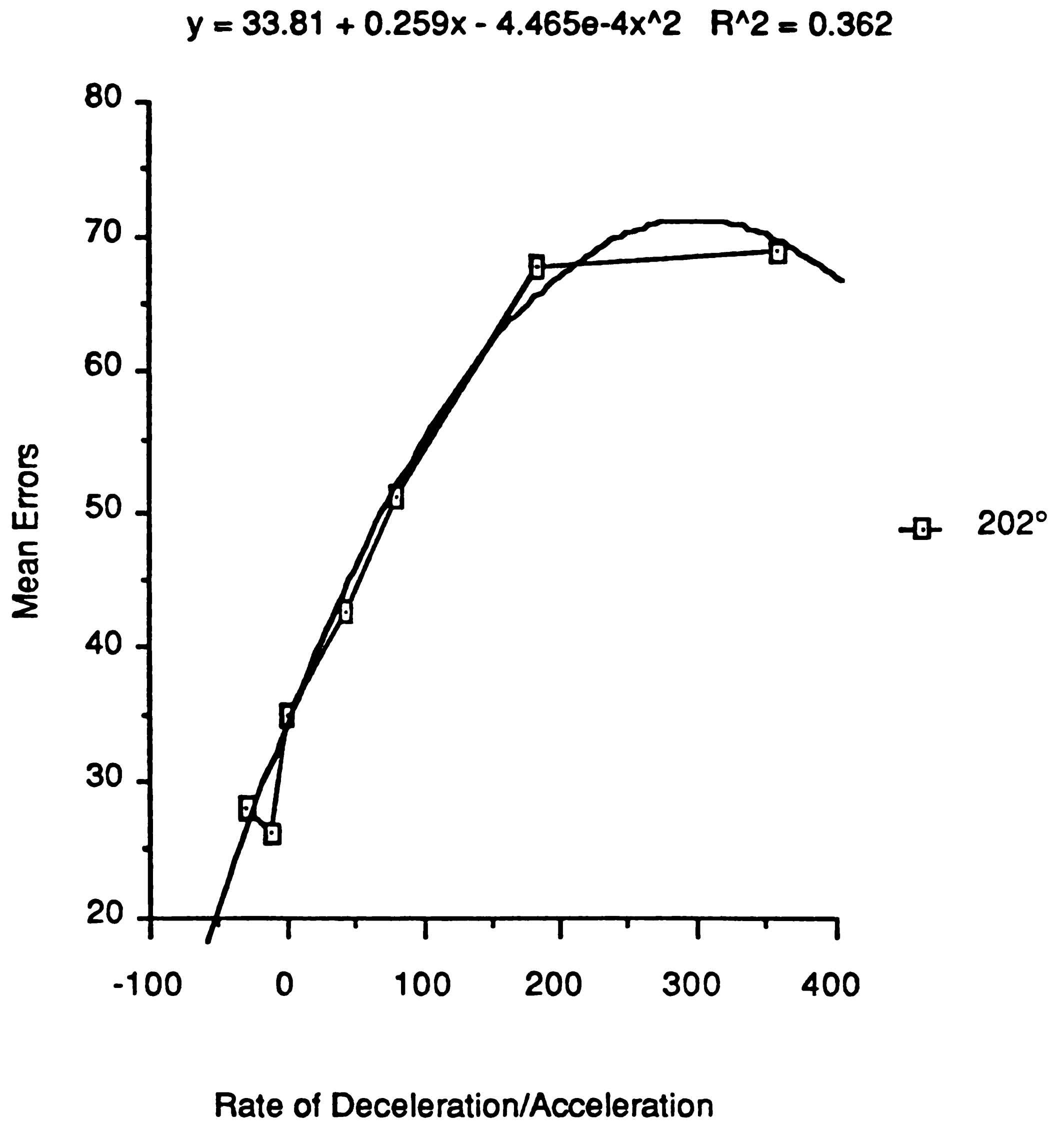


Figure 11c. Mean errors and the best-fitting regression line for the 202° test.

Table 4. Regression Analyses for Each Location

Location	Trend	R	R^2	F-test	x	x^2	x^3	y-intercept
158°	linear	0.52	0.27	52.524***	0.101			19.45
	quadratic	0.55	0.30	30.507***	0.209	-0.000336		18.38
	cubic	0.56	0.31	21.063***	0.303	-0.001	.000002	18.94
180°	linear	0.54	0.29	59.837***	0.114			28.476
	quadratic	0.58	0.34	36.746***	0.254	-0.000436		27.081
	cubic	0.59	0.34	24.415***	0.285	-0.001	7.345e-7	27.266
202°	linear	0.56	0.31	64.515***	0.115			35.235
	quadratic	0.60	0.36	40.088***	0.259	-0.000446		33.808
	cubic	0.60	0.36	26.654***	0.225	-0.0000006	7.96e-7	33.607

*** $p < 0.0001$.

Table 5. Partial F- tests of the Correlation Coefficients

Location	Trend	x	x^2	x^3	$F_p(x)$	$F_p(x^2)$	$F_p(x^3)$
180°	linear	0.101			52.524***		
	quadratic	0.209	-0.000336		21.973***	6.467**	
	cubic	0.303	-0.001	.000002	13.469***	3.076~	1.821 n.s.
180°	linear	0.114			59.837***		
	quadratic	0.254	-0.000436		29.627***	9.904***	
	cubic	0.285	-0.001	7.345e-7	10.767***	0.881 n.s.	0.179 n.s.
202°	linear	0.115			64.515***		
	quadratic	0.259	-0.000446		32.716***	11.081***	
	cubic	0.225	-0.0000006	7.96e-7	7.151*~	0.007 n.s.	0.225 n.s.

*** $p < 0.001$
** $p < 0.005$
*~ $p < 0.01$
~ $p = 0.05$

terms and of the partial-F tests support the observation that quadratic functions best fit the data.

An F-test at each location (shown in Table 4) was conducted to determine if a large and significant portion of the variance of error scores (y) was explained by regression on speed (x). In each test, the F-score obtained was significant at the 0.0001 level. These F-tests indicate that for each regression, the predicted slope was significantly different from 0, and was positively increasing.

In summary, the regression analysis for each function and the F-tests of each support the hypothesis that the error functions increased with respect to increases in acceleration. Because quadratic functions best fit the data, the interpretation is that there is a decline in the rate at which errors increase at the higher rates of acceleration tested.

Test of Parallelism by Multiple Regression

A closer review of the three best-fitting regression equations reveals the parallel nature of these functions. They are:

$y = 18.38 + 0.209x + -0.000336x^2$ for 158°,

$y = 27.08 + 0.254x + -0.000436x^2$ for 180°, and

$y = 33.81 + 0.259x + -0.000446x^2$ for 202°.

The coefficients of x (speed) describe the slope of these functions and they are virtually identical (0.209, 0.254 and 0.259) and are not significantly different by a Tukey-Kramer test of coefficients (Sokal & Rohlf, 1981). In addition, the coefficients of x^2 (speed ^{2}) describe the curvature of the functions, and these coefficients are also almost identical (-0.000336, -0.000436, and -0.000446) and are not significantly different by the Tukey-Kramer test. In short, the functions are virtually the same, with the important exception of the y-intercept. The y-intercept values increase as the location of testing increases. By plotting 95% confidence intervals around each y-intercept as a function of its standard error, it was determined that none of the confidence intervals overlapped, and even the highest value of each interval did not overlap with the lowest value of the next successive y-intercept as a function of increased location. The confidence intervals were as follows: for 158°, 18.403 +/- 4.167; for 180°, 28.819 +/- 2.796; and for 202°, 35.069 +/- 2.392. The y-intercepts were distinctly different from each other. From these observations, the functions seem parallel and separate.

To statistically evaluate the parallel nature of these functions, a nonforced stepwise multiple regression was conducted. The following equation was entered into the analysis:

$$y = a + \beta_0 x_1 + \beta_1 x_1^2 + \beta_2 x_2 + \beta_3 x_1 x_2 + \beta_4 x_1^2 x_2$$

where a = y-intercept, β_i = beta- coefficient,

x_1 = speed (testing for linearity of the functions while ignoring location),

x_1^2 = speed^2 (testing curvilinearity, ignoring location),

x_2 = location (testing linearity by location, ignoring changes in speed),

x_1x_2 = speed * location (testing parallel linearity), and

$x_1^2x_2$ = speed^2 * location (testing the parallel quadratic nature of the functions).

A nonforced stepwise regression was employed so that those variables of this set of five that account for most of the variance would be selected in combination, while the others would be ignored. Order of variable entry is not manipulable in a nonforced stepwise regression, for the test selects the variables to enter on the basis of the amount of variance accounted for or gained by the variables.

The equation produced by the multiple regression that best fit these functions was:

$$y = 1.089 + 0.284x_2 + 0.0003x_1x_2 + -0.0000004436x_1^2x_2$$

where x_2 = location,

x_1x_2 = speed * location, (parallel linearity) and

$x_1{}^2x_2$ = speed^2*location (parallel curvilinearity).

The R^2 term for this equation was 0.379, and the partial- F test for each ß-coefficient was highly significant (see Appendix A for details). The variable first selected that accounted for most of the variance in the three functions was x_1x_2, or the variable accounting for parallelism of the linear functions ($R^2 = 0.295$). The second variable selected was location ($R^2 = 0.339$), and the third variable, $x_1{}^2x_2$, was the variable accounting for parallelism of the quadratic functions ($R^2 = 0.379$). The variance accounted for by speed (x_1) and by speed^2 ($x_1{}^2$), after taking all functions into consideration and parcelling out the effects of the other three variables, was minimal and nonsignificant by partial-F tests (see Appendix A for details). In short, the functions are clearly parallel.

Discussion and Interpretations

In this experiment, novel delays were presented in violation trials in order to determine if time-based characteristics such as rate were represented as an analog perceptual characteristic of movement. A basic quality of an image is that it maintains the physical structure of the entity that it represents. In this case, timing, or rate of change, was tested as a critical structure in the image. The tested violation trials were met with approximately the same level of percentage of correct responses as were the trained trials, as confirmed by an analysis of variance of the percent correct scores. The conclusion from this analysis was that subjects' acquired cognitive strategy for estimating movement could not be perfectly applied to these novel conditions, but it was applied well enough for a general result of positive transfer to occur. Percent correct scores did vary widely within the tested violation trials, indicating that the representational process was not finely tuned to subtle changes in rate during the delay. So, the characteristic of movement representation responsible for the significant response changes was sought. Errors, i.e., failures to discriminate, have been used to infer the nature of the psychological dimensions along which objects or events are perceived to vary (Treisman, 1986). The goal of the analysis of errors in this experiment was to reveal the nature of the psychological dimensions along which objects and events are represented as varying.

One characteristic of movement represention identified from pilot testing that resulted in response changes was a linear relationship between errors as a function of increases in the acceleration during the delay. The relationship, when fully described and analyzed in this experiment, is quadratic: Errors increase with increases in speed, but the amount of increase decreases at the higher speed conditions tested. Once errors exceed 50 percent over all responses, the functions start to flatten. There is no indication in these analyses that the functions eventually drop back down, forming an inverted-U. Since this was not indicated, the inference that subjects confuse acceleration with constant velocity until some critical accceleration rate is met and then they discriminate more accurately again remains unsupported. Curiously, the data indicate that pigeons confusion of acceleration with constant velocity increases with increases in acceleration until it reaches its limit (somewhere between 70 and 100 percent)! If this were the case, it is hard to believe that the pigeon would have survived flight, or could have survived predators (i.e., incoming hawks). This strategy does not harness the sensitivity of the highly developed movement detection system in the pigeon's visual cortex either (Granda & Maxwell, 1979).

It is clear in this study that high rates of acceleration produced inaccurate responding. What is implied in the data is that the higher rates of acceleration produced so much inaccuracy that subjects abandoned their trained discrimination altogether. The explanation that fits the data is that in the case of very short delays indicating fast accelerations (i.e., $>50°/s^2$), pigeons simply responded on the left key (the constant velocity key) . In fact, as acceleration is increased, the tendency to respond by this simple discrimination appeared to increase, producing an increasing function of errors to increases in acceleration. This makes intuitive sense if subjects were following a strategy such as this: if there is no delay (or a very short delay), respond on the constant velocity key.

While the explanation regarding a change in the pigeons' strategy to a simpler discrimination accounts for the general shape of the functions, it does not sufficiently account for error rates to accelerations depicted early in each function (i.e., to accelerations less than 44°/s^2), for in these subjects are responding <u>most often</u> to the right key to increases in acceleration. At this level, it seems that subjects are using the strategy trained, and that was to discriminate constant velocity (left key responses) from aberrations from constant velocity (deceleration OR acceleration, right key responses). Even with an acceleration of 44°/s^2, subjects still respond on the right key 70 percent of the time in the 158° condition, 64 percent of the time in the 180° condition, and 57 percent of the time in the 202° condition.

The shape of the functions in this area of speeds indicates that subjects tend to confuse acceleration with constant velocity more often than they confuse it with deceleration. There is an asymmetric distribution of errors around constant velocity with more errors to acceleration than to deceleration. This distribution could be normalized if some acceleration constant (of between 10°/s^2 to 30°/s^2) were applied to the data . With an adjustment of an acceleration constant, all represented movement is increased, making true deceleration seem exaggerated and true acceleration seem more like "constant velocity" which is represented as increasing. This kind of adjustment would make deceleration discriminations quite easy, even for slight aberrations from constant velocity (i.e., -10°) but it would make acceleration discriminations more difficult.

But this kind of adjustment would also make representations of true constant velocity nonveridical, because the appropriate orientation at which the stimulus appears on imagery trials should appear late. In other words, if acceleration resembles represented constant velocity, then the test locations of imagery trials imply a slight deceleration. Why subjects respond to these trials as if the stimulus moved at constant velocity is not explained by the acceleration constant notion.

Another explanation is that there is a category of "constant velocity" with some accelerations lying within its boundaries. If an acceleration constant is psychologically applied to movement represented, then some decelerations lie within these boundaries as well -- because with an acceleration constant applied, real constant velocity appears as a slight deceleration. The psychological boundaries that define deceleration seem more distinctive than those defining acceleration, for in no case was a true deceleration confused with constant velocity, but in many cases, a true acceleration was confused with constant velocity.

To large increases in accelerations, subjects abandon the estimation strategy and respond more often on the left key (and incorrectly) to greater increases in acceleration. This strategy is a simple generalization in response to very short delay and no delay conditions. A model which describes subjects' overall strategy in this experiment is twofold: a constant velocity-aberrations discrimination with a tendency to confuse acceleration with constant velocity is applied in the tested area around 0 acceleration, and a simple delay discrimination is used in the area testing greatly increased accelerations ($>50°/s^2$).

A constraint on the representational process of accelerations has been identified. It should be noted here that the error results do not necessarily imply that an image was used, for a category for constant velocity could exist out of context of imagery. However, other behavioral evidence of "mental rotation" further strengthens the argument that imagery is employed in the task.

Cooper and Shepard (1973), Metzler and Shepard (1974), and Shepard (1975) have viewed the process of mental rotation as an internal analog of the process that occurs when the rotation of an external object is perceived. They reported as evidence of mental rotation that the time required by human subjects to determine whether two visual stimuli are the same in shape or mirror images increases linearly with increases in the angular difference between the orientations of the visual stimuli. Hollard and Delius (1982) reported that reaction times of pigeons in the same task do not increase with increases in angular difference, rather they remain the same across the tested orientations. They concluded that pigeons may not use a strategy like mental rotation to evaluate the location of a represented stimulus, but that pigeons have some parallel processing strategy for making such estimations that does not involve step-wise internal processing. There are problems with the conclusions of this study, due in part to the fact that reaction time has not been extensively collected and accepted as a dependent variable reflecting cognitive processing in pigeons (Herrnstein, 1985), and in part because the design of the experiment assumed tacit knowledge of static rotations of stimuli with which their subjects may not have been equipped. It should also be noted that Cerella (1987) could not obtain evidence of rotational invariance in pigeons at all, nor has Herrnstein (see Cerella, 1987), and Hollard and Delius's results are currently being disputed.

The experiment reported here displays simulated rotations of stimuli, and requires subjects to extrapolate the location of the rotating stimulus in its absence to accomplish the task. Increases in angular difference, the variable of interest in Shepard and his colleagues' studies as well as in Hollard and Delius 's (1982) and Cerella 's studies (1987), was manipulated here by changing the test location to which subjects must extrapolate rotation from 158° to 180°, and to 202°. The dependent variable which was systematically affected by changes in angular difference was subjects' errors. The test of parallelism of the error data indicates that some constant error rate is added to error functions as the test location is moved from 158° to 202°. Note that this error increase is not a result of increases in the length of time during whicl subjects must transform the stimulus from 90° to the test location, for the delays used were roughly counterbalanced across location conditions. Rather the error increase is a result of an increase in the distance through which subjects must transform the stimulus, irrespective of time for processing. This result provides indirect evidence of mental rotation in pigeons: for if pigeons are mentally rotating the stimuli during stimulus absence, then the farther they must rotate the stimuli, the more errors they make.

The evidence of "mental rotation" provided by the significant test of parallelism further strengthens the argument that imagery is the mechanism used in extrapolating the trajectory of movement in this task. Such evidence clearly indicates that distance is being represented, and that the process of estimating stimulus location requires analog transformations through which increased errors are made with increases in space for transformations. This evidence supports the conclusion made by Hollard & Delius (1982) that pigeons do have the capacity for rotational transformations, and it refutes the conclusions drawn by Cerella and others (Cerella, 1987; Herrnstein,1985) that rotational transformations are not possible by pigeons. Rotational transformations are obtained if pigeons are trained to recognize rotated versions of stimuli as rotated, and evidence of mental rotation as a process (not obtained by Hollard and Delius, 1982) is possible if errors are the variable of interest.

Experiment Two:

The Effects of Changes in Velocity on the Representational Process

The task of the second experiment was to further test the notion that imagery is the controlling process for movement estimation, and to examine other possible constraints of the representational process. In this experiment, the speed of visible stimulus rotation was manipulated. Accurate responding to these novel movement conditions demonstrates that the representational process has considerable plasticity, in that it can be applied to different speeds. It has already been demonstrated that transfer from trained trials to test trials was , in general, positive to different delays (Experiment 1, this plan of study) and to different locations (Experiments 1, 2 and 3 of the introduction). However, errors occurred within testing in Experiment 1 that revealed a constraint of accurate representation of time and a constraint on representing movement through farther distances of represented space. As in Experiment 1, imagery is investigated here by a test of transfer from a trained speed to novel speeds, and the internal model of movement representation is investigated here by an examination of error patterns to the tested speeds.

The imagery hypothesis assumes a dynamic representation of movement during stimulus absence. An imagery strategy predicts positive transfer from training to the test cases in which faster or slower perceptual displays of movement are presented. Alternatively, a timing strategy would not result in positive transfer to the novel movement conditions. The experiment was designed so that a timing strategy based on terminal counts associated with specific locations predicts negative transfer, or would result in below chance responding to the novel movement conditions. The assumption underlying the description of imagery in this paper is that an imagery process applies perceptual information about movement during stimulus absence. Using this strategy, transfer to the novel movement conditions should be positive, or there should be rapid acquisition.

Method

Subjects

The eight subjects from Experiment 1 participated in this experiment. They were maintained under the same conditions as were described in Experiment 1.

Apparatus

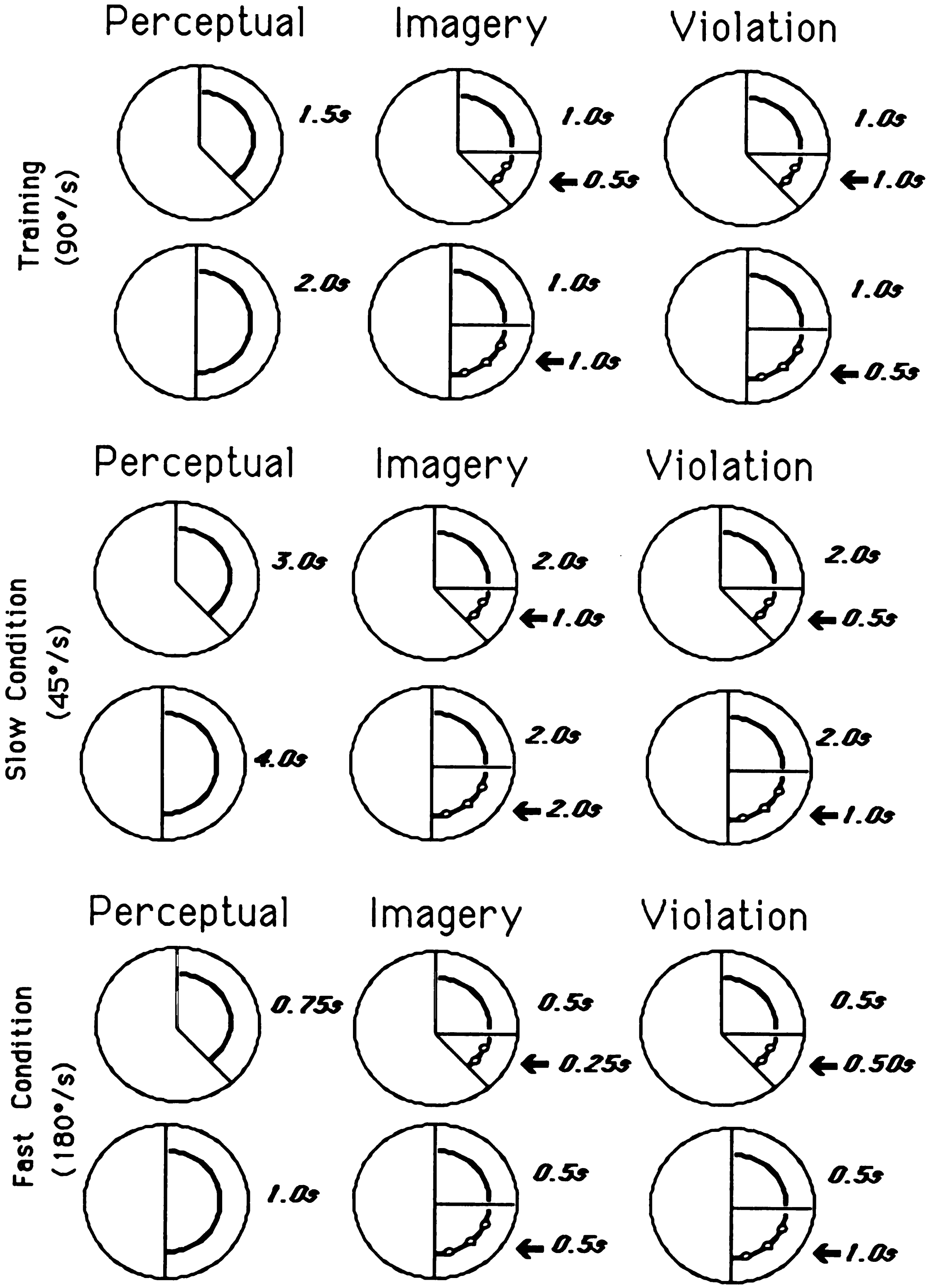
The same two chambers described in Experiment 1 were used in this experiment.

Procedure

The procedure of this experiment was to probe-test new fast and slow velocity conditions within standard training sessions. The procedure was the same as had been employed in all of the experiments: first, subjects were trained to respond accurately to 135° and 180° location conditions, and then novel trials were presented infrequently within these training sessions and response accuracy to the novel trials was noted. The novel trials introduced two new rates of constant velocity, 45°/s and 180°/s, in the familiar 135° and 180° conditions.

Figure 12 depicts the trial types employed in Experiment 2. The top panel of this figure shows the 135° and the 180° trials presented in training. The delays printed to the right of each stimulus represent the time it took the stimulus to be rotated. The delays with arrows represent the times during which the stimulus was absent. In training, the stimulus rotated at a rate of 90°/s, and so it took 1.5s for the stimulus to be rotated from 0° to 135° and it took 2.0s for the stimulus to be rotated from 0° to 180°. Imagery trials used the same durations of time to prese movement as did the perceptual trials. The only difference was that in imagery trials, the stimulus rotated to a 90° orientation in 1.0 s, and disappeared for the remainder of the time it took it to reach its final destination (another 0.5s for 135° and another 1.0s for 180°). In the violation trials, the durations of delays during which the stimulus was absent violated the constant velocity conditions maintained in these trial types. For example, in the 135° violation trial, the stimulus disappeared for 1.0 s and then reappeared at 135° instead of at 180°. The tria progression for these types was the same as that described in Experiment 1, and right key responses were reinforced in violation trials, while left key responses were reinforced in perceptual and imagery trials. Locations for training (135° and 180°) were alternated daily. Eac session consisted of 64 trials, including 16 perceptual, 16 imagery and 32 violation trials, to insure that equal amounts of right key and left key responses were required per session.

Figure 12. Training and test trials employed in speed testing in Experiment 2.


Perceptual
Imagery
Violation
Training (90°/s)
1.5s
1.0s
← 0.5s
1.0s
← 1.0s
2.0s
1.0s
← 1.0s
1.0s
← 0.5s
Perceptual
Imagery
Violation
Slow Condition (45°/s)
3.0s
2.0s
← 1.0s
2.0s
← 0.5s
4.0s
2.0s
← 2.0s
2.0s
← 1.0s
Perceptual
Imagery
Violation
Fast Condition (180°/s)
0.75s
0.5s
← 0.25s
0.5s
← 0.50s
1.0s
0.5s
← 0.5s
0.5s
← 1.0s

Once subjects responded with 80 percent accuracy to both 135° and 180° training trials, the slow and fast conditions were introduced within training sessions. One location was presented per day, so 135° slow or fast trials were presented as probes only within 135° trainin sessions, while 180° slow or fast trials were probed only within 180° training sessions. This constraint on testing allowed for the manipulation of one specific variable: speed of rotation.

Probe-testing was accomplished in blocks of testing sessions. The slow and fast conditions at 135° and 180° were tested within training sessions for 12 sessions each. In these blocks of testing, 135° training and 180° training sessions were alternated daily, just as in training. Slow test trials at 135° and 180° were introduced within their respective training sessions. The middle panel of Figure 12 displays the slow trials at 135° and 180°. In these, the rate of movement was 45°/s. It took 3.0 s for the stimulus to be rotated to 135° at this speed, and it took 4.0 s for it to be rotated to 180°. Again, the imagery trials supported the constant velocity condition of 45°/s movement by presenting the appropriate delays for movement to these two locations. But in the violation trials, the stimulus was absent for a period of time that was too short for it to be rotated constantly and for it to reach its final destination. In both violation trial types in the slow condition, the stimulus actually increased its speed during the delay, or moved at 90°/s instead of 45°/s during the delay.

Note also that the delays used in the slow condition trials provided counterbalancing for the response-delay associations acquired in training. For example, the delay presented while the stimulus was absent in the 135° imagery training trial was 0.5 s, and a left key response was required for reinforcement. In the test for the slow condition, a 0.5 s delay was presented while the stimulus was absent in the 135° violation trial. The test locations in both trials were exactly the same (135°) and the delays during which the stimulus was absent were the same (0.5 s), but the 135° imagery training trial provided reinforcement for left key responses and the 135° slow condition violation trial provided reinforcement for right key responses. The critical difference in the two trials was that the initial movement presented between 0 and 90° in the first case was 90°/s and in the second case was 45°/s, and because of this difference, the trial require opposite choice responses for reinforcement. If subjects applied a strategy timed to a 90°/s speed of rotation directly and ignored the speed of initial rotation in the new movement condition, then they would respond incorrectly to the imagery and violation trials at 135° and at 180°. If, however, they adjusted their strategy appropriately to take into account the new speed of rotation (45°/s), then accurate responding to all trials would be expected.

The bottom panel of Figure 12 shows the test trials to 135° and 180° fast conditions, or when a rate of 180°/s was used. These were presented infrequently within same-location training sessions within an alternating training series. Note again that the delays used in the violations during stimulus absence were of the same duration as those used in the original imagery trials (top panel). If a strategy tied to 90°/s rotation was used, inaccurate responding to these trials is expected. The following table identifies each trial type, the predicted pattern of errors if speed of rotation is noted and accounted for in the representational process, and the predicted pattern of errors if the speed of rotation is ignored and the response-delay associations acquired in training are applied to the novel trials.

Table 6. Predictions of Response Accuracies to Probes

Location	Condition	Type	Imagery Strategy	Timing Strategy
135°	SLOW	imagery	accurate responding	below chance responding
		violation	accurate responding	below chance responding
	FAST	imagery	accurate responding	chance responding
		violation	accurate responding	below chance responding
180°	SLOW	imagery	accurate responding	chance responding
		violation	accurate responding	below chance responding
	FAST	imagery	accurate responding	below chance responding
		violation	accurate responding	below chance responding

Those trials in which below chance responding was expected present a delay associated with a choice response from training which is opposite the response reinforced in the novel movement conditions. Those in which chance responding was expected present a novel delay to which no prior response association could have been acquired.

The slow condition and the fast condition were tested in separate blocks of 12 training sessions per block. A typical test session included 64 training trials and 8 probe trials, for a total of 72 trials per session. The 64 training trials were comprised of 16 perceptual, 16 imagery and 32 violation trials in which the stimulus moved at 90°/s. The 8 probe trials were comprised of 2 perceptual, 2 imagery and 4 violation test trials in which a new speed was introduced. The number of trials per session was planned in this way so that there were equal numbers of left key and right key responses required for each session. Subjects were divided in half pseudorandomly and half received fast speed testing first, followed by slow speed testing; while the other half received slow speed testing first, followed by fast speed testing. In between the two blocks of testing, subjects participated in 135°-180° standard training until 80 percent correct performance was achieved.

The data of interest were average percent correct scores to the novel speed conditions. Positive transfer, or accurate and consistent responding across speed conditions, indicates that the subjects are adjusting their representational process to account for the changes in the speed of rotation.

Results

The question of interest in this experiment was whether positive or negative transfer was obtained to novel movement conditions in the movement estimation task, for this would determine to some extent whether an imagery or a timing strategy was employed. Figure 13

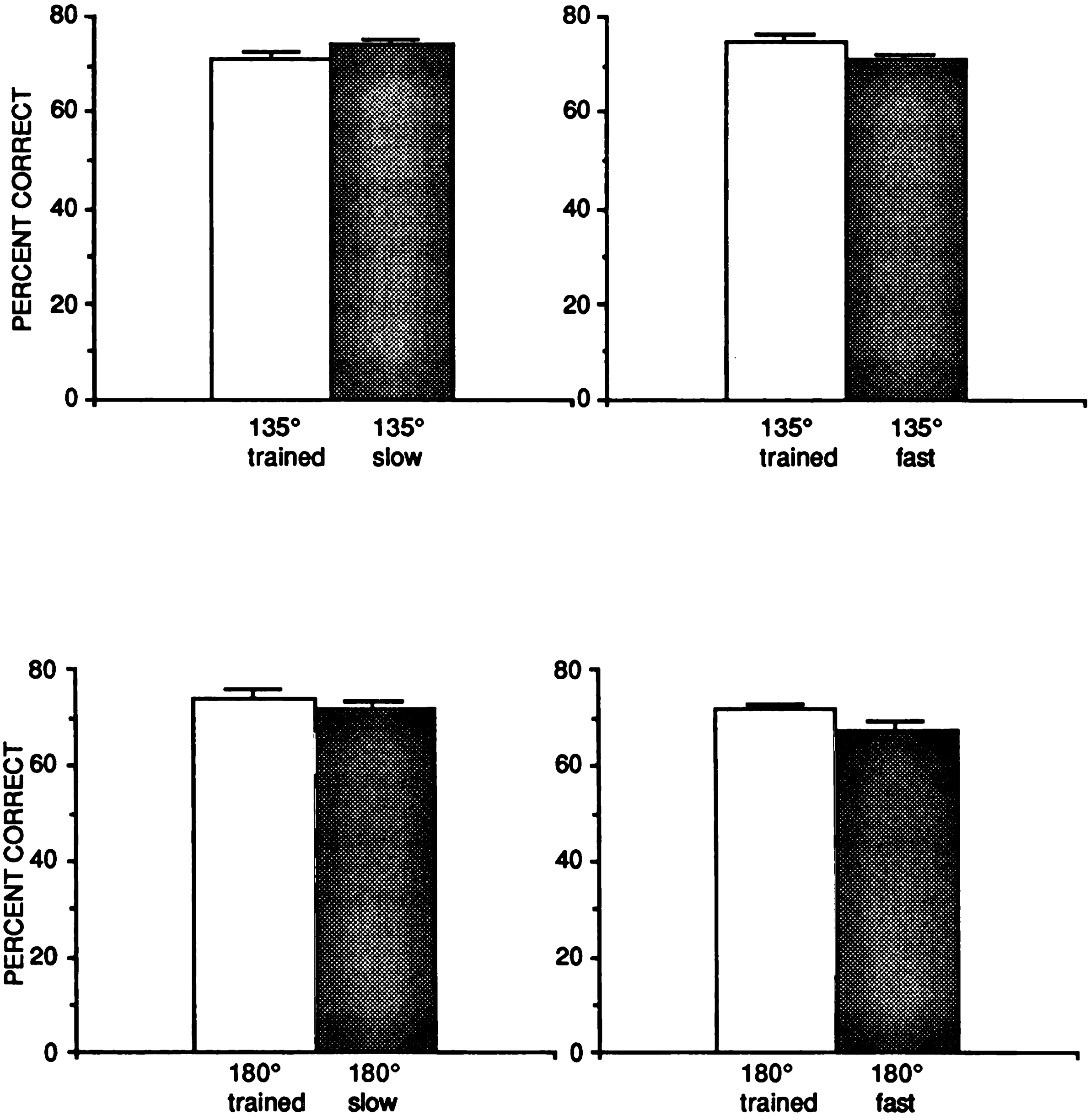


Figure 13. Mean percent correct scores to the trained and novel speed conditions at 135° and 180°.

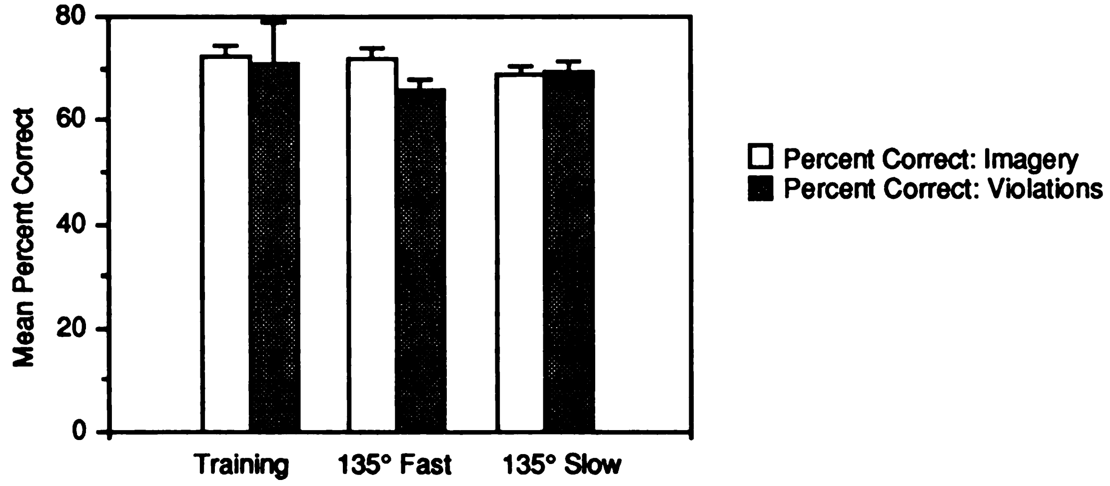
shows the mean percentage of correct scores from all subjects to the trained and tested speed conditions. Separate bars are drawn for response accuracies to two trained conditions: one in which the trained speed (90°/s) was presented within slow speed testing, and one in which the trained speed was presented within fast speed testing. It is apparent from the figure that positive transfer was obtained for all conditions: the mean percent correct scores ranged from 67% to 75% across speed conditions and were clearly greater than chance, or 50%. All trials produced above-chance responding, and the prediction of negative transfer made by a timing strategy (Table 6) was not supported by the data. Figure 14 shows the percent correct scores for each condition to perceptual, imagery and violation trials.

Two 3-way repeated measures analysis of variance (ANOVA) were conducted to test for positive transfer. The differences examined were: speed of rotation (45°/s vs. 180°/s vs. two trained speed conditions (90°/s) , one paired with fast speed testing and one paired with slow speed testing), order of testing (fast/slow vs. slow/fast) and sessions (n=6, to examine acquisition) within each location tested (one ANOVA for 135° and one for 180°). Positive transfer was obtained if there were no significant differences between percent correct scores to the various novel and trained speed conditions.

<u>Results of the 135° Test</u>

For 135° testing, the ANOVA showed a nonsignificant effect of speed ($F_{3,108} = 2.169$, $p>0.10$) indicating that there were no significant differences between responses to novel and trained speed conditions. In addition, the session effect was not significant in this ANOVA ($F_{5,36} = 0.745$, $p > 0.60$). These findings are consistent with the argument that transfer to the novel speeds was positive and immediate in 135° testing. In addition, the interactions of these variables, as well as with order of testing, were not significant (see Table 7 for the ANOVA statistics in detail).

A surprising result of this ANOVA was a significant effect of order of testing ($F_{1,36} = 6.756$, $p < 0.02$). Upon closer examination of the relevant data, it was clear that this was the



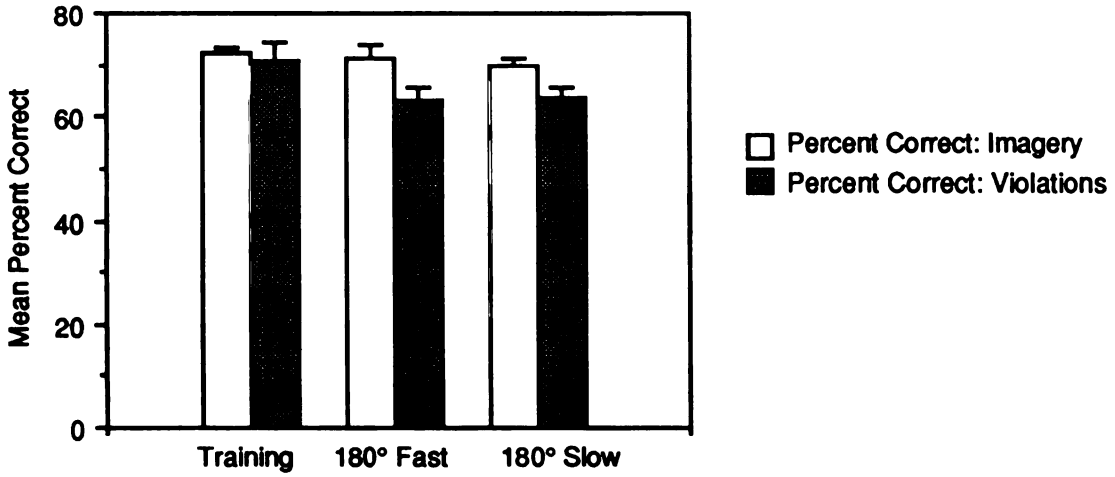


Figure 14. Mean percent correct scores to perceptual, imagery and violation trials.

Table 7. Anova table for the 135° Test and the 180° Test

Anova table for the 135° Test

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Order of Testing (A)	1	832.756	832.756	6.756	.0135
session (B)	5	459.052	91.81	.745	.5951
AB	5	470.992	94.198	.764	.5816
subjects w. groups	36	4437.307	123.259		
LOCATION (C)	3	482.059	160.686	2.169	.0959
AC	3	343.15	114.383	1.544	.2074
BC	15	1081.905	72.127	.973	.488
ABC	15	1104.781	73.652	.994	.4668
C x subjects w. groups	108	8002.672	74.099		

Anova Table for the 180° Test

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Session (A)	5	1165.772	233.154	1.243	.3098
Order of Testing (B)	1	565.111	565.111	3.012	.0912
AB	5	572.34	114.468	.61	.6927
subjects w. groups	36	6754.605	187.628		
Repeated Measure (C)	3	1090.118	363.373	4.043	.0091
AC	15	1067.43	71.162	.792	.6841
BC	3	318.207	106.069	1.18	.3208
ABC	15	639.433	42.629	.474	.9488
C x subjects w. groups	108	9705.744	89.868		

result of a change of response accuracy to the slow condition, depending upon whether it was tested first or second. If it was tested first, the slow condition in 135° testing yielded an average (taken across training and testing) of 69.77 percentage correct responses, but if it was tested second (i.e., after the fast speed had been tested) it was met with an average of 76.01 percentage correct responding. Fast speed testing produced an average of 76.44 percentage correct responses both when it was tested first and second.

Tukey comparisons of response accuracies to the trained and test conditions by order of testing revealed that the significant effect of order was a result of a significant change in responses to test trials and to training trials when the slow speed was first introduced. Response accuracies to trained trials during slow speed testing were 61.54 and 66.42 in correspondence with the slow speed test occurring first or second, respectively. There was a significant reduction in response accuracy to trained trials when slow speed testing was introduced first ($q_{4,36} = 4.885$, $p < 0.05$). Average response accuracies to the slow speed probes were 65.92 and 71.98 to first and second tests, and were significantly different by a Tukey comparison ($q_{4,36} = 6.052$, $p < 0.05$). All other comparisons of probe data by order of testing, as well as of training data by order of testing were not significant.

Figure 15 illustrates the relationships between training and test mean percent correct scores by order of testing. It is evident in this illustration that the significant order effects found in the Tukey comparisons were caused by response differences in the violation trials, but not in the imagery trials. In training and in testing, the order of testing did not differentiate percent correct scores to imagery trials. However, the mean percent correct scores were quite different with respect to the order of testing in violation trials.

In sum, the fast and slow speeds tested at the 135° location produced accurate responding with no differences in general found between trained and tested conditions. By a significant order of testing effect it was revealed that responses to trained and test trials within slow speed testing were not quite as accurate as were those to the other speed conditions, but

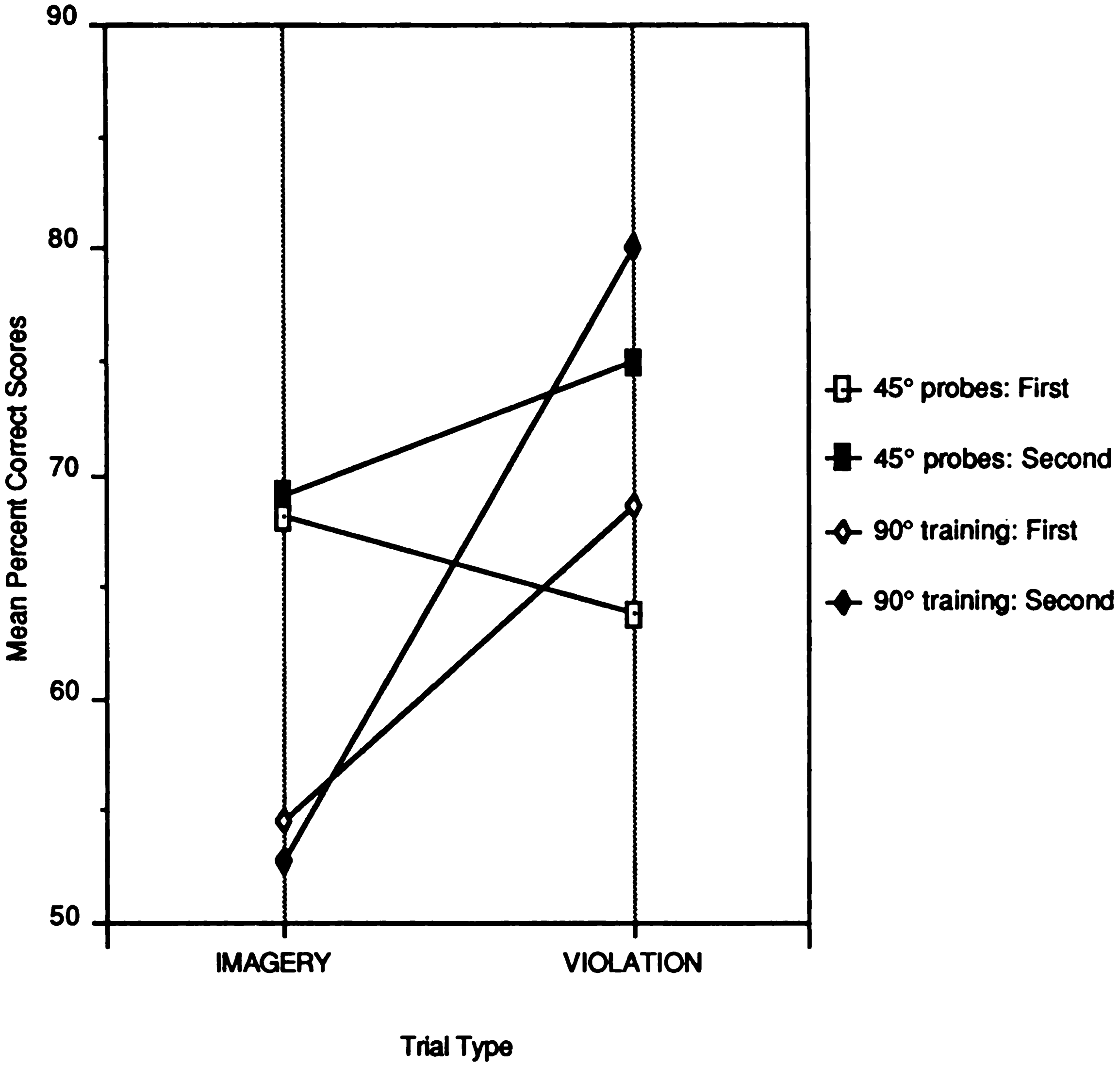


Figure 15. Mean percent correct scores to imagery and violation trials within slow speed testing to compare first and second order of testing.

this effect was evident only when the slow speed was the first novel speed introduced, and, only to the violation trials. These results imply that the pigeons could respond accurately to novel movement conditions, but that there was more initial interference to trained and test violation trials when a slower speed was introduced first.

Results of the 180° Test

The results of the ANOVA for the 180° location were slightly different than those obtained in the ANOVA for the 135° location (see Table 7 for statistical detail). First, the order of testing effect at 180° was not significant ($F_{1,36} = 3.012$, $p > 0.05$). But the speed effect was significant ($F_{3,108} = 4.043$, $p < 0.01$), indicating that response accuracies to the fast, slow and the trained speeds in 180° testing were different. This result works against the hypothesis of positive transfer to novel speed conditions, since there was a significant difference found between response accuracies to the trained and test speed conditions. Tukey tests of all the meaningful comparisons of this effect were conducted (i.e., to response accuracies to trained and test trials in the slow condition, to trained and test trials in the fast condition, as well as to slow vs. fast test trials, and to the two trained conditions). All of these comparisons produced nonsignificant calculated q values. After some post-hoc unplanned comparisons were made, it was determined that the significant effect found in the ANOVA was the result of a significant difference between a test and trained condition that were not meaningful to compare. Specifically, a significance at the 0.005 level was obtained with a Tukey test of average response accuracy to training trials within slow probe testing (the bar on the far left of the 180° histograms in Figure 13) and average response accuracy to fast probes (the bar to the far right in Figure 13, $q_{4,48} = 4.799$). Because of this, the significant effect is spurious in nature.

The session effect in the ANOVA at the180° location was nonsignificant ($F_{5,36} = 1.243$, $p > 0.30$) and all the interaction effects of speed, order of testing, and of sessions were nonsignificant in this ANOVA, just as in 135° testing.

A Comparison of Errors to 135° and 180°

The error data from Experiment 1 revealed that there was a curvilinear relation between errors and rate of acceleration or deceleration presented during the delay in the movement estimation task. Specifically, the error functions were increasing with a quadratic trend with respect to increases in acceleration, and they were parallel with respect to location of testing, with farther distances producing more errors.

The plotting of the error data from Experiment 2 along a deceleration/acceleration axis reveals any similarities between estimating movement at the rate of a trained speed and at novel speeds. An obvious change in error rates to violation trials as a function of location is displayed in Figure 16. Here, the mean errors to the imagery trials across new speeds are very similar, but the error scores to the violation trials are quite diverse. One important implication is that there are increased errors to tested decelerations with novel speeds. The functions seem more symmetric with respect to discriminations of acceleration and deceleration than they did in Experiment 1 with the trained speed. A relation which seemed to pop out of the graph is shown by the arrows drawn between the pairs of functions. These arrows point out a change in the mean error rate as the location of testing is increased from 135° to 180° within speed testing. While the functions no longer appear parallel with a constant error rate separating them with location increases as they did in Experiment 1, they still increase with increases in the distance through which processing must occur. The new conjecture to add to the description of movement representation is that with a novel speed, the errors increase and the shape of the function changes with increases in location.

Discussion and Interpretations

The positive transfer to novel speeds in Experiment 2 indicates that pigeons' representational process for estimating movement is quite flexible and fairly accurate. The

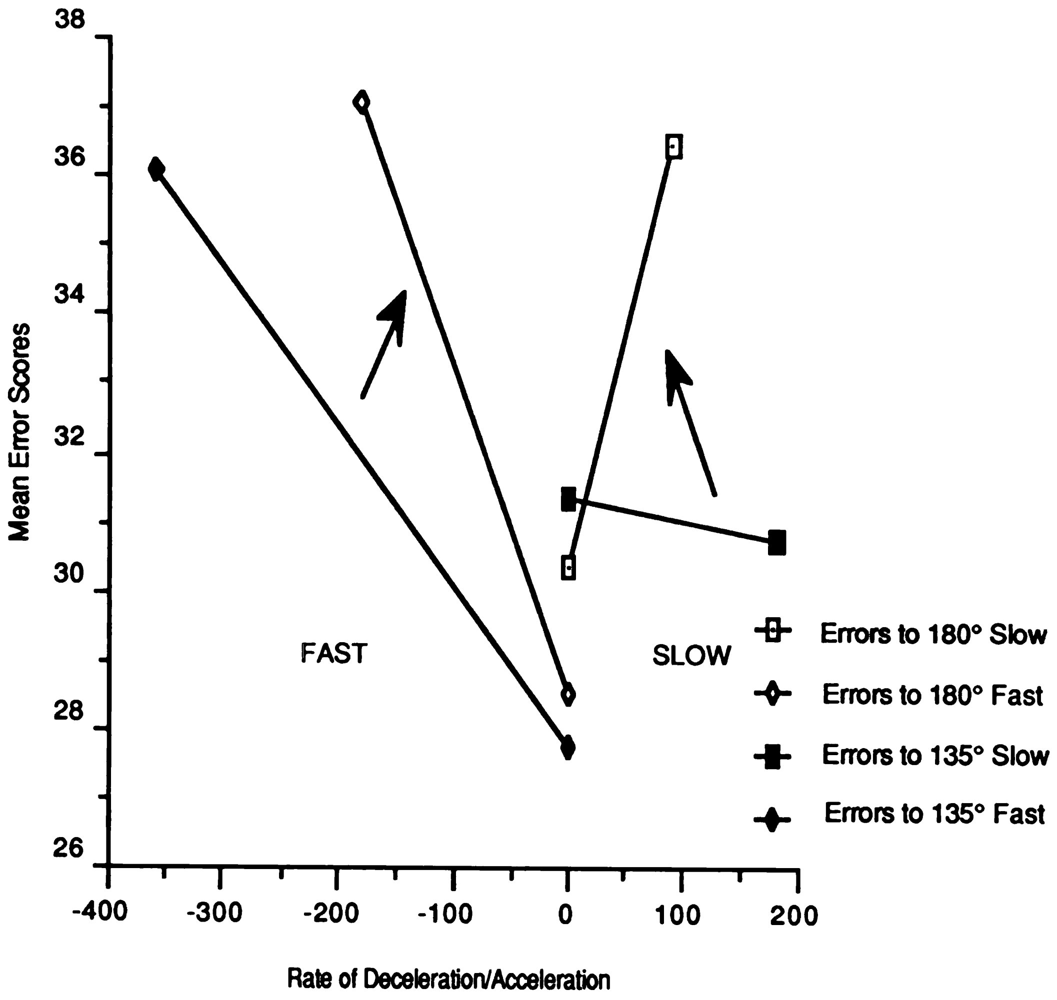


Figure 16. A comparison of mean errors to fast and slow probes at 135° and 180°.

positive transfer obtained supports two of the criteria of the definition of imagery put forth at the beginning of this paper: 1) the structural assumption , that pigeons maintain an accurate perceptual description of the mov ing stimulus in memory , and 2) the functional assumption, that pigeons can mentally transform the stimulus accurately even at the newly perceived rates. The interactive assumption, that perception interacts with imaging was not tested in this experiment. However, the experiment did reveal that perception had a positive influence on the imaging process, for perceived changes in velocity were immediately incorporated in the image. Still, a timing strategy tuned to the perceptual display could account for the positive results obtained.

Are the results of Experiment 2 consistent with the description of pigeons' representation of movement of Experiment 1, or do they require a modification of the description of movement representation developed so far?

The asymmetric discrimination between constant velocity, deceleration and acceleration found in Experiment 1 was not supported by the pattern of errors in Experiment 2. Rather, increased errors to increases in deceleration appeared as a new characteristic. However, the data are insufficient to calculate a full function to describe this effect, so this finding is only mentioned in passing.

The general finding that errors increase with increases in location is consistent across the speed tests of Experiment 2, and this finding is consistent with the notion that an analog process of estimating movement is employed. However, when new speeds were introduced in Experiment 2, the error functions increased and changed shape qualitatively with increases in location, so the parallel-like functions (i.e., the constant increase in errors to increases in represented distance) were not obtained.

Some qualitative changes in the process of representing movement occur when the rate of movement is varied. With one trained speed (i.e., in Experiment 1), there is an asymmetric discrimination of constant velocity from acceleration and deceleration. There are increased errors to increases in acceleration, and there is a constant increase of errors to increases in the distance through which processing must occur. With new speeds, the error functions become more symmetric with respect to the discrimination between constant velocity and acceleration and deceleration. There are still increases in errors to increases in the distance of extrapolation, although the shape of the functions also changes with increases in the distance of extrapolation for novel speeds. Positive transfer was obtained to the novel speeds, or, in other words, responding remained accurate to the novel speeds. However, the differences in the functions produced by the novel speeds reveals complications in the discrimination resulting from the novel speeds.

A direction of research extrapolated from studies of the psychophysics of movement in humans may help resolve the complication in error rates caused by the introduction of novel speeds. When adapted to a specific velocity (usually with moving sinusoidal gratings), people perceive test velocities that are slower than the adapted rate as slower than their actual rates, and test velocities that are faster than the adapted rate as faster than their actual rates (Pantle & Sekuler,1968; Carlson, 1962; Rapaport, 1964; Thompson, 1981; and for a review, see Anstis, 1986). Obviously, this adaptation effect cannot be applied directly to the present study, since threshold detection methodologies were not employed and a full 15-s ITI interrupted the presentation of the "adapted" or trained velocity and the test faster and slower velocities. Nevertheless, the speculation here is that this adaptation effect may also occur at a higher cognitive level; for example, an organism's judgment of movement may be a relative one, or one that is affected by other observed movements in context. This type of effect could result in qualitative shifts in discrimination efficiency to infrequent presentations of slow velocities or fast velocities within an "adapted" velocity session. Systematic research is needed that tests many points along the deceleration/acceleration axis along with changes in velocity for this speculation to be tested. It is offered here as a possible explanation for the qualitative shift observed to changes in velocity in Experiment 2.

Experiment Three:

The Effects of Removing Perceptual Cues for Movement on the Representational Process

The aim of this experiment was to test whether the perceptual display of stimulus rotation was necessary for accurate responding in the task. On certain probe trials within typical training sessions, the perceptual display of movement was removed from the stimulus presentation. On these test trials, subjects perceived a static presentation of the stimulus at its "start" location (0°), followed by an auditory cue for movement and a delay, and then by a test location. Response accuracies to these trials demonstrated whether there was any influence of the perceptual cues for movement on the representational process. The characteristic of the process quantified by this experiment is its triggering feature. The results help to determine whether the start location and a cue for movement are all that is needed, or if the start location plus a perceptual display of movement are required.

In addition, this experiment attempted to test imagery again as the controlling process by manipulating the type of information available for representation. A timing strategy (even one tuned to the perceptual display, as in Experiment 2) would not necessarily be adversely affected by the removal of the perceptual display of movement, as long as boundary start and stop locations were presented. An imagery process would be affected, because subjects' representation of the rotating stimulus would be restricted to a static display.

The same subjects were employed in this experiment as were used in the previous experiment. To avoid the possibility that subjects would assume different speeds of rotation (as was tested in Experiment 2) during the test condition in which perceptual cues for movement were removed, responses to the trained speed were re-trained until criterion performance was met, and the trained speed was the only speed presented in training and testing in Experiment

3. In addition, an auditory cue was added to the beginning of each trial in the training phase of Experiment 3 to signal stimulus movement. The only kind of movement paired with the auditory cue was the trained speed. This auditory cue was also presented in the test trials in which the perceptual display for movement was removed, and it served the purpose of indicating when the stimulus started its movement. The only type of movement that should have been cued by the auditory cue was the trained speed. Thus the novel speeds tested in Experiment 2 should not interfere with this task.

Method

Subjects

The same 8 subjects used in Experiments 1 and 2 participated in this study.

Apparatus

The two chambers used in Experiments 1 and 2 served as experimental chambers in this study. Subjects tested in Chamber 1 in previous experiments continued to receive training and testing in Chamber 1, and subjects trained in Chamber 2 continued in the experiment in Chamber 2.

Procedure

The variable of interest in this experiment was response accuracy to trials in which the perceptual display of stimulus rotation was removed. The procedure was very similar to that followed in all the other experiments: first subjects were trained to respond accurately to 135° and 180° training trials, and then test trials were presented infrequently within training sessions and response accuracy to these trials was noted. However, the trial progression in training and testing was slightly altered. The standard trial progression had been: a static display at 0° is presented for 5 s, and following a VR-12 to 15 on the middle key, stimulus movement was presented, followed by a delay and/or the presentation of the test location. In this experiment, a 2000 Hz tone was presented for 500 ms after the response requirement was met to the static presentation at 0° and before stimulus movement was initiated. Then, in the test trials, the tone was presented after the response requirement was met, but following it, no perceptual display of movement was presented. The auditory cue was added to insure that subjects had a clear and unvarying cue for the start of stimulus movement (i.e., the response requirement was variable) and for the type of stimulus movement employed. It was added to training and testing so that the only variable manipulated in testing was the display of perceptual cues for movement.

The test trials in this experiment were 135° and 180° imagery and violation trials modifie from training. The modification was that in the test trials, a static presentation of the clock hand was presented at 0°, and after the middle key response requirement and the tone, a delay during which the stimulus was absent was initiated until the test location was presented. The simulated rotation from 0° to 90° that was standard in the training trials was removed in these test trials. Figure 17 diagrams the trial types for training and testing.

First, the eight subjects in this experiment were exposed to alternating sessions of 135° and 180° training until the criterion performance of 80 percent correct for two consecutive days was met. In these training sessions, reinforcement contingencies were the same as were described in Experiments 1 and 2 for training. Sessions included 64 trials, consisting of 16 perceptual trials, 16 imagery trials, and 32 violation trials.

Next, a series of test sessions was presented for 12 days. These test sessions were comprised chiefly of 135° or 180° training trials (i.e., 64 out of 72 total trials were training trials) The remaining 8 trials at either location were comprised of imagery (2) and violation test trials (4) that did not present stimulus rotation, and 2 perceptual trials. The imagery and violation test trials progressed in the following manner: a static presentation of the clock hand was presented

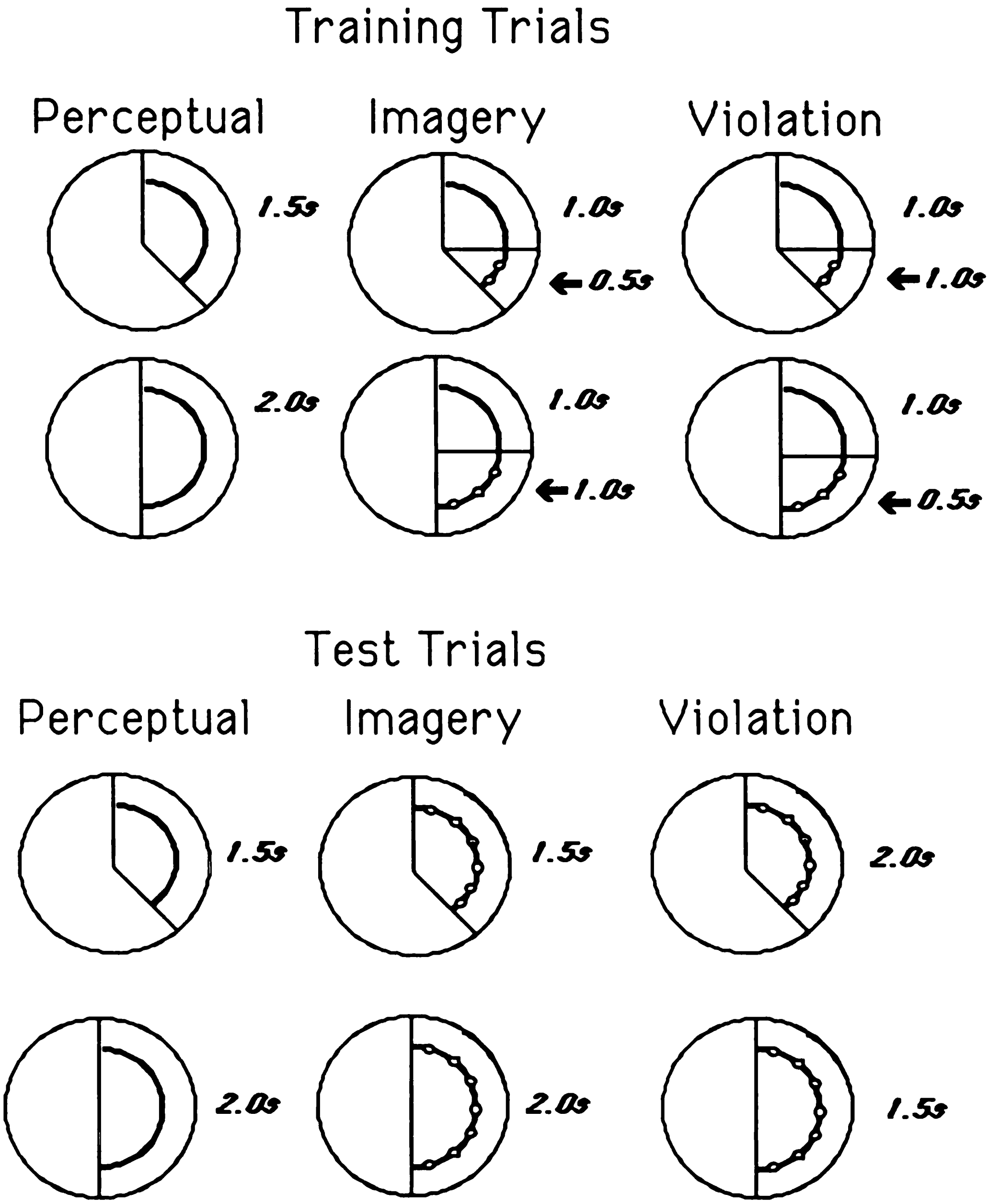


Figure 17. Training and test trials used in test of perceptual cues for movement in Experiment 3.

at 0° for 5 s, and following responses on a VR-12 on the center key, a 2000 Hz tone was presented for 500 ms. Next, the stimulus disappeared during a delay (i.e., one which included the time taken for stimulus rotation from 0° to 90° and rotation to the test location) and then the stimulus reappeared at a test location. These trials were reinforced under the same contingencies as those in training: imagery trials were reinforced for left key responses and violation trials were reinforced for right key responses.

During testing, 135° and 180° training were alternated daily. Test trials at 135° were presented in 135° training sessions, and test trials at 180° were presented in 180° training sessions. A total of 24 exposures to imagery and perceptual trials, and 48 to violation trials was planned in the test series. The data of interest were percent correct scores to the novel test trials, and error scores to those trials.

Results

Figure 18 shows the mean percent correct scores to trained and test trials at the 135° location and at the 180° location, and Figure 19 displays the means to perceptual, imagery and violation trials within these conditions. The means to trained trials appear greater than those to test trials, although all means appear lower than criterion (i.e., less than 80 percent correct responding).

A two-way repeated measures analysis of variance (ANOVA) was conducted to compare percent correct scores from training and testing, and across sessions to each location condition. A significant difference in response accuracy between training and testing, with test accuracy significantly lower than accuracy to trained trials, supports the hypothesis that the removal of perceptual cues for movement debilitated performance. The analysis for each location is discussed in separate sections and is presented in Table 8.

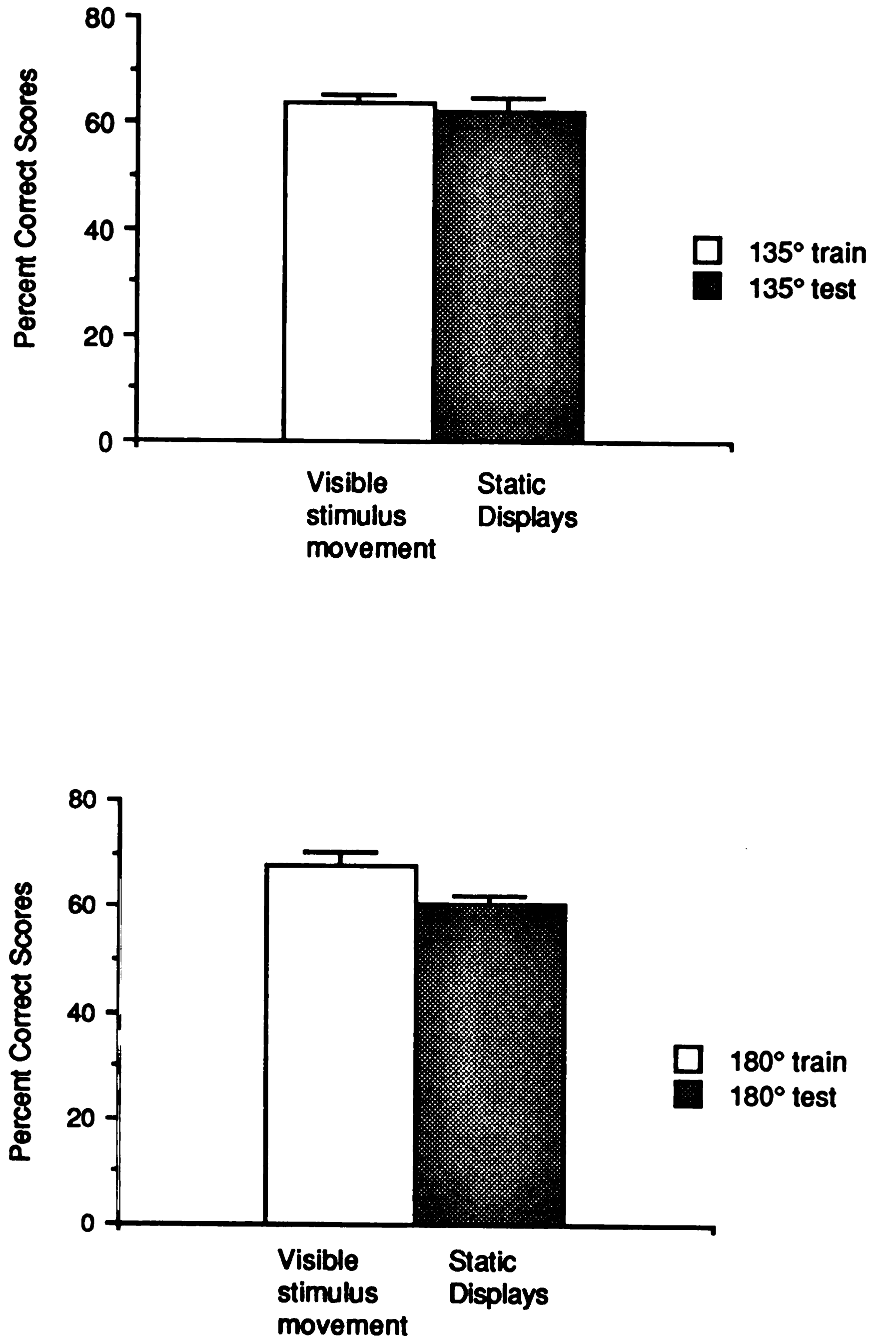
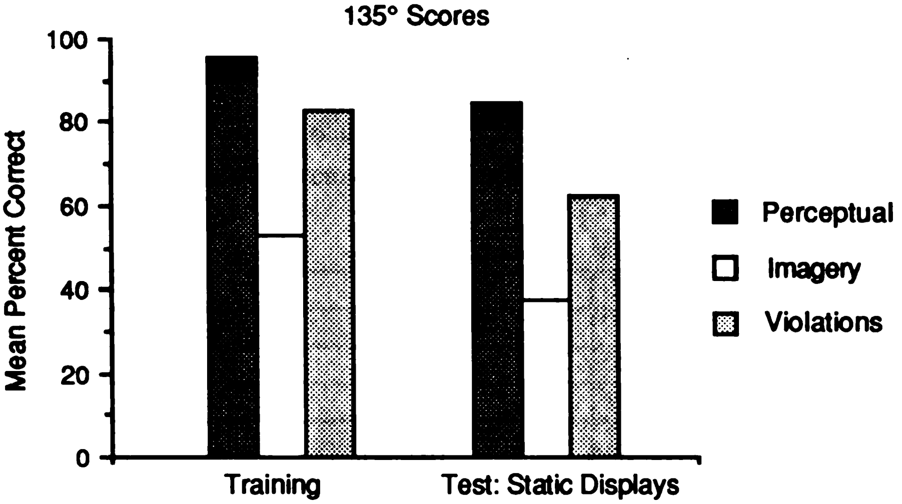


Figure 18. Mean percent correct scores to the trained and test conditions in Experiment 3.



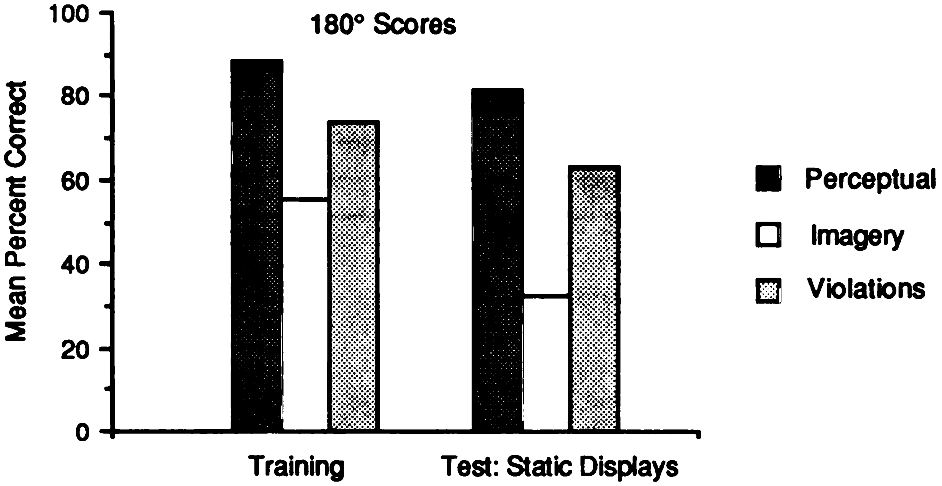


Figure 19. Percent correct scores to perceptual, imagery and violation trials.

Table 8. Analyses of Variance of Percent Correct Scores in Experiment 3.

Analysis of Variance of Percent Correct Scores to Trained and Test Conditions to 135° Trials

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
SESSION (A)	5	1261.069	252.214	1.17	.3397
data w. groups	42	9050.762	215.494		
Trained vs. Test (B)	1	53.417	53.417	.423	.5188
AB	5	760.86	152.172	1.206	.3229
B xdata w. groups	42	5298.556	126.156		

Analysis of Variance of Percent Correct Scores to Trained and Test Conditions to 180°

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
SESSION (A)	5	1046.246	209.249	.979	.4416
data w. groups	42	8974.183	213.671		
Trained vs. Test (B)	1	1147.821	1147.821	6.465	.0148
AB	5	848.239	169.648	.956	.4558
B x data w. groups	42	7456.815	177.543		

The 135° Test

In the ANOVA at 135°, a significant difference was not obtained between trained and test mean response accuracies ($F_{1,42} = 0.423$, $p > 0.50$). This result indicated that the removal of the perceptual cues for movement had no effect on response accuracy. The mean percent correct scores to trained and test trials at 135° were 63.679 and 62.187, respectively. Since response accuracy remained between 75 and 80 percent correct before testing, these scores indicate that there was a general suppression effect of correct performance during testing. To evaluate this, two two-tailed t-tests contrasting the trained and test mean percent correct scores with 50 percent correct responding (i.e., the level of chance) revealed that performance to trained trials was significantly higher than chance ($t_8 = 4.133$, $p < 0.005$) but that performance to test trials was not significantly different from chance ($t_8 = 2.1878$, $p > 0.05$). Although the deleterious effect of the removal of perceptual cues for movement was not revealed in the ANOVA, these t-tests reveal that performance to trials with the perceptual cues for movement removed was worse than was performance to trained trials.

The effects of sessions, as well as the interaction between trained vs. test trials and sessions were not significant in the ANOVA at 135°. Also there were no significant differences found in an analysis of variance testing for subject differences in training ($F_{7,40} = 1.28$, $p > 0.20$) or in testing ($F_{7,40} = 0.848$, $p > 0.50$).

The 180° Test

The repeated measures ANOVA at 180° revealed a significant difference between percent correct scores to trained and to test trials ($F_{1,42} = 6.46$, $p < 0.02$). The mean score to trained trials was 67.74, and the mean score to test trials was lower: 60.825. The result is consistent with the hypothesis that the removal of perceptual cues for movement in test trials debilitated performance. The sessions effect was not significant, nor was the interaction.

At this location of testing, both trained and test means were significantly greater than chance level responding would predict ($t_{8(train)} = 2.948$, $p < 0.01$; $t_{8(test)} = 3.347$, $p < 0.005$). Still, the result of the ANOVA clearly indicated that percent correct scores to test trials were significantly lower than those to training trials.

An analysis of variance conducted to examine subject differences in training and testing revealed significant differences between subjects' training scores ($F_{7,40} = 2.52$, $p < 0.05$) and between subjects' test scores ($F_{7,40} = 3.003$, $p < 0.02$). These effects were brought on by the extremely low percent correct scores of two subjects: labelled #25 and #4. The trained means for these two subjects were 53.98 and 52.32, respectively, while the means to trained trials of all other subjects ranged between 60.00 and 73.78 percent correct. In addition, the test means of these two subjects were 51.19 and 65.47 respectively, while all others' test scores ranged between 62.00 and 81.78 percent correct. These subjects were clearly responding at chance levels to the trained trials, and entered artificially low values into the test data in the ANOVA.

For the purpose of testing the amount of transfer to the test condition as a mean effect of the experiment (i.e., despite the chance performance of two subjects), another two-way repeated measures ANOVA was conducted with the data from these two subjects removed. The results of this ANOVA were virtually the same as the results of the first: a significant difference was obtained to percent correct scores from trained and test trials ($F_{1,30} = 7.29$, $p < 0.02$) and nonsignificant differences were obtained to sessions and to the interaction. The mean scores to trained and test trials were increased from the first test: the trained mean for the 6 remaining subjects was 70.876 and the test mean was 63.382. These scores were also significantly different from chance ($t_{6(train)} = 3.299$, $p < 0.01$; $t_{6(test)} = 4.55$, $p < 0.005$). However, the subject effect found significant in the first analyses of variance disappeared after removal of the two subjects ($F_{5,30\ (trained)} = 1.94$, $p > 0.10$; $F_{5,30\ (test)} = 2.14$, $p > 0.08$).

Regardless of the disparate data of two subjects, the significant effects found at 180° hold: a significantly lower response accuracy to test trials than to training trials. The addition of the data from the two subjects merely produced a significant subject effect, but did not occlude the deleterious effect of removal of perceptual cues for movement on performance.

Comparison of Error Scores

Next, mean errors for all eight subjects were plotted as a function of the speed of rotation evident in the delay for each trial type. Mean errors to imagery trials were plotted at the 0-point of the decleration/acceleration axis seen in Figure 20. The mean errors to the violation trials were graphed on either side of the 0-point. When matched with the error results of Experiment 1 , the mean errors from the trained and test conditions of Experiment 3 appear quite different. Specifically, errors to the imagery trials seem inflated and the mean errors to the violation trials are less, not more, than the errors to the imagery trials. These functions clearly do not possess the parallel and linearly increasing characteristics of the functions of Experiment 1.

On closer examination (see Figure 21), there is a pattern to the errors seen in Experiment 3 that describes the strategy subjects followed in testing. With the introduction of the new delays inadvertently caused by the removal of all perceptual cues for movement, subjects adopted a simpler, albeit less accurate, strategy of response: If there is not a delay, peck the left key; but if there is a delay, peck the right key. This strategy explains the inflated error rates to imagery trials, for in training and testing, subjects responded on the right key (and incorrectly) more often than on the left to any delay. This strategy also explains the more accurate results (and fewer errors) to the violation trials for which right key responses were reinforced.

It is important to note that this strategy was not followed before the removal of perceptual cues for movement, for subjects were responding between 75 and 80 percent correct to 135° and 180° training trials before testing. The removal of perceptual cues for movement on probe trials was so disruptive that subjects abandoned their cognitive strategy for estimating movement and adopted an S-R strategy of response similar to that first applied in preliminary Experiment 1.

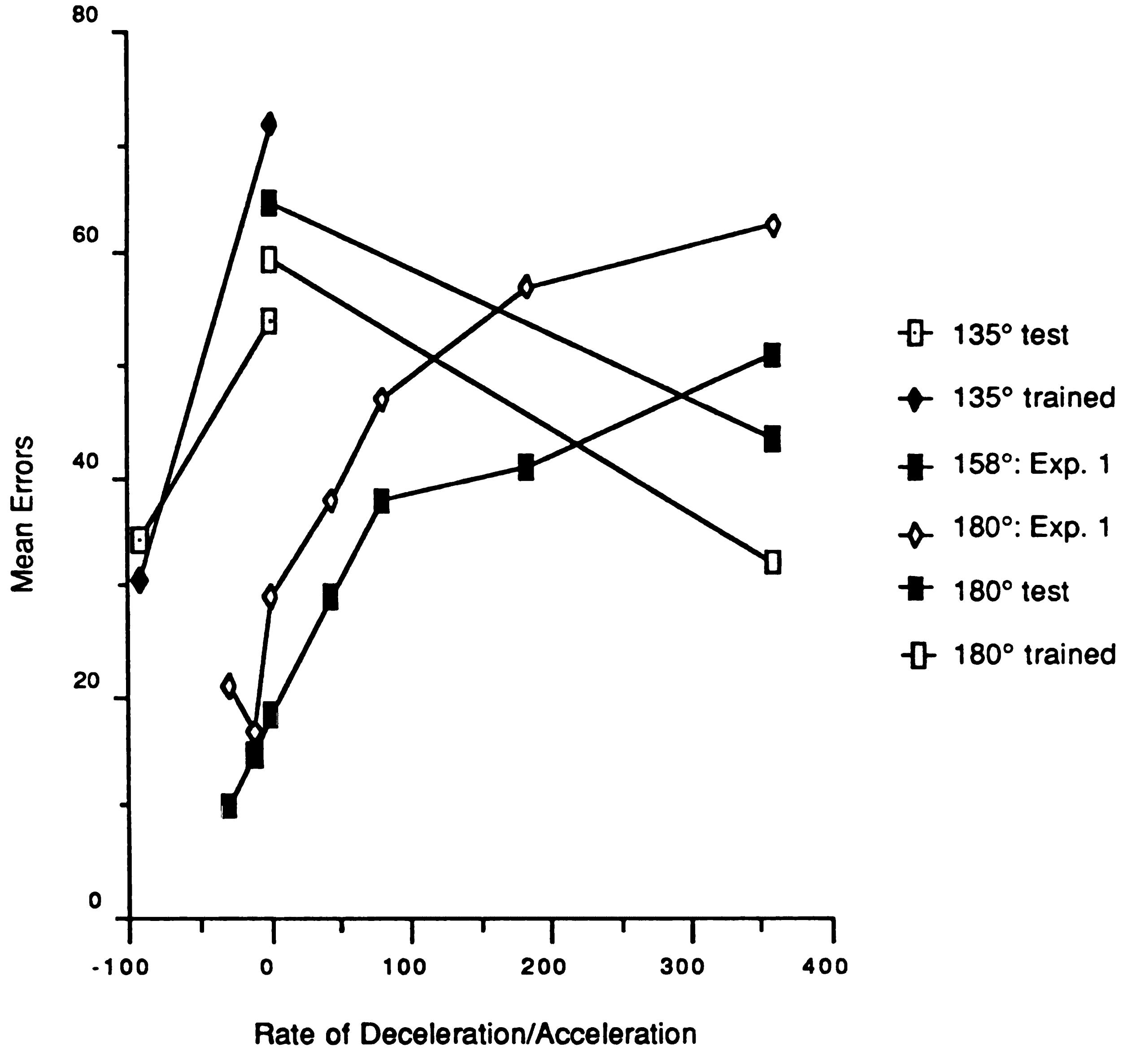


Figure 20. Mean errors to trained and test trials by speed of movement during the delay in Experiment 3, compared to errors made in Experiment 1.

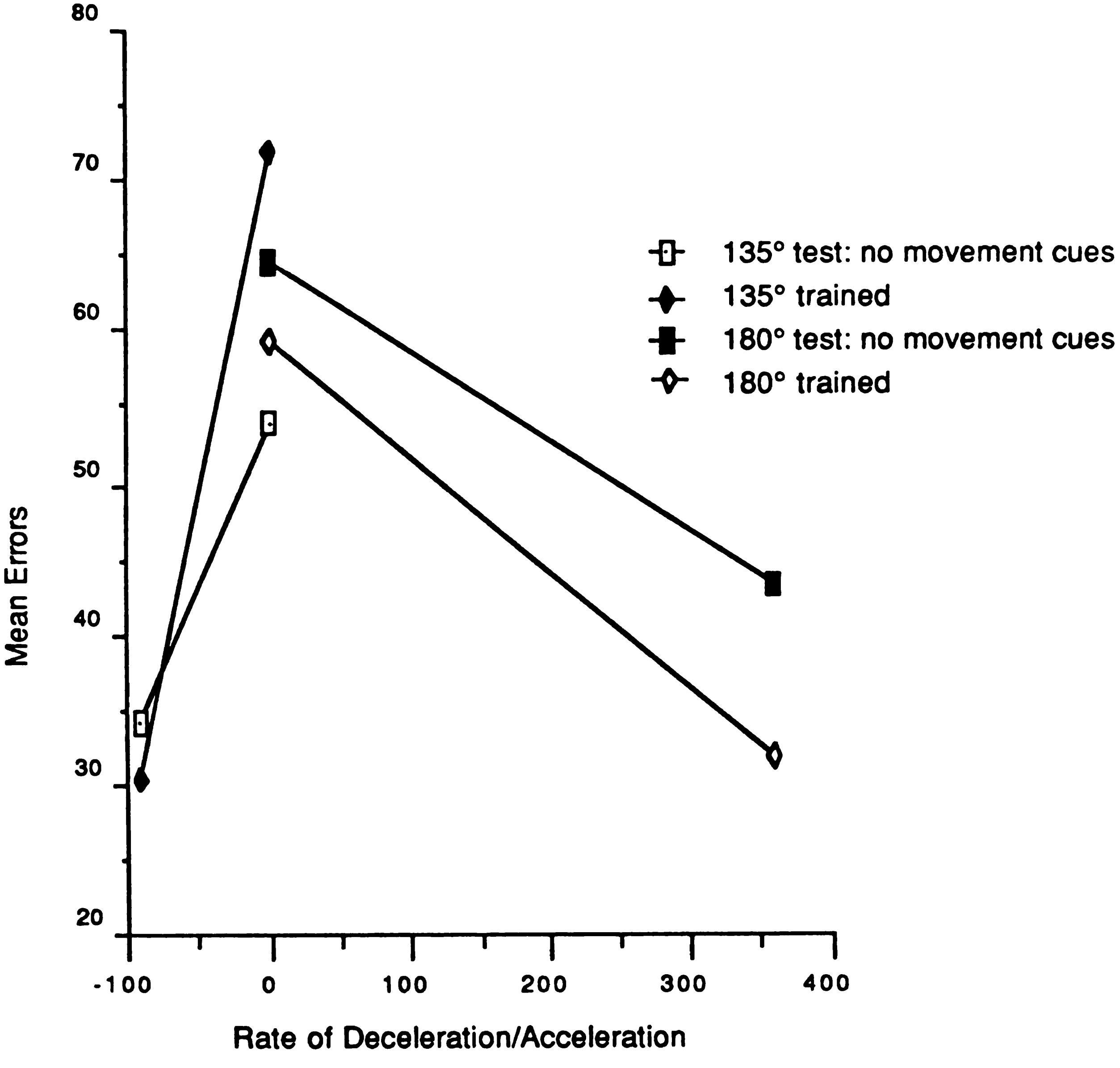


Figure 21. Mean errors to trained and test trials plotted by speed of movement during the delay.

Discussion

Experiment 3 was devised to examine the influence of perceptual cues for movement on the representational process. Removal of the perceptual cues in probe trials resulted in a complete shift of the strategy from cognitive estimation to a less efficient S-R timing strategy. Percentage of correct response scores appeared low for trained and test trials, but the most debilitating effect was to responses to the test trials. The error data revealed the S-R strategy more clearly, due to the inflated error rates to imagery trials and the more accurate response patterns to all violations.

When perceptual cues for movement are present, subjects estimate the location of the stimulus by imaging its movement in its absence. When perceptual cues are absent, a simple strategy is employed in which right key responses are emitted following <u>any</u> delay.

Perceptual cues for movement are a necessary ingredient for representing movement. Further, static stimuli, even when timed accurately to convey movement, are not salient cues for movement in pigeons. Transformational studies in which static stimuli are employed would most likely fail, and poor results have been obtained in almost every case (Cerella,1987).

Summary and Conclusions

A goal of this investigation was to put to a test the characteristics of an imagery process. The structural assumption, that imagery maintains the perceptual characteristics of the stimulus held in memory, was examined in Experiment 1 by a manipulation of the delay intervals which supported the timing component of remembered stimulus movement. Positive transfer, or accurate responding to these delays, was found, but the finding was weakened somewhat by the disparate data within the tested violation trials. This experiment was a fine-grained analysis of the structure of movement in the representational process by a manipulation of delays, and it revealed that the representational process did not always accurately incorporate subtle changes in timing. Imagery was implicated as the process used in Experiment 1 however, by a general effect of transfer across training and test trials.

The functional assumption, that imagery allows for appropriate mental transformations of stimuli, was tested in Experiment 2 by an observation of the effects of new velocities on the process. Positive transfer was observed to fast and slow speeds at 135° and at 180° . The representational process accommodated new transformations at different speeds quite readily. The functional assumption of imagery was supported. In addition, the timing strategy was refuted as an alternative which accounted for pigeons' performance thus far, since the predicted negative transfer of the timing strategy was not realized in the data.

Finally, the interactive assumption, that perception interacts with imaging, was not tested in any of the experiments. The influence of a perceptual display on the representational process was tested in Experiments 2 and 3, by a manipulation of the speed presented in the perceptual display (Experiment 2) and by removal of the perceptual dynamic display (Experiment 3). It was found in Experiment 2 that the representational process used could pick up new information about movement in the perceptual display and use it immediately and readily in the memory process. It was thought that this evidence supported the imagery hypothesis better than a timing strategy because in imagery, perceptual input of the dynamics of movement would be represented realistically, while in timing only particular cues and times would be incorporated. Still, a timing strategy tuned to the perceptual dynamic display could account for the transfer results. The imagery process was again tested in Experiment 3, by a measurement of the effect of removing perceptual cues for movement on the process. The result of this manipulation was a complete shift in the pigeons' strategy from an estimation strategy to an S-R strategy that was not as accurate. Clearly, removal of the perceptual cues had devastating results on the representational process. It appears as if the representational process pigeons employed required a perceptual display for movement for accurate estimation, and since timing would not necessarily require a dynamic display of movement, imagery is thought to be at work here.

Imagery had been defined operationally and two criteria to identify its existence were tested. It is possible that a timing strategy tuned to the perceptual display and requiring perceptual input for timing calibration could account for the data, thus imagery is not isolated as the process by the data. The more parsimonious explanation supported here is that imagery is the process used to represent stimulus movement because the timing strategy does not support all the changes in error rates very easily and because it should not be necessary for a timing strategy to require perceptual dynamic input if timing is preserved in the static input employed. Still, the question is empirical, and begs a return to the interactive assumption, that perception interacts with imaging, for its answer. An experiment in which perceptual input is given while subjects are imaging can reveal whether perceptual input can facilitate or debilitate the representational process. A timing strategy might be influenced by perceptual input during timing, but it should not be as debilitated as would an imagery strategy if that is what subjects are using.

Another goal of this investigation was to attempt to quantify certain characteristics of movement as it is represented in pigeons. The question of interest in this investigation was to what extent pigeons' representation of movement complied with the laws and characteristics of real physical movement. The results of the error analyses in the three experiments delineate certain characteristics of the representational process. A description of pigeons' ability to represent movement, as reflected by the results of these experiments, follows.

To estimate movement at all, the subjects needed a perceptual display for movement (Experiment 3). If one was not presented, subjects responded on the basis of the presence or absence of a delay. After a perceptual display was provided and once the moving stimulus disappeared, subjects transformed a representation of the stimulus through space to its test location, and they made increasingly more errors as the test location was increased (Experiments 1 and 2). To tested rates above 44°/s^2, or to very short delays, subjects adopted a simple delay strategy (Experiment 1). Within their bounds for testing accelerations, subjects have a category for constant velocity in which some accelerations and few decelerations fit. Finally, if a change in visible stimulus movement is noted, this change is accurately represented in the stimulus movement (Experiment 2). And, subjects still make more errors as they transform the stimulus at the new rate through farther distances, but there is a qualitative shift in the increase in response to novel speeds.

This description of movement representation is suggested by the data from the three experiments. A full description of movement as it is represented requires that more is understood about pigeons' perception of movement and movement changes. In addition, a more systematic evaluation of represented movement as it changes over time and distance would test the description offered; certainly it would identify whether an acceleration constant is applied in the process, or whether there is some category for movements applied.

An investigation of movement representation allows for the development of models of perceptual-cognitive function in a direction so far ignored in animal work. In pigeons, as well as in many studied species (macaque monkeys, cats, other avians such as owls), much is known about the neural networks and brain structures involved in movement perception (Granda & Maxwell, 1979). The structuralist view of perception , that percepts are merely additive combinations of color, light, edges, bars, and movement, controls this kind of investigation. While this point of view lends itself to the technique of neural investigation of percepts in intact organisms possible at this time (primarily intracellular recordings) , it may not appropriately describe the perceptual experience of the organism (Hochberg, 1980). It is clear from experiments of illusions and of gestalt psychology with humans that higher level rules of perceptual organization are involved that allow for object constancy across changes in size, orientation, and movement. Object constancy despite change in the environment is a perceptual phenomenon that has clear survival value and there is some evidence that it exists in species other than humans, and specifically in pigeons. An investigation of a moving object as it is perceived and as it is represented begins to explore these issues because in such an investigation, transformations of an object that maintain object constancy are identified. Again, as in the investigation of imagery in pigeons, the goal is to build a model of perceptual-cognitive function.

APPENDIX A

A test of parallelism by nonforced multiple regression analysis.

Stepwise Regression Y_1 :Error Scores 5 X variables

F to Enter	5
F to Remove	5
Number of Steps	3
Variables Entered	3
Variables Forced	0...0

Residual Information Table

SS[e(i)-e(i-1)]:	e ≥ 0:	e < 0:	DW test:
275263.306	223	209	1.597

Stepwise Regression Y_1 :Error Scores 5 X variables

STEP NO. 1 VARIABLE ENTERED: X_4 : parallel.acc*loc

R:	R-squared:	Adj. R-squared:	Std. Error:
.543	.295	.294	21.328

Analysis of Variance Table

Source	DF:	Sum Squares:	Mean Square:	F-test:
REGRESSION	1	81974.108	81974.108	180.213
RESIDUAL	430	195595.167	454.872	
TOTAL	431	277569.275		

STEP NO. 1 Stepwise Regression Y_1 :Error Scores 5 X variables

Variables in Equation

Parameter:	Value:	Std. Err.:	Std. Value:	F to Remove:
INTERCEPT	27.593			
parallel.acc*loc	.001	.0000928	.543	180.213

Variables Not in Equation

Parameter:	Par. Corr:	F to Enter:
SPEED	-.046	.914
speed sqrd	-.22	21.899
location	.25	28.654
quad.acc2*loc	-.249	28.444

Stepwise Regression Y_1 :Error Scores 5 X variables

STEP NO. 2 VARIABLE ENTERED: X_3 : location

R:	R-squared:	Adj. R-squared:	Std. Error:
.583	.339	.336	20.673

Analysis of Variance Table

Source	DF:	Sum Squares:	Mean Square:	F-test:
REGRESSION	2	94220.323	47110.162	110.228
RESIDUAL	429	183348.952	427.387	
TOTAL	431	277569.275		

STEP NO. 2 Stepwise Regression Y_1 :Error Scores 5 X variables

Variables in Equation

Parameter:	Value:	Std. Err.:	Std. Value:	F to Remove:
INTERCEPT	1.089			
location	.298	.056	.211	28.654
parallel.acc*loc	.001	.00009054	.519	173.008

Variables Not in Equation

Parameter:	Par. Corr:	F to Enter:
SPEED	.092	3.654
speed sqrd	-.161	11.412
quad.acc2*loc	-.245	27.309

Stepwise Regression Y_1 :Error Scores 5 X variables

(Last Step) STEP NO. 3 VARIABLE ENTERED: X_5 : quad.acc2*loc

R:	R-squared:	Adj. R-squared:	Std. Error:
.616	.379	.375	20.067

Analysis of Variance Table

Source	DF:	Sum Squares:	Mean Square:	F-test:
REGRESSION	3	105217.548	35072.516	87.095
RESIDUAL	428	172351.728	402.691	
TOTAL	431	277569.275		

STEP NO. 3 Stepwise Regression Y_1 :Error Scores 5 X variables

Variables in Equation

Parameter:	Value:	Std. Err.:	Std. Value:	F to Remove:
INTERCEPT	1.089			
location	.284	.054	.201	27.518
parallel.acc*loc	.003	.0002863	1.141	83.417
quad.acc2*loc	-.000004436	8.488E-7	-.651	27.309

Variables Not in Equation

Parameter:	Par. Corr:	F to Enter:
SPEED	.095	3.88
speed sqrd	.084	3.004

APPENDIX B

Cumulative Record of Sessions in Experiments 1, 2, and 3

APPENDIX B

Cumulative Records of Sessions In Experiments 1, 2, and 3

BIRD #	7	8	9	25	2	14	4	10
Sessions to criterion	10	24	11	12	14	21	16	32
Exp 1	18	18	18	18	18	18	18	18
Sessions to criterion	4	10	16	5	7	6	12	16
Exp 2 (first)	12	12	12	12	12	12	12	12
Sessions to criterion	6	9	2	12	3	12	11	6
Exp 2 (sec.)	12	12	12	12	12	12	12	12
Sessions to criterion	12	3	6	19	8	13	20	17
Exp 3	12	12	12	12	12	12	12	12
TOTAL	86	100	89	102	86	106	125	113

APPENDIX C

SUBJECT TESTS

Experiment 1: ANOVA of subject differences and location differences.

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
subject (A)	7	3355.864	479.409	.335	.9341
data w. groups	48	68735.713	1431.994		
location (B)	2	14095.342	7047.671	10.455	.0001
AB	14	12915.337	922.524	1.369	.1837
B x data w. groups	96	64710.155	674.064		

Note: Subject differences are not significant (p = 0.9341).

Experiment 2: ANOVA of subject differences and speed condition (135°)

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Subject (A)	7	1704.176	243.454	1.819	.2003
data w. groups	40	5353.652	133.841		
Repeated Measure (B)	3	577.625	192.541	2.592	.063
AB	21	2193.279	104.442	1.406	.1051
B x data w. groups	120	8914	74.283		

Note: Subject difference is not significant (p = 0.2003).

Experiment 2: ANOVA of subject differences by speed condition (180°)

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
Subject (A)	7	2948.844	421.264	2.0798	.1044
data w. groups	40	8101.99	202.55		
Speed (B)	3	482.059	160.686	2.367	.0742
AB	21	2386.835	113.659	1.674	.0941
B x data w. groups	120	8145.672	67.881		

Note: Subject difference is not significant (p = .1044).

Experiment 3: ANOVA of subject differences and training vs. testing (135°)

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
SUBJECT (A)	7	1838.965	262.709	1.24	.3043
DATA w. groups	40	8472.866	211.822		
TEST CONDITION (B	1	53.417	53.417	.384	.5389
AB	7	498.198	71.171	.512	.8201
B x DATA w. groups	40	5561.218	139.03		

Note: Subject differences are not significant (p = 0.3043).

Experiment 3: ANOVA of subject differences and training vs. testing (180°)

Source:	df:	Sum of Squares:	Mean Square:	F-test:	P value:
SUBJECT (A)	7	4835.245	690.749	5.329	.0002
data w. groups	40	5185.184	129.63		
Test Condition (B)	1	1147.821	1147.821	6.23	.0168
AB	7	934.99	133.57	.725	.6517
B x data w. groups	40	7370.064	184.252		

Note: Subject difference IS significant (p = 0.0002).
Analyses reported in dissertation are one-way ANOVA's for training and testing. These are presented next, and then the differences when #25 and #4 are removed are shown.

One-Way ANOVA testing subject differences at 180° (n = 8).

Training

Source:	DF:	Sum Squares:	Mean Square:	F-test:
Between groups	7	1415.326	202.189	3.003
Within groups	40	2693.029	67.326	p = .0125
Total	47	4108.355		

Test

Source:	DF:	Sum Squares:	Mean Square:	F-test:
Between groups	7	4354.909	622.13	2.523
Within groups	40	9862.219	246.555	p = .0301
Total	47	14217.128		

One-Way ANOVA testing subject differences at 180° (n = 6).

Training

Source:	DF:	Sum Squares:	Mean Square:	F-test:
Between groups	5	465.56	93.112	1.938
Within groups	30	1441.69	48.056	p = .1174
Total	35	1907.25		

Test

Source:	DF:	Sum Squares:	Mean Square:	F-test:
Between groups	5	2326.691	465.338	2.142
Within groups	30	6518.419	217.281	p = .0876
Total	35	8845.11		

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