ADAPTATION TO VISUO-MOTOR REARRANGEMENT:
A LEARNING PHENOMENON?

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Thesis Declaration

The work reported in this thesis is my own, having been completed within the normal terms of reference in the Faculty of Social Sciences, University of Edinburgh.

JENNIFER FLOOK

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ABSTRACT

This thesis proposes that adaptation to visuo-motor rearrangement is a form of learning. The experimental work reported here supports this view, showing that adaptation in both monkey and man has long-term influences. These take the form of (a) savings on re-adaptation to the same prism, (b) "learning to learn" effects following repeated adaptation to two different prisms presented serially, and (c) accurate prediction of the appropriate response when external cues correlated with the prisms are available. Such effects, analogous to those obtained in conventional learning studies, occur despite the intervention of periods of normal activity between the adaptation experiences. The conventional view that the effects of adaptation are transient, dissipating rapidly following removal of the prisms, is challenged by these findings.

An alternative interpretation is proposed, suggesting that adaptation should be regarded as a form of motor-response learning. This specific proposal is supported by the results of a subsidiary study with squirrel monkeys, in which their ability to differentiate motor responses on the basis of reinforcement contingencies was investigated. It is concluded that the contingencies between self-produced movement and visual consequences, learnt on the basis of response-produced feedback, is the crucial factor in visuo-motor coordination.

CHAPTER 1

WHY STUDY ADAPTATION?

> "Derailments of ontogeny often suggest factors that underlie normal development."
> (Teuber, 1961, p 32).

Research in perception has exploited the use of "derailments" to great effect. The study of spatial perception, for example, has involved the disruption of normal function in the form of "rearrangements" of the relationships between the senses, in particular between vision and the other senses. Such visuo-motor rearrangements consist of the introduction of an optical device, such as a prism, between the perceiver and his environment. An extensive range of transformations may be produced in this way, and the effects of exposure to many of these have been studied: the visual field may be rotated through small angles by prisms (e.g. Mikaelian and Held, 1964), or through 180° by a lens system (e.g. Stratton, 1896); mirrors may be used to produce either inversion or reversal (e.g. Kohler, 1964), wedge prisms to produce lateral displacement (e.g. Helmholtz, 1866) and change of form (e.g. Gibson, 1933); and a lens system or a convex mirror may be used to study the effects of change of size (e.g. Rock, 1965). These transformations of visual stimulation are termed rearrangements since they result in a changed relationship between vision and the other senses. It should be noted that, although the relationship between them is altered, the one-to-one correspondence between visual stimulation and other spatial information is maintained. An object may be seen in a different location from one in which it was seen previously and from which it is felt and heard. However, the topological relationship between the new locations of objects and their old visual positions, still registered by the other senses, is conserved. It is possible that the subject may discover this relationship. Accurate coordination is, however, unknown under conditions in which the one-to-one correspondence is not maintained. Such a situation is termed "disarrangement"(1) and may be produced, for example, by a prism of continuously varying optical power.

Rearrangement situations, therefore, by transforming visual stimulation, disrupt the coordination between vision and the other senses. The effects of such rearrangements may be seen in errors of perceptual judgment when, for example, a subject wearing inverting lenses will make errors when asked whether an object is upright or inverted. Behavioural effects are also apparent when the subject points towards a visual target. After some practice, however, errors of localisation are reduced and coordination between vision and action is restored. This process of adjustment is referred to as adaptation. If adaptation reaches completion, the subject may come to behave as if his vision were undistorted. When the distorting device is removed, however, further errors of localisation will be observed, this time in the opposite direction. These errors are commonly called adaptation aftereffects.

Although this thesis is concerned primarily with visuo-motor rearrangements, adaptation to rearrangements affecting other sensory systems may occur. Investigators of auditory rearrangement (Held, 1955; Freedman et al, 1967) have interpreted their results as

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(1) The term "disarrangement" was originally used by Held (Held & Gottlieb, 1958) to refer to all conditions causing disruption of sensori-motor coordination. Later the use of this term was restricted to cases in which random changes in the relationships between senses are introduced.

involving the same adaptation mechanism as in the visual case. Thus, whilst the experimental work discussed here involves visuo-motor rearrangements, its implications are arguably relevant to the full set of sensori-motor coordinations.

SOME EARLY STUDIES REVIEWED

The earliest experiments on adaptation to visuo-motor rearrangement were reported by Helmholtz:

> "Take two glass prisms with refracting angles of about 16° - 18° and place them in a spectacle frame, with their edges both turned toward the left. As seen through these glasses, the objects in the field of view will all apparently be shifted to the left of their real positions. At first, without bringing the hand into the field, look closely at some definite object within reach; and then close the eyes, and try to touch the object with the forefinger. The usual result will be to miss it by thrusting the hand too far to the left. But after trying for some little while, or more quickly still, by inserting the hand in the field and, under the guidance of the eye, touching the objects with it for an instant, then on trying the above experiment again, we shall discover that now we do not miss the objects, but feel for them correctly. It is the same way when new objects are substituted for those with which we have become familiar. Having learned how to do this, suppose now we take off the prisms and remove the hand from the field of view, and then, after gazing steadily at some object, close our eyes and try to take hold of it. We find then that the hand will miss the object by being thrust too far to the right, until after several failures, our judgment of the direction of the eyes is rectified again."
> (Helmholtz, 1866/1962, p 246).

This is the clear precursor of the technique employed recently in studies of hand-eye coordination in the form elaborated by Held and Gottlieb (1958). During the intervening century, however, investigators concentrated on rearrangements producing inversion and reversal of the visual field.

The tradition of studying major rearrangements derives from the work of Stratton (1896, 1897a, b, 1899). At that time, theories of perception assumed that the inversion of the retinal image by the lens system of the eye was essential to the perception of an upright world. Stratton's work was an attempt to test this assumption by studying the effects of the substitution of an upright retinal image. Although Stratton wore inverting lenses continuously for considerable periods of time, and recorded all his perceptual experiences, his work does not provide a conclusive answer to this question. He experienced considerable behavioural adjustment, recording on the fourth day that:

> "actions appropriate to the new visual perception frequently occurred without any conflict or apparent tendency to react by a misinterpretation of visual positions. My hands, in washing, often moved to the soap or to the proper position in the basin, without premeditation or any need of corrective movement."
> (Stratton, 1897a).

Stratton also appears to have experienced a certain amount of phenomenal change for he reported "harmonious" experiences during active manipulation of objects in the visual field. Such effects seem to have resulted from a re-alignment of felt position with vision rather than a visual change:

> "As long as the new localisation of my body was vivid, the general experience was harmonious and everything was right side up."
> (Stratton, 1897b).

However it is not clear from these accounts whether the inverted visual field came to be perceived as upright, or whether Stratton modified his behaviour to suit a world which remained phenomenally inverted. This distinction between the overt behavioural achievements of the subject and the phenomenal visual experience, considered by later investigators as crucial to the interpretation of adaptation, is obscured by the nature of Stratton's reports.

Other investigators have also tried to demonstrate that "normal" vision could occur under such rearrangement conditions (Ewert, 1930; Peterson and Peterson, 1938; Snyder and Pronko, 1952). These studies all showed considerable behavioural adjustment in the form of increasing accuracy on various tasks involving visuo-motor coordination, e.g. card sorting, peg manipulation, etc. Perceptual adaptation was, however, less successful. Peterson claimed that the world continued to appear inverted, and Ewert reported no change in tests involving judgments of up and down, and left and right, inversion responses being made consistently by all subjects. Snyder and Pronko, however, noted a somewhat ambiguous effect. A subject who was reported to be "adequately adjusted" to right/left, up/down inverting lenses, when asked if the world appeared upside down, replied:

> "I wish you hadn't asked me. Things were all right until you popped the question at me. Now, when I recall how they did look before I put on these lenses, I must answer that they do look upside down now. But until the moment that you asked me I was absolutely

> unaware of it and hadn't given a thought to the
> question of whether things were right-side-up or
> upside-down."
> (Snyder and Pronko, 1952, p 113).

This phenomenon of a spontaneous feeling of "correct" vision experienced by subjects when not concentrating critically on the visual appearance was also found by Erismann and Ivo Kohler in their extensive work on adaptation to various types of rearrangement (Kohler, 1964). As with Snyder and Pronko's (1952) subject, when questioned on their visual experiences, these subjects also became confused. For example, one subject, after wearing left/right reversing spectacles for fifteen days, had the following experience:

> "'It seems that everything in vision is the way it really is; ..... just as they would feel if I were to touch them.' Professor Erismann comments: 'Did you experience this visually?' But this critical question is too much. The subject withdraws: 'Please ..... I can't say I saw this correctly ..... I sat in the car and didn't think about anything in particular, and suddenly I thought that people walked by on the correct side, and not through me.'"
> (Kohler, 1964, p 154).

The work of investigators such as Kohler reflects a move away from the specific problem of the inversion of the retinal image into the domain of spatial perception in general. Such a move permitted a change in the type of rearrangement under investigation. Major rearrangements such as inversion of the visual field require exposure periods of days or even weeks to achieve adaptation. Adaptation to lateral displacement, on the other hand, as Helmholtz (1866) discovered, occurs within minutes. The use of such minor rearrangements, permitting the independent manipulation of different vectors of space, e.g. up/down, left/right, has the advantage that adaptation is not only rapid, but occurs progressively, providing a quantifiable error profile. Thus the development of a technique such as that elaborated by Held and Gottlieb (1958), provides a practical means of obtaining significant adaptation following brief exposure to prismatic rearrangement effects. Held's work marks a revival of interest in this field, inspiring research which continues to the present day, and the following chapter is devoted to a discussion of his theory and findings.

CHAPTER 2

HELD'S POSITION

Held developed his technique (Held and Gottlieb, 1958) to show that adaptation need not be explained by "some variant of that classical paradigm of learning - trial, error, and correction", for he believed (on the basis of results from a previous experiment (Held, 1955)) that adaptation could occur without the subject receiving information about his errors of localisation. Following Helmholtz's (1866) report of adaptation to lateral displacement of vision produced by wedge prisms, Held developed a procedure whereby the subject, looking through prisms, watched his hand move in an otherwise empty visual field. No targets or boundaries were visible, only the hand. The head was fixed by the use of a bite-board, and so no parallax information was available. This "exposure" condition therefore allowed no opportunity for the subject to obtain error information for use in "trial-and-error" learning. Measurements of the adaptation could also be made without the subject seeing his errors. This was achieved by the use of a mirror arrangement, which allowed the subject to mark the image of targets while seeing neither his hand nor the marks he made. Held's technique provides a means of obtaining accurate measures of the amount of adaptation occurring under a variety of possible conditions. Exposure periods of three to five minutes result in significant shifts in localisation. Held comments that "The technique should prove useful for isolating the conditions of exposure that produce adaptation." (Held and Gottlieb, 1958). The determination of these conditions was the subject of a series of experiments which followed.

These experiments (Held and Hein, 1958; Held and Schlank, 1959) compared "active" and "passive" conditions of prismatic exposure. In the active conditions the subjects made the movements themselves, whereas in the passive conditions the experimenter moved the subject's arm. Significant adapation was found only in the active conditions. Held concludes that:

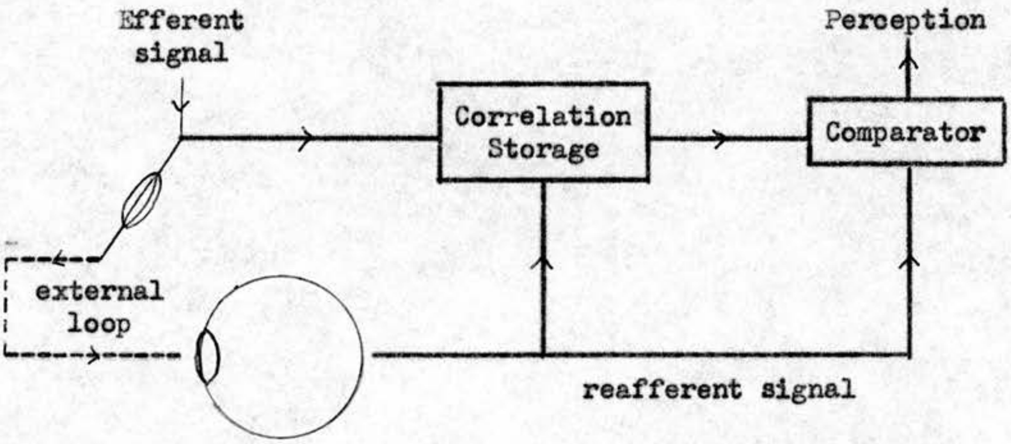
> "not simply movement, but self-produced movement with its contingent reafferent stimulation is the critical factor in compensation for rearrangement."
> (Held and Bossom, 1961).

The conceptual content of Held's work consists of a model of visuo-motor coordination based on the use of visual feedback accompanying movement. This model is an extension of von Holst's work on the relationship between the Central Nervous System (CNS) and the peripheral senses and muscular movement (von Holst, 1954). Von Holst distinguished between efference (motor impulses) and afference (impulses produced by stimuli in the receptors of the organism). Afferent signals have two sources: stimulation produced by muscular activity of the whole or part of the body, which is termed "reafference"; and stimulation produced by external factors - "exafference". He further proposed that the efferent signal leaves an "image" of itself (the Efference Copy) somewhere in the CNS to which the reafference of this movement may be compared in a summation process. Since the two signals are complementary, if they are equal they will compensate exactly. Any difference will be registered and influence either the movement or perception.

Held (1961) adapted von Holst's model to the case of visuo-motor adaptation by adding the "Correlation Storage" as shown in Figure 1. The skeletal muscle represents any motor system that can be a source of reafferent visual stimulation. The Correlation Storage is introduced in place of the summation between monitored efferent and reafferent signals in von Holst's model. According to Held:

> "the reafferent signal is compared (in the Comparator) with a signal selected from the Correlation Storage by the monitored efferent signal. The Correlation Storage acts as a kind of memory which retains traces of previous combinations of concurrent efferent and reafferent signals. The currently monitored efferent signal is presumed to select the trace combination containing the identical efferent part and to activate the reafferent trace combined with it. The resulting revived reafferent signal is sent to the Comparator for comparison with the current reafferent signal. The outcome of this comparison determines further performance."
> (Held, 1961, p 30).

Figure 1.



Schematised process assumed by Held to underlie the consequences of rearrangement, neonatal development, disarrangement and deprivation on visuo-motor coordination (from Held, 1961).

This model is basically a servo-mechanism which operates as a self-correcting process maintaining the coordination between the visual and motor systems. Any mismatch between the current reafferent signal and the revived signal provides the basis for adjustments to future behaviour. In the rearrangement situation atypical combinations of efference and reafference are registered. As adaptation proceeds, these new combinations are stored, with the result that: "The same monitored efferent signal may now revive either an old or a new reafferent trace or both." With further experience of the new conditions "this ambiguity is gradually eliminated in favour of the more recent combinations." (Held, 1961).

Held claims that his model represents the mechanism underlying three processes:

> "(1) the development of normal sensorimotor control in the young, (2) the maintenance of that control once it has developed and (3) the adaptation to changes or apparent changes in the data reported by the senses of sight and hearing."
> (Held, 1965).

In order to support this claim, Held has devised experiments to show that the same critical factor - active, self-produced movement - is involved in all three processes. Experiments on adaptation have been described above. Disarrangement, produced by the use of prisms varying continuously in optical power, has been shown to produce deterioration in hand-eye coordination after active, but not passive exposure (Held and Freedman, 1963). This was interpreted as support for the involvement of active movement in maintaining coordination.

This distinction between active and passive movement is applied to the development of visuo-motor coordination in an experiment (Held and Hein, 1963) which involved rearing pairs of kittens whose only experience in the light was in the experimental apparatus. This consisted of a "carousel" which allowed one kitten to locomote around the chamber while its movements were transferred to a gondola which transported the passive kitten. Both kittens travelled along equivalent paths and so received equivalent visual stimulation from the uniform striped environment. The gondola occluded the passive kitten's body from view. Tests of visuo-motor coordination revealed that the passive kittens failed to develop normal coordination whereas the active members of each pair were successful. Held's interpretation of this experiment is that active, self-produced movement with its accompanying visual feedback is essential to the development of visuo-motor coordination.

Held's model and technique have been widely accepted as the "paradigm" (1) for studying adaptation to rearrangement of visuo-motor coordination. The widespread acceptance of this paradigm has produced a proliferation of experiments:(Efstathiou et al, 1967; Freedman et al, 1965; Freedman et al, 1967; Graybiel and Held, 1970; Hardt et al, 1971; Held, 1962; Held and Bossom, 1961; Held et al, 1966; Held and Mikaelian, 1964; Held and Rekosh, 1963; Kalil and Freedman, 1966; Mikaelian, 1971, 1974a, b; Mikaelian and Held, 1964). These experiments, which follow the paradigm

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(1) Kuhn's account of the progress of science includes the concept of the paradigm: "On the one hand, it stands for the entire constellation of beliefs, values, techniques and so on shared by the members of a given community. On the other, it denotes one sort of element in that constellation, the concrete puzzle-solutions which, employed as models or examples, can replace explicit rules as a basis for the solution of the remaining puzzles of normal science." (Kuhn, 1970, p 175).

closely, by studying, for example "Interpedal generalisation of rearranged eye-foot coordination" (Mikaelian, 1971), demonstrate, perhaps, the activity of "puzzle-solving" which Kuhn has shown to be typical of "normal science", (1) but do not show any conceptual advance.

In summary then, Held's model has two main features: (1) a servo-mechanical process is proposed as the basis of the coordination system, and (2) this single mechanism is proposed as the basis for the three processes of adaptation, maintenance and development of visuo-motor coordination. Held and his colleagues have reported many experiments which they have interpreted as supportive of this position. However, there are empirical findings which challenge various features of the model. Some of the more controversial points will now be considered.

The evidence against Held's model

Several investigators have challenged the necessity for active movement by demonstrating adaptation under several "passive" exposure conditions (Howard et al, 1965; Templeton et al, 1966; Wallach et al, 1963). In Howard's experiment, for example, subjects who were hit repeatedly in the mouth by a rod while wearing prisms showed significant adaptation, whereas a control condition in which the rod was stopped before touching the face produced no effect. The adaptation seems to have resulted from the conflicting sight and felt position of the rod. Thus Howard and Templeton conclude:

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(1) "Normal science does not aim at novelties of fact or theory, and when successful, finds none." (Kuhn, 1970, p 52).

> "discordant exafferent stimulation, which gives a passive subject 'information' regarding optical distortion, may lead to at least some visuo-motor adaptation."
> (Howard and Templeton, 1966, p 393).

Held attempted to defend his model by claiming:

> "The conditions which have so far been shown to produce adaptation to rearrangement without self-produced movement do not appear to have the generality of the motor-sensory feedback loop. As far as is known these conditions do not yield full and exact compensation, and they do not appear relevant to the development of the neonate."
> (Held and Mikaelian, 1964).

However, Held's own experiments with "active" exposure of similar duration resulted in small amounts of adaptation: Held and Hein (1958) and Held and Mikaelian (1964) reported adaptive shifts of 7.3"/22" and $4.9^{\circ}/11^{\circ}$ respectively. Thus, although it is true that the "passive" conditions did not produce complete compensation, the adaptation appears comparable in magnitude to that obtained by Held after a similar period of exposure.

Significant adaptation of this sort obtained under conditions in which no active movement is permitted has been interpreted as based on "informational discrepancy" (Wallach, 1968) or "discordant exafferent stimulation" (Howard and Templeton, 1966). Thus it is Held's model, requiring reafferent feedback, which may not have sufficient generality. By contrast, a model which can use information from any available source as the basis of the compensation seems to be demanded by the empirical evidence.

Held's second reason for claiming that adaptation obtained under passive conditions differs from that obtained by self-produced movement is the assumption that the same process underlies the development of visuo-motor coordination. However, a close examination of the evidence reveals that Held's studies do not in fact show that visual feedback from active movement is essential to normal development.

Held's experiment (Hein and Held, 1963) on neonatal development of visuo-motor coordination in kittens shows that the passive condition in the "kitten carousel" does not permit the development of normal coordination. However, when the "passive" condition is examined more closely it becomes apparent that these kittens were able to make active movements, for example, turn their heads and move their legs, although these were not coordinated with the changes in visual stimulation they experienced. The passive kittens were in fact in a "disarrangement" condition where no invariant contingency relationship existed between their movements and visual stimulation. Thus this experiment should be taken as evidence for the effect of <u>disarrangement</u> under conditions involving <u>active</u> exposure!

Held has also reported rearing studies with monkeys (Held and Bauer, 1967, 1974; Bauer and Held, 1975). In these experiments young rhesus monkeys were reared wearing opaque collars preventing sight of their hands and bodies. These monkeys failed to show normal hand-eye coordination when released. In the original study, while wearing the collars, the monkeys were given training in which they were taught to extend an arm when a feeding bottle was presented. In a discussion of this experiment Walk and Bond (1971) comment:

> "their procedure essentially taught the animals that visual objects had no relation to the position of the hands, since their animals were not required to reach in the direction of the bottle."
> (Walk and Bond, 1971).

Thus it is hardly surprising that when the collar was removed these animals failed to take any account of visual information about the location of the feeding bottle, but instead produced the stereotyped arm movement they had been rewarded for during the experimental period. Failure to develop normal visuo-motor coordination may not be due therefore to lack of visual feedback from active movement, but due to the learning of some abnormal relationship between visual stimulation and motor responses.

In their own experiment, with the same rearing conditions, Walk and Bond (1971) successfully trained monkeys to reach for a stick that extended upwards into the visual field and downwards into the tactual field. This stick was presented in several position. Following this training, reasonably accurate visual reaches were shown when the collar was removed. Considerable transfer to the untrained hand was also observed. Thus they concluded that deprivation of sight of the hands does not prevent the development of visually guided reaching.

Held and Bauer's (Held and Bauer, 1974; Bauer and Held, 1975) subsequent studies involved a modified training procedure in which an accurate response was required to visual stimulation during the experimental period. In this apparatus the monkey was trained to reach for, and pull, a manipulandum situated below a food reward. Training was given in one position and with one hand only. Generalisation tests showed decrements in accuracy, as did tests for intermanual transfer.

Control subjects reared under the same conditions, but with a transparent collar permitting sight of the limbs and body, showed no such decrements on these tests. Bauer and Held (1975) interpreted these results as showing that monkeys reared without sight of their limbs or body could be conditioned to reach with one hand in a given direction. This learning was specific to the training condition, showing a generalisation gradient when tested on new directions. The control monkeys did not show such specificity of learning. However, the apparatus was such that it is not surprising that the experimental animals did not reach in the direction indicated by the food reward. How could they know that the manipulandum which had been presented in one position, and which they could not see, was attached to the slide arrangement which brought candy to their mouths? The control animals had at least the opportunity of seeing that the two might be related.

In general, therefore, Held's rearing studies have shown that neonatal kittens and monkeys can learn an arbitrary relationship between vision and reaching. However this does not prevent them from "adapting" to the normal environment when released: both kittens and monkeys showed normal coordination within a few days of their release from the experimental conditions. Thus Held's conclusion that "the sight of the moving hand is responsible for calibrating the metrical space of vision and that of reaching" (Bauer and Held, 1975) does not appear fully justified.

An evaluation of Held's theoretical position

Held (1961) claims that a servo-mechanical process is adequate to account for all three processes of adaptation, maintenance and development of visuo-motor coordination. A servo-mechanism is a self-correcting process using feedback information to maintain a specified state despite external pressures which may cause change. The basic principle is that if any mismatch is registered between the current and desired states an adjustment is made to reduce this discrepancy. This ensures that the system operates within a limited band-width of error, fluctuations being compensated for as soon as they are recorded. Such a system can therefore <u>maintain</u> an established coordination within a certain range of error. However, regulation within a certain band-width of error round a particular specified state is <u>all</u> that such servo-mechanical processes are capable of. The servo-mechanism was conceived originally in an engineering context as a model of a control system which can

> "appreciate continuously the discrepancy between the state of the machine realised at a given moment and the final aim assigned to it by its constructor." (Paillard, 1960).

Clearly the control system has no capacity for specifying the aim or desired state, this must come from an external source. Thus Thomson (1977) has criticised theories of visuo-motor control, e.g. Bernstein's (1967) model of the regulation of movements, which rely on servo-mechanical feedback loops. (1) Thomson suggests that the desired state, or "Sollwert" in Bernstein's terminology, must be formulated

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(1) Bernstein in fact concluded that: "how and by what physiological means the image of the envisaged or required effect of the movement may function as a guiding principle of the motor structure of an act, and as a program for the direction of the effector element, is a problem to which there are as yet no signs of any concrete or determinate answers." (Bernstein, 1967, p 133).

on the basis of visual information. This takes the form of a "program" for action which can then be run off without need of further visual information in the form of the continuous monitoring required by servo-mechanical control. Intermittent sampling from the visual array would then be sufficient to maintain accuracy.

The problem of how the organism formulates such an action program on the basis of visual information is the subject of this discussion. From Thomson's analysis it is clear that this operation is not under servo-mechanical control. Ruch, too, following a detailed analysis of servo-mechanical processes, concluded that <u>output-informed feedback</u> control is inadequate and suggested that "what may be called input-informed" processes are required (Ruch, 1951). Thus Held's model cannot account for the <u>development</u> of either the initial coordination in the neonate nor the new adaptation coordination in the mature organism under rearrangement conditions.

What function then might a servo-mechanism play in adaptation? It is clear that the rearrangement causes discrepancies between vision and the other senses and between current and previous visual stimulation. Such mismatches may be registered on the basis of feedback information as suggested by Held (1961). However, the errors in this situation fall outwith the range previously encountered in normal conditions. How then does the system cope with this novel situation? Held's model does not specify the type of "adjustment" which occurs to reduce the registered discrepancy and there appears to be no feature of the control system which could translate this discrepancy into either a <u>behavioural</u> adjustment or a <u>perceptual</u> change.

Thus Held's (1961) model is considered unsatisfactory as an account of the relevant findings. For a servo-mechanical control system is incapable of producing a new coordination, its only function being the maintenance of accuracy within a well-defined coordination system. Although Held's approach now seems inadequate, his work continues to be regarded as the established "paradigm" in the field. As Kuhn (1970) points out, the life of a paradigm does not end when contradictory evidence is reported. A new model, which provides a more comprehensive account of the data and suggests new directions for research, must emerge to take its place. Does such an alternative to Held's work exist in the domain of adaptation research? The following chapter reviews several different approaches in an attempt to answer this question.

CHAPTER 3

Held's (1961) model of adaptation is based on changes mediating the interaction between afference (input) and efference (output). The models reviewed in this chapter as alternatives to this established view are presented according to whether they involve changes on the input side, i.e. within the *perceptual* system (Gibson, 1966; Rock, 1966; Dodwell, 1970), or on the output side, i.e. *behavioural* adjustment (Kohler, 1964; Taylor, 1962). The position of "perceptual" theories on adaptation is predictable from their epistemological view that knowledge comes through the senses and that accurate registration of the external world is a *perceptual* achievement which subsequently prescribes action. To act appropriately, on this view, it is first necessary to perceive appropriately. Hence, adaptation to sensory distortion must proceed from perceptual accommodation. By contrast, *behavioural* accounts of adaptation are free to subscribe to an epistemological position which holds that one important source of knowledge is obtained through action and feedback. On this view, the relationship between action and perception is "conditional", i.e. perception does not entail particular behaviour. Applied to the problem of adaptation, behavioural theories would insist that the role of action is at least equal to that of perception in establishing new sensori-motor correlations.

ADAPTATION AS A PERCEPTUAL CHANGE

Gibson's model

J. J. Gibson (1959, 1966) suggests that a process of normalisation or veridicalisation of perceptual experience follows continuous exposure to stimuli deviating from the perceptual "norms". These norms, or neutral values, provide the framework for perceptual judgments in a way similar to the operation of "adaptation levels" described by Helson (1964). Gibson claims that perceptual adaptation to any situation which differs from "normal", i.e. that to which the perceiver is accustomed, consists of a process of extraction of the new invariants, or constants, specified by the visual array. The result of this process is that the norm, or adaptation level, of each perceptual quality is reset to the current mean of the environmental values.

The research which led to this interpretation began with a study of adaptation to curvature:

> "... a curved line, when perceived for any considerable period of time, becomes phenomenally less curved than it was at the beginning of the period, and at the end of the period an objectively straight line will seem curved in the opposite direction. This fact holds whether the curvature is actually in the object, or is induced by the distorting effect of prisms. The immediate inference was that we were dealing with a phenomenon strikingly similar to simple sensory adaptation of the type exhibited by color and perhaps temperature. We apparently have to look within the perceptual process itself for the explanation of the adaptation."
> (Gibson, 1933).

Similar effects were subsequently obtained with tilted lines (Gibson and Radner, 1937; Gibson, 1937). Further experiments extending the similarity with sensory adaptation demonstrated simultaneous contrast effects, and the restriction of the aftereffects to the specific area of the field occupied by the curved or tilted line.

These effects were re-interpreted by Köhler and Wallach (1944) as examples agreeing with their "satiation" theory of sensory adaptation. This model predicts that a particular pattern of excitation gradients in the visual projection system will result from prolonged presence of a contour in a constant retinal position. Gibson (1937), however, showed that his aftereffects occurred with or without eye movements, and transferred, with some loss, to the previously unexposed eye. Such findings are incompatible with the satiation model.

A further important finding was the occurrence of these aftereffects following inspection not only of prismatically induced curvature or tilt, but also of stimuli which were *objectively* deviant from the norm. This rules out the possibility of conscious correction or behavioural adjustment as contributing factors. Hence the interpretation of these effects as due to some normalising *perceptual* process appears justified. Such a process, however, requiring only prolonged inspection of the distorted stimuli, cannot readily account for the results obtained from exposure to rearrangements such as lateral displacement and rotation of the visual field (e.g. Kohler, 1964). In these cases it seems likely that other types of adaptation are involved.

Empirical evidence in support of this view has been reported by Held (1962) and by Mikaelian and Held (1964). Gibson's negative aftereffects result from mere *inspection* of visual stimuli deviating from the norm. In an experiment designed to investigate the different effects of active and passive exposure to optical rotation of the visual field, Held (Mikaelian and Held, 1964) discovered two types of adaptation. The first corresponded to Gibson's negative aftereffect, and appeared to be a purely visual effect resulting from passive inspection of a structured visual field rotated by 20°. This effect was small, not exceeding 3°. Active movement under the same conditions resulted in full compensation. These two types of adaptation were further distinguished by the fact that active movement in an unstructured environment, containing only randomly positioned luminous spheres, resulted in significant adaptation. Passive inspection of this environment produced no effect, confirming Gibson's (1959) statement that the aftereffect requires exposure to an environment deviating from normal along specifiable dimensions.

Thus it appears that a normalising effect, resulting from mere inspection of deviant visual stimulation, may occur under conditions in which a structured environment is viewed. This effect is small, however, and reaches an asymptotic value within a few minutes. It can be distinguished therefore from the process referred to as adaptation, which reduces errors of localisation and, given sufficient exposure time under appropriate conditions, restores accurate visuomotor coordination.

Rock's model

Rock's (1966) model of adaptation is based on a different type of change within the perceptual system. Like Gibson (1966) he views adaptation as the attainment of "veridical" perceptual experience despite the presence of the optical distortion. For Rock, adaptation is:

> "... a change in the direction of normal perception. If adaptation were complete, the world would appear as it did before it was viewed through the distorting device. It would look exactly as it looks to us." (Rock, 1966, p 1).

Rock argues that there is no a priori reason why veridical perception should not result from visual input received in any form which maintains a consistent relationship with the spatial attributes of objects in the external world. Such attributes are not specified in absolute terms in the retinal image, but only with respect to other objects and to the perceiver. Thus the ordering of the objects may be specified, but not the direction of the order. Rock concludes, therefore, that the orientation of the retinal image is irrelevant to the information necessary for "upright" vision. Since the distortions, or rearrangements, commonly employed in adaptation studies do not alter the relative spatial attributes of objects in the visual field, this argument leads to the proposition that no change in perceptual attributes should be experienced as a result of a transformation of the entire image. Perceptual disruption is experienced, however, when distorting spectacles are first worn, e.g. subjects wearing inverting lenses consistently report that the world looks upside down. To cater for this finding, Rock suggests that past experience may be implicated:

> "... memory carries some record of the specific or absolute nature of the stimuli that previously gave rise to the experiences in question (the stimulus copy aspect of the memory trace, in contrast to the representational aspect of the memory trace), by virtue of such traces, the transformed proximal stimuli lead to non-veridical experiences."
> (Rock, 1966, p 251).

Thus disruption of perceptual experience results from the change in the relationship between proximal and distal stimulation. Adaptation should therefore be possible when the perceiver discovers the new form of this relationship.

For Rock (1966) therefore the adaptation process is regarded as a progressive build-up of new memory traces which supplant the old ones. He considers this to be analogous to an A - B, A - C transfer of learning paradigm, where the same proximal stimulus (A) must be associated with a new "response" (C). Since frequency must favour the old traces and recency the new ones, a stage in which the two associations are of equal strength will occur, resulting in "double localisation" during adaptation (Held, 1955; Held and Bossom, 1961). Rock suggests that a process analogous to the resolution of physical forces may produce perceptual judgments which appear to be a compromise between the two "responses", the resultant being closer to the stronger of the two determinants. Such a process could also account for the gradual progress of adaptation towards veridical judgments.

The new traces are built-up on the basis of visual information as to where objects are actually located in relation to the perceiver. Rock suggests that such information might be available from three sources: (1) direct sight of the body, (2) movement of the observer even when the body is not directly visible, and (3) the presence in the visual field of familiar objects whose actual size, orientation or shape is known. Thus the adaptation is based primarily on visual information, although if this is ambiguous, Rock suggests that proprioceptive information may be a contributing factor. If appropriate information is available adaptation will occur, and veridical perceptual experience will be restored once "traces of the transformed image have been associated with veridical information about the properties of objects." This association, once formed, does not require the continued presence of the information on which it was based - sight of the body etc - but continues to operate until a further change occurs. Thus Rock's interpretation of adaptation does not involve a transformation of the visual input itself, but rather a change in the association between perceptual experiences and proximal stimulation.

Dodwell's model

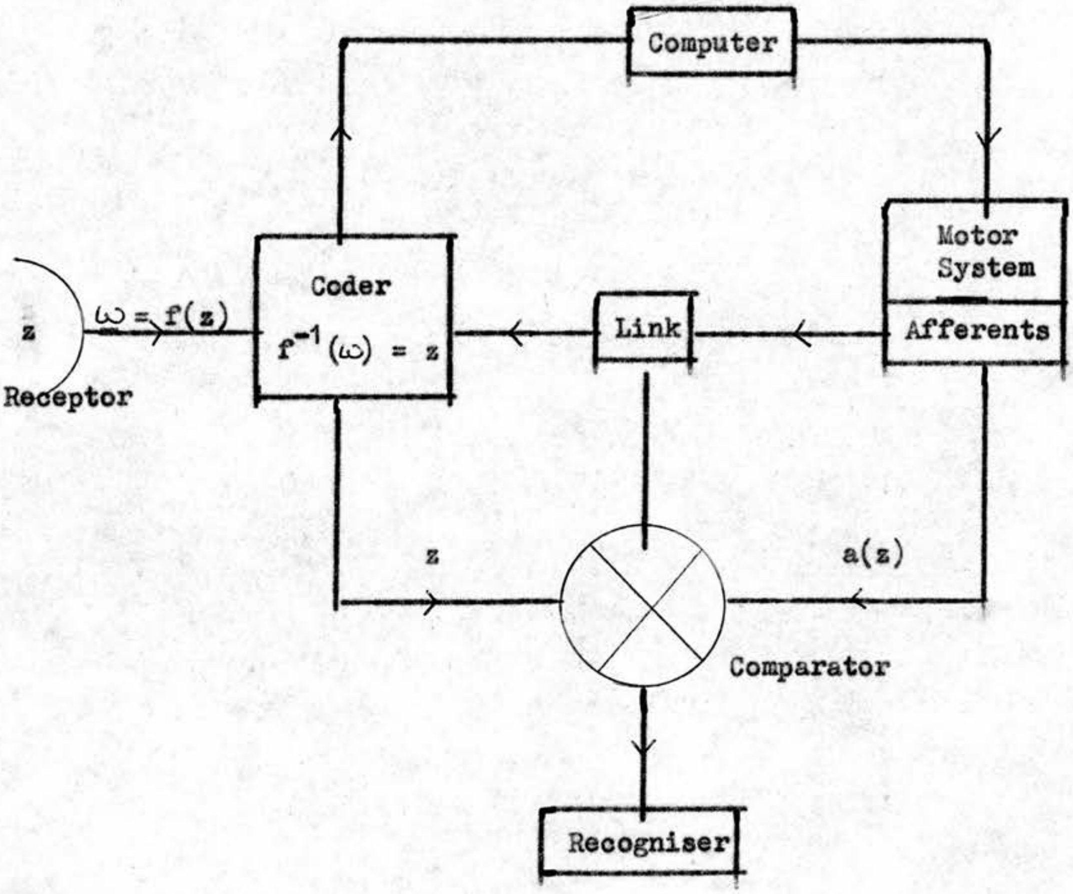
This model has been presented in the context of a theory concerned primarily with pattern perception. Dodwell (1970) presents no empirical evidence of his own, but assumes the following findings to be accepted:

> "1. Whole-field distortions produced by lenses, prisms and mirrors are adapted to, at least partially, by most human observers.
>
> 2. Virtually complete adaptation can occur, even to 'radical' distortionssuch as inversion of the field, in the sense that in time the observer is able to coordinate his movements with the distorted visual input, and apparently to behave normally in the distorted visual environment.
>
> 3. There are numbers of cases where complete <u>phenomenal</u> adaptation has been reported, even to 'radical' distortions. That is, the observer reports that his visual world <u>appears to be normal</u>, and this is evidently not necessarily the same condition as the coordinative adaptation described in item 2.
>
> 4. Some degree of adaptation can occur quite rapidly, if the distortion is a 'mild' one such as displacement of the visual field to one side by a few degrees.

> "5. Typically, however, adaptations are partial, and established gradually. For example, if visual directions are displaced x^o to the right, the subject adjusts as if the displacement were cx^o, $c < 1$. But this partial adaptation tends to be <u>consistent</u>, that is, the observer does not fluctuate between 0^o and x^o of adaptation.
>
> 6. Most devices which produce 'static' distortions (changes of apparent visual direction for points in the visual field with the head and eyes being held still) also produce 'dynamic' distortions when the head moves. These also can be adapted to in both ways (items 2 and 3).
>
> 7. On removal of the distorting medium a reverse distortion appears, and is equal and opposite to the adaptation to the initial distortion.
>
> 8. The reversed distortion itself dissipates with time, until 'normality' is restored.
>
> 9. Adaptation occurs to a variety of distortions which are continuous spatial functions of the normal input; where, however, a sudden break in the distorted visual field is introduced, poor adaptation occurs in the neighborhood of the discontinuity." (Dodwell, 1970, p 159).

In outlining his thesis, Dodwell proposes that adapation consists of a change in the translation from retinal image, or proximal stimulus, to visual perception. He has shown that all the distortions to which adaptation has been achieved can be represented mathematically by "conformal" transformations, or a combination of such transformations, of the normal visual input. In mathematical terms, a conformal transformation, or mapping, is expressed by the relation $\omega = f(z)$, where $z = x + iy$, a complex number. For each such transformation there exists an inverse function, $f^{-1}(\omega) = z$, which maps points in ω onto z. A one-to-one correspondence holds between points in ω and z in each direction. Dodwell proposes that the major component of the adaptation process is the retransformation of the distorted visual input to its normal form by the operation of the appropriate inverse function. A schematic representation of such an adaptation process is shown in Figure 2.

Figure 2.



A model for the adapting visuomotor system (from Dodwell, 1970).

The operation of this system is described as follows:

> "When the normal input z reaches the coder, this 'veridical' representation of the visual field passes to the computer which controls motor output. This in turn produces reafferent stimulation a(z) which is matched with the coder's output by the comparator. If the two agree, events in the visual field are recognized, and the link is not activated. However, when the input to the coder is $f(z) = \omega$, visual and proprioceptive information do not match, the link is activated, and its function is to cause the coder to apply some $\phi(\omega)$ to the visual input, so as to reduce the mismatch. If the coder attains $\phi = f^{-1}(\omega)$, then visual and proprioceptive information again agree, stable recognition occurs, the link is shut off, and $f^{-1}(\omega)$ continues to be applied until further mismatches occur in the comparator."
>
> (Dodwell, 1970, p 173).

Dodwell distinguishes between two categories of distortion. "Mild" distortions, e.g. displacement, conserve the spatial ordering within the visual field. "Radical" distortions, e.g. inversion and reversal, change this ordering. The conformal transformations which describe these two categories of distortion can be distinguished by the fact that mild distortions are represented by functions involving constants in an additive or multiplicative operator, whereas radical distortions require operators which include values of the argument (x and y), e.g. logarithmic functions. In practical terms this means that mild distortions can be reduced by a gradual process of successive approximations, while radical distortions will involve step-functional processes. This distinction does not necessarily imply that different processes must be involved in the adaptation to the two types of distortion, but rather that different profiles of the progress of adaptation may be observed.

In a further elaboration of this model, designed to fit the adaptation process into his wider, multistage model of visual pattern perception, Dodwell included the possibility of changes in the visuo-motor coordination system in addition to the changes in visual coding. This modified version provides the basis for two types of adjustment, i.e. in visuo-motor coordination and in phenomenal adaptation. It was suggested that the visuo-motor coordination system may adapt more rapidly, resulting in behavioural adjustments before perceptual adaptation is complete. This accounts for the two forms of adjustment reported by Kohler (1964) and Hay and Pick (1966). In Dodwell's model they appear to be independent, although both operate on the information from any mismatch registered by the comparator.

Thus Dodwell's model includes the possibility that adaptation may involve more than one type of recalibration. Since there has been considerable controversy surrounding the exact nature of the changes which occur following exposure to rearrangement, this possibility has some plausibility. Dodwell (1970), however, does not elaborate the conditions necessary for each type of adaptation, the relative importance of the different components, or the possibility of interaction between them.

An evaluation of the perceptual approach to adaptation

The case advanced by the proponents of models of adaptation based on changes within the perceptual system is far from convincing. The changes demanded by this position should manifest themselves as alterations in perceptual judgments which occur either in the absence of behavioural adjustment, or at least prior to it. Although Gibson (1933) demonstrated such changes in the perception of curvature, it has been shown that these effects are not representative of adaptation to visuo-motor rearrangement. Similarly, the "immediate correction" effects reported by Rock (Rock et al, 1966) cannot be considered true adaptation. In this case, the effects can be attributed to a change in the environmental reference, rather than to a change in the perceived relationship between objects and the self - Rock's (1966) own definition of adaptation. Since Dodwell (1970) reports no evidence of his own, the assumptions of the perceptual approach remain unsubstantiated by empirical data.

In conclusion, it may well be that a theoretical concern with how the world comes to appear "normal" may be misplaced since some rearrangements do not in fact produce abnormal visual stimulation. Lateral displacement of the visual field, for example, causes the subject to experience a view of the world which is normally experienced by a different orientation of the eyes. This scene is, however, visually normal, assuming that there are no extraneous effects due to the optical device. The rearrangement does not produce visually abnormal stimulation, it merely produces a new relationship between the same visual stimulation and the orientation of the eyes and head. This produces a change in the relationship between vision and the other senses, since objects are seen as displaced to one side of their felt position. This is the crux of the matter - it is not just the visual appearance of the world which must be adapted to, but rather the relationship between vision and the other senses. The perceptual interpretations of adaptation discussed so far propose that this discrepancy is reduced by a change in visual perception. An alternative interpretation is that changes occur in the felt position of the relevant parts of the body. Such an interpretation was proposed by Stratton to account for the changes he experienced in egocentric localisation (Stratton, 1899). More recently Harris (1963, 1965) has developed this account of adaptation in terms of changes in position sense, which he termed proprioceptive changes.

Harris' model

Harris (1965) proposes that adaptation is based on a change in the felt position of various parts of the body. He uses the term proprioceptive to describe such changes in an attempt to distinguish between the position sense of relative locations of parts of the body, and the perception of movements of parts of the body, which may be called kinesthesis. Such changes result from a perceived discrepancy between visual and proprioceptive information regarding the position of a part (or parts) of the body. When these two senses conflict, proprioceptive changes occur so that the subject comes to feel that his limb is where he saw it through the prism. This results in non-veridical position sense of that limb, as the subject's judgment of its position relative to the rest of the body is now incorrect.

In his original statement of this hypothesis (Harris, 1963), only the hand-eye coordination system was considered. Harris argued that if a subject adapted to lateral displacement using only one arm, then the unexposed arm should not be affected by any proprioceptive change. Experimental evidence was reported to support this prediction: lack of transfer of the adaptation to the unexposed arm suggested that the adaptive change did not occur within the visual system, but the possibility existed that the change involved a recalibration of the visuo-motor correlation (Held, 1961). However, the adaptation transfered to auditory targets, indicating that the change affected more than the visual or visuo-motor coordination systems. The adaptation also transfered to new target positions and so was not due to the learning of specific motor responses.

Subsequent research showed that when head movements are permitted during the exposure period, some intermanual transfer occurs (Hamilton, 1964). The proprioceptive-change hypothesis was therefore extended (Harris, 1965) to include changes in the felt position of any part of the body involved in the movements in the exposure situation. Thus the muscles of the neck or eyes may be involved in the adaptive change.

This proprioceptive-change hypothesis assumes that vision is the dominant sense, with proprioception changing to accord with it, even though this may produce non-veridical proprioceptive impressions. Support for the dominance of vision is found in studies demonstrating 'visual capture' (Rock and Victor, 1964; Rock and Harris, 1967). When visual and tactile impressions were put into conflict experimentally, no change in visual judgments was found, whereas tactile judgments were altered and brought into line with vision. These new tactile judgments continued when the subject closed his eyes, indicating that the information from touch was not blocked or ignored when it conflicted with vision, but was transformed to produce new perceptions consistent with those from vision (1).

---

(1) It should be noted that Rock (1966) cited these experiments as evidence <u>against</u> a model of visual adaptation based on proprioceptive information. This interpretation assumed the existence of <u>visual</u> adaptation, a point which has already been questioned.

Harris' proprioceptive-change hypothesis is also able to account for the results obtained by those working within Held's paradigm. For studies of the accuracy of position-sense have shown that judgments depending on proprioceptive information are:

> "... significantly more accurate and less variable after self-induced displacement of the positioned hand than after passive displacement."
> (Paillard and Brouchon, 1968).

Thus changes in felt-position would be expected to occur to a greater extent under exposure conditions involving self-induced movement as compared to equivalent exposure with passive movements - exactly what has been found. Paillard and Brouchon's (1968) work indicates that some information regarding position-sense might be available from passive movement and so the occurrence of adaptation under such exposure conditions is not incompatible with Harris' interpretation.

Harris' (1965) proprioceptive-change model appears therefore to be reasonably successful in accounting for many of the empirical findings. Position sense, or proprioception, may, however, have both afferent and efferent components: receptors, muscles and tendons in the joints, for example, supply afferent information which may be used to indicate position; in addition, certain patterns of muscle efference typically result in the movement of parts of the body to certain positions. This second "central" component has been shown by Taub (Taub, 1968; Taub and Berman, 1968; Taub and Goldberg, 1974) to provide accurate position sense in the absence of any peripheral, or afferent, stimulation. His work also shows that deafferented monkeys are able to adapt to visuo-motor rearrangement. Thus the proprioceptive component of adaptation may be rooted in fact in an <u>efferent</u> change, i.e. subjects may obtain a different phenomenal impression of their limb positions as a result of adjusting their behaviour. This possibility not only alters the interpretation of Harris' work but also suggests a purely behavioural approach to adaptation. In the following section some such behavioural models are considered.

BEHAVIOURAL APPROACHES TO ADAPTATION

Adaptation viewed from a behavioural perspective is a process by which the organism comes to behave appropriately to the rearranged stimulation whatever its phenomenal content. The sole criterion of adaptation is that a subject has regained accurate visuo-motor coordination. Behavioural accounts of adaptation have generally regarded the process as involving the acquisition of new patterns of muscle efference through some form of learning, which has led some investigators to study the acquisition of particular motor skills under rearrangement conditions. For example, Snyder and Pronko (1952) found that a subject wearing spectacles causing up/down inversion, left/right reversal and reversal of depth cues showed initial disturbance followed by improvement on several tasks involving visuo-motor skills, e.g. card-sorting, mirror tracing and the Minnesota Rate of Manipulation Test. The amount of disruption, rate of improvement, final performance and persistence of after-effect following removal of the spectacles depended on the specific test. Adaptation, as measured by improvement, was found in all test situations. Further work on the effects of rearrangement on visuo-motor skills by Smith and Smith (1962) showed that not only do the effects of rearrangement differ according to the task, but also that adaptation was found to be limited to the type of motor responses involved in the training period. In general, the quantitative data obtained in such studies show the course of adaptation, as measured by improvement on tasks requiring visuo-motor coordination, to follow profiles similar to those found in the acquisition of motor skills, e.g. mirror drawing (Starch, 1910; Siipola, 1935). The finding that transfer to different tasks is limited is also consistent with this interpretation of adaptation.

Some perceptual effects, however, have also been reported, e.g. the rather confused comments by Snyder (Snyder and Pronko, 1952) which were mentioned earlier, and these have led to the interesting thesis of Kohler's (1964) that perceptual adaptation may be _mediated_ by behavioural adjustment.

Kohler's model

Kohler's account of adaptation isbased on work carried out in Innsbruck in a project which has continued forhalf a century. This programme of research, begun by Erismann and continued by Kohler, has investigated a wide variety of rearrangement situations and includes many long-term studies of adaptation. Kohler (1964) interprets the results of these studies as showing the development of perceptual adaptation through three phases.

(1) The initial disruption caused by the rearrangement is followed first by a period of _behavioural adjustment_. During this phase subjects learn to behave appropriately although they report no change in visual perception. For example, the behaviour of a subject who wore up/down inverting spectacles was described as follows:

> "During a simulated fencing match, the subject parried all blows correctly, even though the opponent was seen upside down."
> (Kohler, 1964, p 31).

This subject was also able to ride a bicycle and ski successfully, although he experienced visual perceptions as the right way up only occasionally.

(2) The second phase consists of a change in visual perception in which the up/down or left/right directions become confused. This ambiguous phase often results in contradictory perceptions as objects which are actually inverted or the right way up might <u>both</u> be perceived as upright. Further investigations of this transition phase reveal three factors which influence perception. Any object viewed and touched simultaneously is perceived in its correct orientation. Similarly, the experience of <u>gravitational</u> pull, for example holding a plumb line, or driving up a steep hill in a car, produces upright perception. Familiarity proves to be a third factor: a candle appears upright when lit, and smoke rising from a cigarette indicates the upright direction of the visual field.

(3) The final stage is "veridical" vision, achieved by some subjects. This stage is characterised by appropriate motor behaviour, coupled with correct perceptual judgments of the direction or orientation of visual stimuli. Subjects who achieve this stage of <u>perceptual adaptation</u> report aftereffects following removal of the spectacles. One subject of Kohler's reported that people appeared to be suspended head downwards from the "ceiling", and

> "... while taking a walk outside, the subject reported that the reflection of a house and tree seen in a puddle appeared considerably more upright than the house and tree itself."
> (Kohler, 1964, p 32).

Behavioural though his theory may be, Kohler's approach to the study of adaptation relies for the most part on introspections from subjects concerning both their behaviour and their perceptual experiences. This concentration on introspective report rather than more objective measures is illustrated by the following example of what was claimed to show "veridical" perception:

> "'When I stand close to the wall the street looks right!' We tried to test this assertion and gave Grill the instruction to stand near the wall. This being done, he walked to the curb and stumbled off the sidewalk. To our astonished query he replied, 'I saw the wall there (points left) and thought, well now you go right, since that's the way to be sure to get there. This proves to me that I saw the wall correctly in the first place and that I don't have to make any more corrections!'"
> (Kohler, 1964, p 155).

Kohler has, however, failed to provide objective evidence of such perceptual adaptation. He explains this by suggesting that a critical attitude to immediate vision on the part of the subject, for example when he is asked if the world appears normal, evokes pre-experimental memories. Thus he regards the errors in perceptual judgment recorded in controlled tests in the laboratory situation as the result of a disturbance of the new visual impression by this taxing environment. Kohler claims that when the test situation resembles the everyday world accurate perceptual judgments occur, reflecting perceptual adaptation.

Although Kohler claims that such perceptual adaptation occurs, he attributes the basis of adaptation, and also the development of visuo-motor coordination, to behaviour. Kohler interprets Stratton's accounts of his experiences with inversion, for example stamping his foot to aid localisation, as follows:

> "Always there is the same emphasis upon the effects of movements, of even the mere intention of movements, upon the harmonisation of vision and bodily behaviour." (Kohler, 1964, p 161).

Thus although Kohler claims that <u>perceptual</u> adaptation does occur, as opposed to merely learning new motor habits, this is achieved by the mediation of behavioural adjustment.

Kohler's work also contains evidence for two phenomena which may be interpreted according to a motor learning approach to adaptation. First, he reported the occurrence of "piece-meal" adaptation, i.e. adaptation which is limited to a particular aspect of the situation. This might involve restriction to specific motor responses, so that a subject who had learnt to ski successfully while wearing the spectacles could not automatically drive a car or ride a bicycle. Such lack of transfer between different tasks has also been reported by other investigators, e.g. Smith and Smith (1962). Alternatively, the adaptation might be limited to particular stimuli, for example one subject reported that cars were perceived as driving on the right (correct) side of the street but that their number plates were seen in mirror writing. Kohler interprets such findings as showing that adaptation proceeds by including progressively more "behavioural connections" between visual and tactile localisations of objects. In the final stage of adaptation, objects not directly accessible to touch are included in the new visual experience.

Kohler has also reported <u>intermittent</u> aftereffects when the distorting spectacles are removed following adaptation. This effect, termed the "<u>situational aftereffect</u>", occurs following adaptation to split-field spectacles where, for example, the upper half of the visual field might be viewed through a wedge prism and the lower half through plain glass. On removal of such spectacles, the aftereffects are confined to the part of the visual field viewed previously through the prism. This "situational" effect cannot be attributed to some form of partial adaptation affecting only part of the retina since the eyes are free to move in any direction behind the spectacles, with the result that most of the retina receives both normal and distorted visual stimulation. Thus the adaptation which follows exposure to this rearrangement is differential with respect to the direction of gaze, but occurs within the same area of the retina. Kohler interprets this "gaze-contingent" adaptation as resulting from a conditioning process:

> "... the occurrence regularly coincides with the presence of absence of certain other conditions belonging to the same total stimulus situation ..... such deviant sensory responses have the characteristics of conditioned reactions: they occur or do not occur, although the same visual stimulus is always impinging on the same retinal area."
> (Kohler, 1964, p 26).

Kohler's account of adaptation is therefore based on the development of a new visual perception of the world through behavioural adjustment. The operation of learning processes seems to be implicated in this development, being evidenced in such effects as the situational aftereffect and piece-meal adaptation.

Such an interpretation has been developed in a slightly different form by Taylor in his theory of perceptual development (Taylor, 1962). Taylor's work has received much less recognition than that of Kohler, or of the American investigators such as Held. This may be partly due to the rather daunting nature of his approach - a behavioural account of perception, using notation from set theory, a Hullian framework and concepts derived from Ashby's theory of multistable systems!

Taylor's model

Taylor's (1962) theory of perception is firmly based on conditioning principles. His approach is primarily behavioural, regarding visuo-motor coordination as the association between visual stimulation and a class, or sub-system, of responses. These connections are assumed to be established through learning during early development. The rearrangement situation alters these relationships and the old associations become subject to extinction, due to lack of reward, and suppression due to punishment. New associations, which are rewarded by producing accurate behaviour, must be developed again through learning processes.

This approach, therefore, involves the association of motor responses to the transformed visual stimulation. Such motor learning is not limited to a single, stereotyped response but refers to a sub-system, or class of responses, defined by the activity involved, for example pointing to visual targets, or by the use of a particular part of the body:

> "It was soon realised that the adaptation of one sub-system does not at all guarantee the adaptation of other sub-systems ..... The subject learned to move the foot that was indicated by the flicking of a stick toward it. We then tested the subject by asking him to move parts of the body not previously included in the training program, such as the knees,

> shoulders, and elbows, and in every case the first response was wrong."
> (Taylor, 1962, p 199).

Taylor interprets such findings in terms of Ashby's (1952) theory of "multi-stable" systems in which sub-systems may act independently of one another.

In common with Kohler, Taylor developed his model beyond the behavioural level, regarding complete adaptation as a state in which visual perception is consistent with spatial perceptions deriving from other modalities. Such perceptual adaptation is also achieved through learning, the transformed visual stimulation becoming associated with new classes of perceptual response. Here again the sub-systems may adapt independently:

> "... anomolous experiences, such as the perception of a building in its correct position while at the same time the inscription on it is seen as mirrored ..... since the apparently conflicting perceptions do not belong to one and the same sub-system ..... further strengthening of the responses on which the perception of the position of the building depends does not have any direct effect on reading behaviour."
> (Taylor, 1962, p 207).

Taylor has therefore provided an account of adaptation which proposes that the development of a new visuo-spatial perception is achieved through learning processes and is based on behavioural compensation. The same process is assumed to apply to the developing organism, with the proviso, however, that the neonate differs from the mature adult in its lack of previous experience and hence undeveloped state of its multi-stable system. One feature which he suggests to be of importance, with obvious relevance to the difference between adaptation and neonatal development, is that the mature human subject can understand and use language. Taylor insists that the process of adaptation to rearrangement is not independent of the state of the system as a whole. Thus an exact statement of the transformation applied to the afferent function may be necessary to calculate the effect on the system, but it is not sufficient.

CONCLUSIONS

The established paradigm in adaptation research, the work of Richard Held (e.g. Held, 1961), has been subjected to several criticisms but has as yet withstood the challenge. The approaches reviewed in this chapter, while providing plausible accounts of the results obtained within their own frameworks, have not succeeded in producing a model of sufficient power to take its place. Held's work, based on the simple distinction between active and passive movement, has a breadth of application unrivalled by his competitors: not only adaptation, but the development of coordination in a comparative context (Held and Hein, 1963; Held and Bauer, 1967) and the maintenance of coordination (Held and Freedman, 1963) are included. His techniques, too, contain novel and ingenious features (Held and Gottlieb, 1958; Held and Hein, 1963) and provide excellent "shared examples" (Kuhn, 1970) of the paradigm. Thus Held's work has exerted an extremely powerful influence in the domain of adaptation research, an influence so strong that investigators have not questioned the underlying assumptions in Held's thesis:

(1) that adaptation is transient, rapidly cancelled out when the rearrangement device is removed and normal coordination restored;

(2) that adaptation is not a form of learning.

These assumptions have not been submitted to empirical test by any investigator, even when seeking to contradict Held's model. Only those working from a behavioural approach might be in a position to dispute them, but an open challenge has not yet been forthcoming.

CHAPTER 4

A CHALLENGE TO THE CONVENTIONAL VIEW OF ADAPTATION

There is little empirical justification for the relative exclusion of learning from consideration as a causal factor in adaptation. Held, in fact, had been traditionally mute on this point, as Taub (1968) observes:

> "To our knowledge, no one of Held's papers contains a definite statement on whether or not prism compensation involves learning."
> (Taub, 1968, p 86).

A recent comment by Held (Held and Bauer, 1974), however, indicates that his position on the role of learning in adaptation is obscure. In a discussion of the performance of monkeys reared without sight of their limbs, Held suggests that their achievements in developing visuo-motor coordination were:

> "... based on slow and pains-taking conditioning, consistent with the relatively rapid extinction of this capability when training and testing were discontinued for a few weeks and then resumed. The capabilities of the control animals did not suffer at all from one month of post-testing deprivation of sight of their limbs ..... If one insists upon calling the calibration process, contingent upon the free vision of limbs and body, a form of learning, then that form must be carefully distinguished from the process by means of which the experimental animals improved their performance during the training procedure."
> (Held and Bauer, 1974).

Thus it remains unclear whether Held endorses the view that the calibration of the visuo-motor system is a form of learning, and if so, what precise form such learning (1) might take.

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(1) It should be noted that conditioning is not always a "slow and pains-taking" process, although sub-optimal conditions may permit only inefficient learning.

It appears that the only evidence which might embarass a learning view has been reported by Lazar and van Laer (1968). Their failure to obtain positive inter-prism transfer, or "learning to learn" effects, may, however, be attributed to the limited experience given to their subjects (ten trials on each of only three prisms); by contrast, conventional learning set studies (Harlow, 1949) require the presentation of over a hundred problems before any positive transfer is recorded. Given the limitations of this work and the general lack of evidence, therefore, the question of whether adaptation involves learning processes may be considered an open one.

The further assumption that adaptation is a transient phenomenon with no long-term durability is implicit in the use of *within-subject* experimental designs by many investigators, i.e. the same subjects receive exposure to the same, or different, rearrangements under a variety of conditions. The exposure phases are commonly separated by periods of at least one day (e.g. Held and Bossom, 1961). This procedure assumes that once normal coordination has been restored through a process of "de-adaptation" (Held, 1961), the subject can be considered as "back to normal" and no longer affected by the rearrangement experience. It came as a surprise to a group of investigators using this conventional procedure, therefore, to find that the aftereffects of brief exposure to rearrangement persisted despite intervening periods of normal activity:

> "... the authors tested subjects in different conditions spaced two days apart. This was done as a matter of convenience, with the assumption that the *effect of prior training would dissipate* during the intervening days as a result of practice with hand movements in everyday life. However, it appeared that this was not the case."
> (Klapp *et al*, 1974, my italics).

Klapp (Klapp et al, 1974) went on to show that such aftereffects may persist for as long as two weeks, evidence which seriously challenges the conventional view of adaptation as a transient phenomenon. A further challenge to the assumptions in Held's work comes from research instigated by McGonigle (McGonigle et al, 1974, see Appendix D) on the different, but not unrelated, topic of cross-modal matching. Following a claim by Ettlinger that rhesus monkeys fail on such tests (Ettlinger and Blakemore, 1967) McGonigle proposed the development of a new technique, involving the use of laterally displacing prisms, to avoid certain problems inherent in Ettlinger's task. The most important of these problems concerns the spatial dissociation between the original stimulus and the set from which the match is to be selected, for such a form of presentation incurs the risk that the two sets of stimuli might be identified as different on the basis of their spatial locations. McGonigle suggested, therefore, a procedure which makes use of the error in localisation induced by prismatic displacement in tasks involving visually elicited reaching. If the subject (in this case a squirrel monkey) were "prism-sophisticated", i.e. could correct this mistake after only a single error under conditions of visual feedback of the terminal position of the pointing limb, tests could then be made on his ability to use haptic information to correct similar mistakes under conditions without terminal visual feedback. Thus, successful retrieval of the target object would require the integration of the visual information which elicited the reach with haptic information concerning the terminal position of the limb. To achieve the necessary level of prism-sophistication, while still ensuring that reaching errors would occur, a training procedure based on the "serial-reversal" learning paradigm (e.g. McGonigle *et al*, 1971) was devised (see Appendix D). The results of this work proved to be of great relevance for the study of adaptation:

(1) The adaptation profiles of the two squirrel monkeys indicate that the effects of exposure to lateral displacement are *not transient*: savings on re-adaptation, in the form of smaller errors and more rapid attainment of accurate reaching, were recorded. So significant was this effect that accurate *first trial* reaching was recorded on several occasions, indicating that the adaptation was conserved despite the intervention of normal activity in the home cage during the period between test sessions.

(2) *Learning* influences, specifically "learning to learn" effects in the form of positive inter-prism transfer were observed when two prisms were presented according to a "serial-reversal" training procedure. Terminal performance in this situation included accurate *prediction* of the correct adaptation response on the first trial of each new prism presentation, i.e. without error feedback.

These findings, if substantiated by further empirical work, would clearly violate both assumptions underlying the conventional view of adaptation, particularly if human as well as monkey subjects were involved. The experiments reported in this thesis constitute an attempt, therefore, to establish conclusively the existence of these effects in monkey and man. In the first part of the experimental section which follows, data are reported which show that adaptation in squirrel monkeys includes long-term effects and is susceptible to learning influences. In the second section, human data showing an essentially similar profile are presented.

EXPERIMENT 1 - ADAPTATION IN SQUIRREL MONKEYS

Subjects

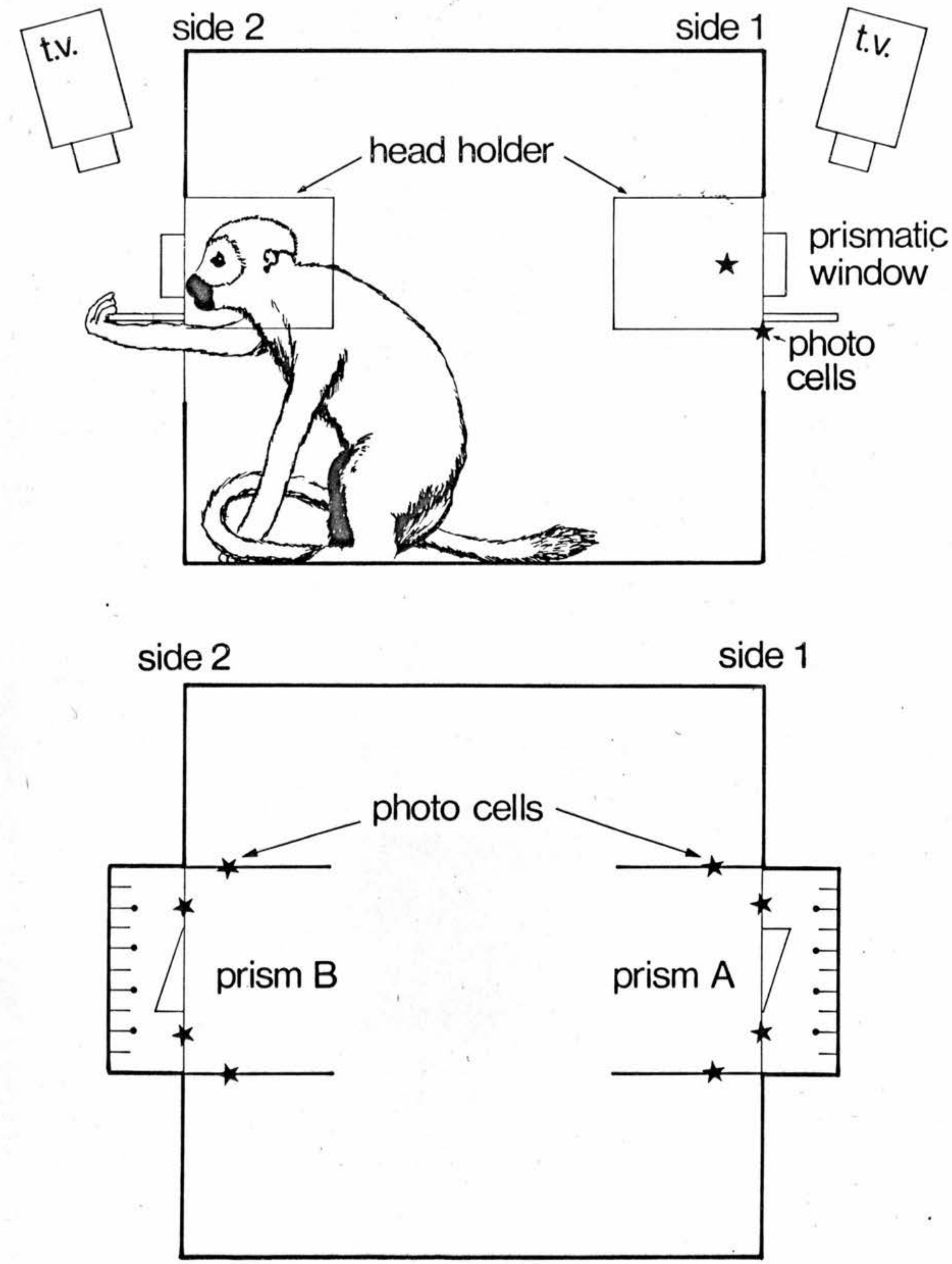
Five male squirrel monkeys (Saimiri scuireus) approximately five years old served as subjects. They were experimentally sophisticated in test situations involving the Wisconsin General Testing Apparatus (WGTA) where they had undergone extensive investigations in which size, brightness and pattern stimuli were used (see e.g. McGonigle and Jones, 1975). They were naive, however, with respect to the apparatus described below, and had never previously taken part in any sensory rearrangement experiment. They were maintained on MRC diet 2, on which they were fed ad libitum.

Apparatus

Subjects were placed in a metal chamber (55 cm long x 40 cm wide x 55 cm high) which had a small circular window (3.2 cm in diameter) at each end (see Figure 3). Through each window the monkey could see a ledge (7.5 cm deep x 19 cm long) protruding from below it, with four foodwells (2.5 cm apart) countersunk into its surface. The ledge was painted matte black with white strips (0.5 cm apart) showing on its upper surface. Immediately below the ledge was an aperture (3.2 cm deep x 19 cm long) through which the monkey could reach to the upper side of the ledge. Outside the window was fitted a slide holder on which were mounted two 30 diopter wedge prisms (base-right and base-left) and a plain glass block. Each ledge was illuminated constantly by a shaded 5 Watt white bulb. A click generator gave the cue (lasting 5 sec) for the start of a reaching trial. Television cameras were installed in front of each ledge to record the reaches of the subjects at their termini. Errors were

Figure 3

Schematic representation of the apparatus used with squirrel monkeys for studying adaptation.



later measured by means of a Sanyo Video Tape Recorder allowing frame-by-frame analysis.

Procedure

(a) Pretraining. The monkeys were pretrained to look through the window, locate the position of a peanut on the ledge and reach for it through the slit aperture located below the window. The ledge occluded the subject's view of its pointing limb until it appeared at the terminus of its reach. Pretraining was carried out at both ends of the test apparatus.

(b) Testing. Subjects were required to reach for a peanut which was located at any one of the four positions on the ledge as per a 'predetermined' random sequence. They were permitted to correct their mistakes in the course of any given 'trial'. A new trial (signalled by the click generator) began with the target (peanut) in the new position. During the intertrial interval (ITI) of 15 seconds the experimenter occluded the window of the test chamber. Forty trials were given on each testing session. Testing was carried out five days per week (Monday to Friday).

It should be noted that this testing procedure conforms to the stringent criteria outlined by Howard (1968) for adaptation research, These may be summarised as follows:

(1) The use of a 'terminal display with target' procedure rather than any of the others Howard criticises.

(2) Pointing to several targets in a random order so as to avoid stereotyped movements.

(3) Preventing the subject from viewing his own body through the prism, as the sight of it displaced to one side may itself 'induce

behavioural changes in the subject quite apart from any effect due to sensorimotor discordance'.

(4) Fixing the subject's head so as to prevent complex parallax effects in the field of view during movements of the head (and prisms).

(5) The use of (a) two parallel mirrors instead of prisms or (b) simple visual targets restricted to the region of the median plane, in order to remove apparent curvature of straight vertical lines and compression of horizontal distances towards the base of the prism ((b) is satisfied here).

(6) The use of targets at eye level because it is only this plane which suffers no tilt distortion when seen through vertical prisms.

<u>Design</u>

Three groups of subjects were involved. Two monkeys (Group 1) were first trained to alternate between two prisms displacing in opposite directions (Prism A and Prism B) located at opposite ends (Sides 1 and 2) of the box (AS condition) (1); following this they were given training with both prisms on the same side (Side 1) of the apparatus (SS condition). Two subjects (Group 2) began with training on the same side (SS condition) followed by training on opposite sides (AS condition). One monkey (Group 3) was simply overtrained (OT) on one prism (Prism A) at one side (Side 1) of the apparatus to record the degree of conservation of adaptation over successive sessions. Later he was given AS and then SS training. The design is summarised in Table 1.

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(1) This presentation, involving <u>different spatial locations</u> for the two prisms, was found to produce the greatest improvement in adaptation performance in the preliminary study (see Appendix D).

Table 1

Design for Experiment 1: (a) shows the conditions presented to each group of subjects, (b) defines each condition in terms of the location of the prisms.

(a)

Group	Phase	
	1	2
1	AS	SS
2	SS	AS
3 (OT)	AS	SS

(b)

	Side of Apparatus	
Condition	Prism A	Prism B
AS	1	2
SS	1	1
OT	1	

It was decided to use a "fixed trials" rather than a "performance criterion" design as this allows comparison between subjects after equal amounts of exposure to the prisms. Thus for each prism exposure a fixed number of trials was given. The number of trials per session was kept constant (forty trials), whereas the number of trials per prism presentation varied over four stages of training: Stage A involved 80 trials per prism, Stage B 40 trials, Stage C 20 trials, and Stage D 10 trials. Thus for Stages A and B only one prism (A <u>or</u> B) was presented in any given session, whereas for Stages C and D both prisms were presented in the course of each session (once for Stage C, twice each for Stage D). If performance on Stage D was good enough, a further stage (E) was given, in which the rate of changing between prisms was increased dramatically such that the subjects were required to alternate between the prisms with only a single trial exposure to each. The number of sessions for each stage was determined by the performance of the subjects (apart from Stage A which was fixed at four sessions,(1) i.e. two prism exposures). Thus for Phase 1, twelve sessions were given for Stage B, five for Stage C, and two for Stage D. In Phase 2, eight sessions were given for Stage B, five for Stage C, and two for Stage D. The details of this procedure, showing the number of times each prism was presented per stage for each phase of the experiment, are summarised in Table 2.

Table 2.

Details of the design for Experiment 1, showing the number of times each prism was presented for each stage.

Stage	No of Trials per Prism	No of Prisms per Session	No of Times each Prism was Presented	
			Phase 1	Phase 2
A	80	1	2	2
B	40	1	12	8
C	20	2	10	10
D	10	4	8	8
E (Altns)	1	40	80	80

One subject from each group was given training on the base-right prism first (Prism A), with Prism B as base-left; the other subjects were trained with Prism A as base-left and Prism B as base-right. Thus any asymmetries in performance due to differences in base-right and base-left prisms *per se* should not affect comparisons between

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(1) From the results of the preliminary study it was decided to give forty trials per session, and to give eighty trials (two sessions) for the first two prism exposures, to allow the subjects to adapt successfully to each prism.

conditions or groups. Since the errors induced by these two prisms are in opposite directions, the error analysis is in terms of absolute values only, to permit direct comparisons between relative accuracy on Prisms A and B for all subjects.

Results and Discussion

Two measures were taken from the frame-by-frame analysis of the video-tape recordings. The first involved measurements of the initial error (distance between the target and the middle finger of the monkey's hand) for each trial. A second profile was produced by recording the number of trials on which a "correct" response was produced (i.e. the subject hit the peanut with any part of the hand on the first attempt).

The results support both findings from the preliminary study:

(1) Adaptation in the squirrel monkey is not transient but has long-term effects. This is shown by the savings effects on re-adaptation to a single prism by the subject in Group 3 on the OT condition. The performance of this subject reached the maximum level of accuracy within ten sessions, i.e. no further reaching errors were recorded with this prism (see Figure 4 (a)).

(2) "Learning to learn" effects, which also indicate long-term influences in adaptation, are shown by the inter-prism transfer effects recorded by all subjects on the "serial-reversal" training involving two prisms (see Figures 4 and 5).

A more detailed profile of this learning effect is revealed by statistical analysis, which included a six-factor analysis of variance carried out on the error data from subjects in Groups 1 and 2. The F ratios for the main effects and the significant interactions are presented in Table 3. For further details of this analysis see

Appendix A. The main features of this "learning to learn" effect are as follows:

(a) Improvement in adaptation performance occurs over the four stages (A to D) of training ($p < .01$).

(b) The experience of "switching" between the two prisms seems to be implicated in this learning effect since "overtraining" on a single prism (OT condition Group 3) did not produce facilitation on subsequent reversal training (Figure 4 (a)).

(c) Analysis of the performance on the first trial of each prism presentation (see Table 4) reveals that for the AS condition the serial improvement in adaptation included prediction of the correct response without need for error feedback.

(d) Performance on the SS condition (no spatial dissociation) does not show the same "learning to learn" profile as the AS condition (Condition x Stage interaction $p < .01$). Although some improvement was recorded on Stages A and B, performance deteriorated when the rate of switching between prisms increased so that more than one prism was presented per session (see Figure 5 (c)). This disimprovement is much less marked in Group 1 (Figure 5 (b)) who experienced previous training on the AS condition. This relationship between the order of presentation of the two conditions and the learning profiles is shown in Figure 6 where the significant ($p < .05$) Order x Condition x Stage interaction is represented graphically.

(e) Performance on the two prisms differs significantly ($p < .05$), with superior performance on Prism A.

Figure 4

Percentage of trials correct for Group 3 (a) per session for OT condition; and for successive prism exposures for Stages A to E: (b) AS (c) SS conditions.

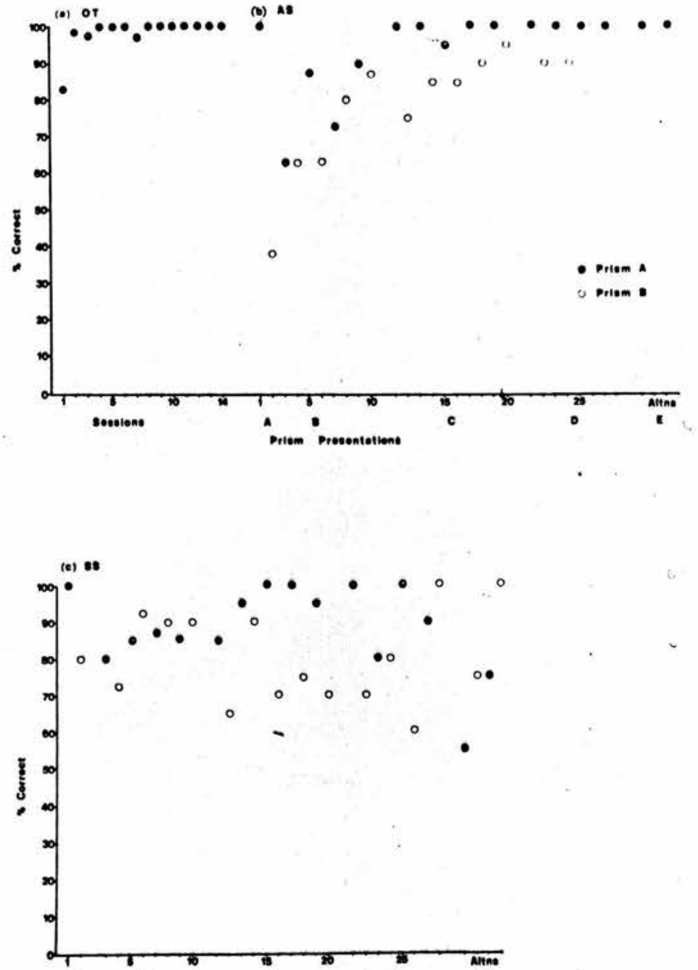

Figure 5

Percentage of trials correct for successive prism exposures for Stages A to E: for Group 1 (a) AS (b) SS; for Group 2 (c) SS (d) AS conditions.

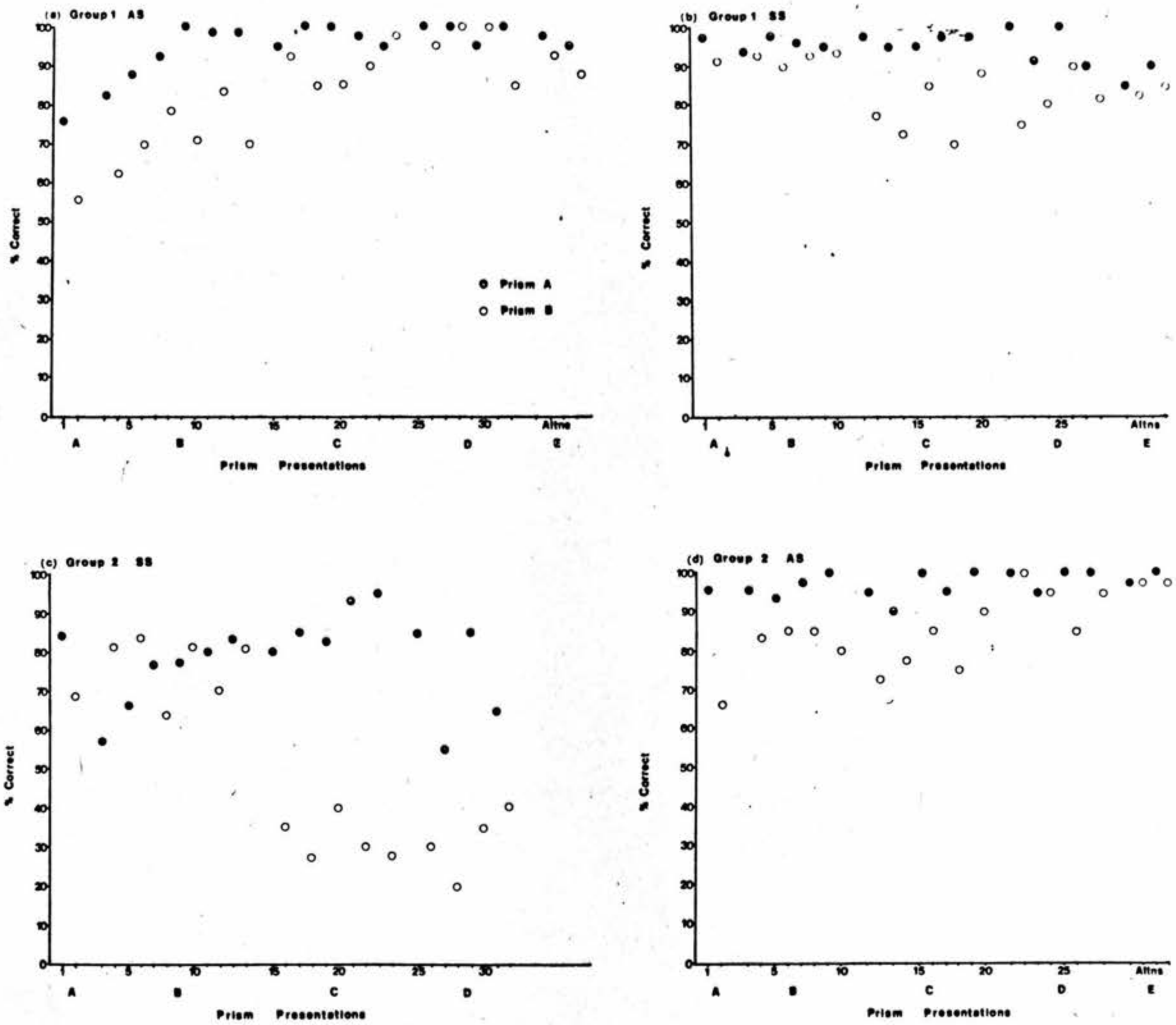

Figure 6

Order x Condition x Stage interaction

Mean Errors (cm) per stage for each condition for (a) Order (Group) 1 (b) Order (Group) 2.

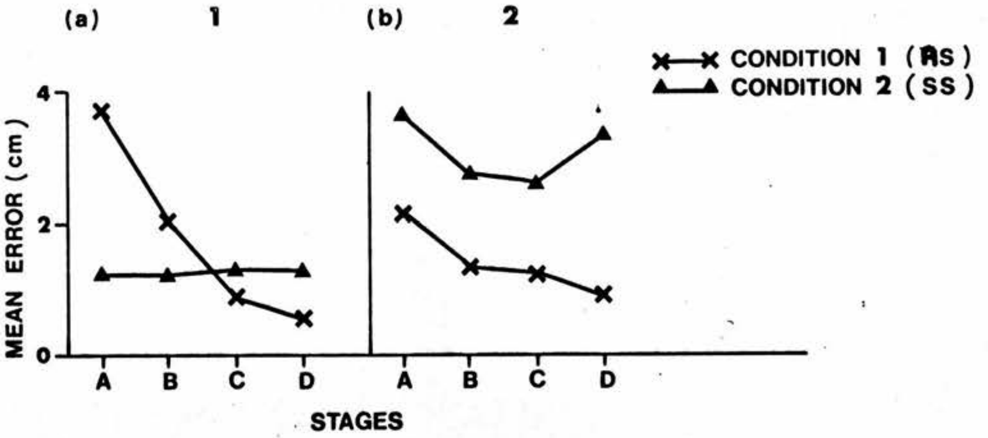

Table 3

Main effects and significant interactions from the six-factor analysis of variance on the error data from Groups (Orders) 1 and 2.

Source	MSerror	df	F	p
Main Effects				
Order*	40.978	1,3	4.293	ns
Condition*	69.282	1,4	1.678	ns
Prism*	40.091	1,4	10.460	<.05
Stage	3.983	3,6	24.463	<.01
Trial*	6.012	1,89	4.218	<.05
Subject	3.983	2,6	7.506	<.05
Significant Interactions				
Order x Cond*	41.939	1,4	8.925	<.05
Cond x Stage	5.185	3,6	11.478	<.01
Prism x Trial*	2.562	35,95	1.669	<.05
Prism x Subj	4.852	2,6	5.314	<.05
Stage x Trial	1.374	57,114	3.186	<.01
Order x Cond x Stage	5.185	3,6	6.204	<.05

* Quasi-F calculated from the expected Mean Squares (see Appendix A).

Table 4

Percentage of first trials correct per prism presentation (a) Groups 1 and 2, (b) Group 3.

(a)

Stage	Group 1				Group 2			
	AS		SS		SS		AS	
	Pa	Pb	Pa	Pb	Pa	Pb	Pa	Pb
A	0	0	100	0	0	0	100	0
B	58	26	38	38	0	17	65	50
C	80	90	80	40	50	0	60	50
D a	100	100	100	75	75	0	100	100
b	100	100	75	50	25	50	100	100

(b)

Stage	Group 3				
	OT	AS		SS	
		Pa	Pb	Pa	Pb
A	0	100	0	100	0
B	100	0	25	0	50
C		100	20	80	20
D a		100	50	100	0
b		100	100	0	100

a refers to the first presentation of the prism for the session.
b refers to the second presentation of the prism for the session.

These results suggest that powerful learning mechanisms may operate in the adaptation process. The profiles in the "multiple" adaptation condition, showing initial interference (negative transfer) between prisms on the first presentations followed by dramatic improvement (positive transfer) on subsequent "reversals", are essentially similar to those obtained in standard serial reversal learning studies (e.g. Mackintosh et al, 1968). The lack of positive transfer from the "overtraining" condition parallels a finding reported by McGonigle et al (1971) and interpreted by them as indicating that serial reversal improvement is a process by which:

> "... the subject 'learns to learn' to change response attachments to the outputs of the relevant analyser (in Mackintosh's terms(1)): in particular, the speed with which subjects extinguish response attachments to the formerly reinforced stimulus is deemed critical." (McGonigle et al, 1971).

Thus it is not the training to associate a specific cue with reward which underlies serial reversal improvement, but the experience of switching between the different reinforcement contingencies, which establishes the appropriate responses firmly in the subject's repertoire, that seems to be fundamental. Applied to the adaptation situation, this view predicts that repeated exposure to a single prism

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(1) Mackintosh (1965) proposed a two-stage model of learning known as "attention theory" - discrimination learning is seen as involving two distinct processes: (1) learning to attend to the relevant stimulus dimension, the stage of "switching in" the relevant analyser, and (2) learning to associate appropriate responses with specific stimulus values on this dimension, the stage of "response attachment".

will facilitate re-adaptation to that prism, and reduce aftereffects when the prism is removed, since the responses to both these conditions become well-established in the subject's repertoire. Similarly, the experience of switching between the two prisms in the multiple conditions establishes the two adaptation correlations, permitting more rapid adaptation on subsequent presentations of these prisms. The role of switching is demonstrated by the subjects in Group 2, who were trained first on the SS and then on the AS condition. For although their performance on the SS condition is inferior to that of subjects trained on the AS condition, positive transfer was recorded when they subsequently received AS training. Thus switching *per se* seems to be an important factor in the process of serial reversal improvement.

"Learning to learn" effects of this sort, however, may not transfer to different rearrangements since these would involve different adaptation responses. Further experiments are necessary to determine the generality of such "learning to adapt" effects. An indication that the effect may be specific to the particular prism, however, is given by the predictive performance of subjects in the AS condition. This situation, in which the two prisms are presented in different spatial locations, may be regarded as analogous to a "conditional discrimination" in which a subject is required to change his response to particular stimuli when an external cue is changed (e.g. Riopelle and Copelan, 1954). Thus the adaptation profile shows not only "learning to learn" effects in the form of learning to adapt more rapidly, but also involves the conservation or *storage* of the adaptation correlations.

The predictive nature of the performance suggests that two components are involved in this multiple adaptation state. First, the adaptation correlations must be established on the basis of response-produced feedback. Switching between the prisms provides experience of the different adaptation responses which may then become associated, through a process analogous to "classical" conditioning (Pavlov, 1927), with correlated external cues. The results of this experiment indicate that an effective cue can be provided by the presentation of the two prisms in different spatial locations. Once the multiple adaptation state is established, however, the spatial cues are no longer essential to predictive performance, as the profile from subjects transferred from the AS to the SS condition reveals. Perhaps less salient cues, colour fringes, compression of the visual field, parallax effects for example, which are also produced by wedge prisms, may have been sufficient to indicate which adaptation response was appropriate.

Finally, the asymmetrical performance on the two prisms may be attributable to the order of presentation of these prisms since Prism A, for which superior adaptation performance was recorded, was always presented <u>first</u>. In the AS condition, this primacy effect is apparent in the initial stages where the prisms were presented on separate days. Only Prism B suffered negative transfer, suggesting that the adaptation to this prism might be derived from the adaptation to Prism A rather than from the normal state. This is possible since (1) a generalisation test carried out in the preliminary study showed transfer of the adaptation to a single prism from Side 1 to Side 2 of the apparatus, (2) larger errors were recorded when

Prism B was first presented, although the magnitude of the displacement is the same as for Prism A. Thus the adaptation to Prism B may be established, not directly from the normal state, but from the adaptation state appropriate to Prism A. The base-line for this second adaptation, therefore, fluctuates according to the adaptation achieved following the exposure to Prism A and the extent to which this adaptation transfers to performance with Prism B. The asymmetrical effect in the SS condition, by contrast, is recorded when more than one prism is presented per session (Stages C and D). On these stages the number of trials per prism exposure is reduced and so it is not clear whether "learning to learn" in the absence of salient external cues requires more intra-problem training or whether the temporal interval between reversals is an important factor.

In conclusion, both long-term conservation of adaptation to a single prism and "learning to learn" effects with several prisms have been recorded in the adaptation performance of squirrel monkeys. Since the possibility that either different eyes or different hands might be involved in the multiple adaptations was checked and discounted, it may be concluded that several visuo-motor coordinations, involving the same visual and motor systems, are acquired and maintained by these monkeys. The important question is whether such findings are species-specific or whether they can be extended to the human domain. In the following experiment, therefore, an attempt is made to demonstrate similar effects with human adults.

EXPERIMENT 2 - LONG-TERM ADAPTATION IN THE HUMAN ADULT

Introduction

This experiment follows a preliminary study with human subjects (see Flook and McGonigle, 1977, Experiment 4) which showed that adaptation performance improved following repeated exposure to either one or two prisms within a single session. Performance on the multiple adaptation condition, however, failed to improve above the level of the original adaptation within the limited period of training available, the improvement merely reducing the negative transfer between the prisms. In the following study a more extensive attempt was made to replicate the findings obtained with squirrel monkeys. The experiment is in two parts. In part 1, long-term adaptation effects to a single prism are investigated. The second part is devoted to multiple adaptation training.

Subjects

The subjects were thirty-four adults aged twenty to thirty years, undergraduates and postgraduates at Edinburgh University. Subjects were tested for accuracy on the pointing task before the experiment. Those who required corrected vision continued to wear their spectacles or contact lenses throughout the experiment. Subjects always used their preferred hand and preferred eye (see Table 5).

Apparatus

An Imhof stand was used to support an aluminium panel which housed a small circular window (3.3 cm in diameter). When the subject looked through the window he could see the edge of a second panel 40 cm away, which extended obliquely from the bottom of the upright panel. This second panel occluded the subject's pointing limb from view until the terminus of his reach. The edge of this panel served as a target board 50 cm wide and calibrated in units of 1 cm. A removable board could be attached to it to provide a condition with no visual feedback of pointing errors. A white plastic chess piece (1.5 cm high) with a magnetic base was used as the target. A slide holder on the back of the window (on the upright panel) held two 30 diopter wedge prisms (base-right and base-left) and a plain glass block. The window could be occluded between trials. The subjects sat on a chair which was adjusted so that the window was at eye level.

Table 5

Preferred hands and eyes used by subjects in Experiment 2 (a) males (n = 18), (b) females (n = 16).

(a)

Eye	Hand	
	Right	Left
Right	14	0
Left	3	1

(b)

Eye	Hand	
	Right	Left
Right	11	0
Left	4	1

Procedure

Subjects pointed at the target in five different positions (midline, 3 and 6 cm to right and left of midline) presented in 'predetermined' random sequences. The sequences were generated by the random selection of positions from the pool of ten items consisting of two representations of each target position. Thus each target position was presented twice per ten trials. The experimenter started each trial by removing the occluder from the window and the subject responded by pointing towards the target. Visual feedback was available only at the terminus of the reach, when the pointing finger was visible above the edge of the target board. No corrections under visual control were permitted. The subject returned his hand to his lap after any error had been noted. The experimenter recorded the errors as the distance between the middle of the subject's pointing finger (marked with a dyed stripe for ease of measurement) and the target position.(1) When this measurement had been taken the occluder was replaced and the experimenter moved the target to the next position. The inter-trial interval was ten seconds.

Testing sessions consisted of a number of blocks of ten trials each. Every such 'Trial-Block' was followed by a rest period of 1.5 minutes during which the subject was free to carry out normal activities (e.g. smoke a cigarette, drink coffee). There was an interval of three days between testing sessions. All subjects were given a practice session of two Trial-Blocks with the glass condition (and visual feedback of errors) before the experiment proper. This provided a record of their normal pointing accuracy and also served to familiarise them with the procedure.

PART 1: Long-term adaptation to a single prism

Design

This part of the study involved one group (Group 1) of six subjects who were given repeated exposure to a single prism

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(1) Although both magnitudes and directions of the errors were recorded the results presented here are in terms of magnitudes, or absolute values, only. The directions of the errors were attributable to the direction of displacement of the prism, and in the case of the glass condition, to the prism presented in the previous condition.

(base right) for five training sessions. Each session consisted of forty trials with the prism, presented in four Trial-Blocks, each of ten trials. Retention tests, of one Trial-Block only, with the same prism were given after intervals of two and four weeks.

Aftereffect (AE) measures were also taken for comparison with the adaptation scores, and to comply with the conventional procedure(1). This test consisted of a single Trial-Block with the glass condition and no visual feedback of errors. Two subjects were given such a test both before (retention of previous session's AE) and after (AE) the four training Trial-Blocks with the prism. The other four subjects were given no such tests during the five training sessions to allow comparison between the adaptation scores with and without the possible interference of the presence of the glass condition. All subjects were given an aftereffect test on each of the retention test sessions.

The training for all subjects consisted of several sessions on different days. Since subjects were generally available only from Monday to Friday each week, a break of at least two days for every weekend had to be incorporated into the training procedure. It was

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(1) "When localising with unaided eyes following exposure, compensation for the prism-induced error is usually evidenced as an increased error of localisation (sometimes called an aftereffect of exposure). Under properly controlled conditions, the measurements taken with prisms differ from those taken without prisms by exactly the amount of lateral deviation introduced by the prisms. Measuring with unaided eyes is convenient for a number of reasons of which the most important is that of a control against the presence of unwanted cues as to the objective direction of the target. The subject who shows increasing errors of localisation cannot be utilising such cues."
(Held and Bossom, 1961).

decided that sessions should be separated by, on average, three days for each subject. This had the added advantage that any effects obtained between sessions would be the result of long-term adaptation effects over three days of normal activity, a period longer than that frequently employed to ensure no interference effects between different conditions by other investigators. For example, Mikaelian and Malatesta (1974) separated their four exposure conditions by "at least twenty-four hours".

Results and Discussion

This part of the experiment was successful in that long-term effects of adaptation to a single prism were recorded. The pointing errors (cm) for each trial for all six subjects(1) were analysed according to an analysis of variance (including repeated measures) using the computer program BMD08V (BMD, 1971). This analysis involved three factors: Session (five levels, fixed); Block (four levels, fixed); Trial (ten levels, fixed). These were defined as follows:

Session - training sessions 1 to 5

Block - the four Trial-Blocks per session

Trial - trials 1 to 10 within each block

All main effects and interactions were found to be significant (see Table 6), indicating improvement between and within both sessions

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(1) The adaptation scores for the two subjects given pre- and post-exposure tests with the glass condition on each session did not show any significant deviation from those of the other four subjects. The scores of all six subjects were therefore analysed together as a single group.

Table 6

Analysis of Variance (including repeated measures) with three factors: Session (five levels, fixed); Block (four levels, fixed); Trial (ten levels, fixed).

Source	MSerror	F	df	p
Session (S)	3.019	23.032	4,20	<.01
Block (B)	1.667	31.461	3,15	<.01
Trial (T)	0.823	8.382	9,45	<.01
S x B	1.457	13.452	12,60	<.01
S x T	0.716	4.472	36,180	<.01
B x T	0.839	4.434	27,135	<.01
S x B x T	0.732	1.669	108,540	<.01

and trial-blocks. The significant three-way interaction, Session x Block x Trial, may be interpreted as showing that the improvement over trials not only changed according to the session, but also depended on the particular trial-block within the session. The graphic representation of the data (see Figure 7) shows that on the early sessions improvement occurred within at least two trial-blocks, whereas by the fifth session no improvement was recorded at all, since the performance had reached the level of normal accuracy. Thus significant savings effects on re-adaptation were recorded between sessions despite the intervention of three days of normal activity. This long-term adaptation effect is illustrated clearly in Figure 8 where (a) the mean Total Errors (corrected for practice errors for each subject) and (b) the First Trial Errors (uncorrected) are shown for each Trial-Block per session.

Figure 7

Mean Error (cm) per trial for Group 1 for (a) Session 1 (b) Session 5, which also shows the mean error per trial for the aftereffect (AE) and the aftereffect retention (AE Ret) tests for the two subjects averaged over the five training sessions.

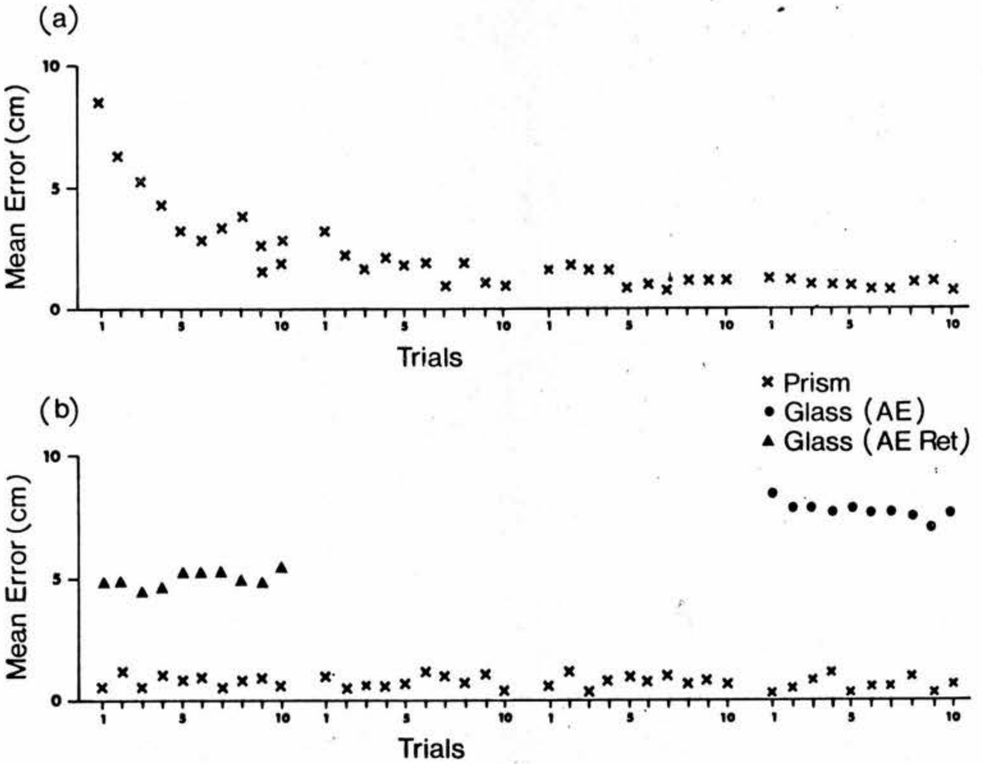
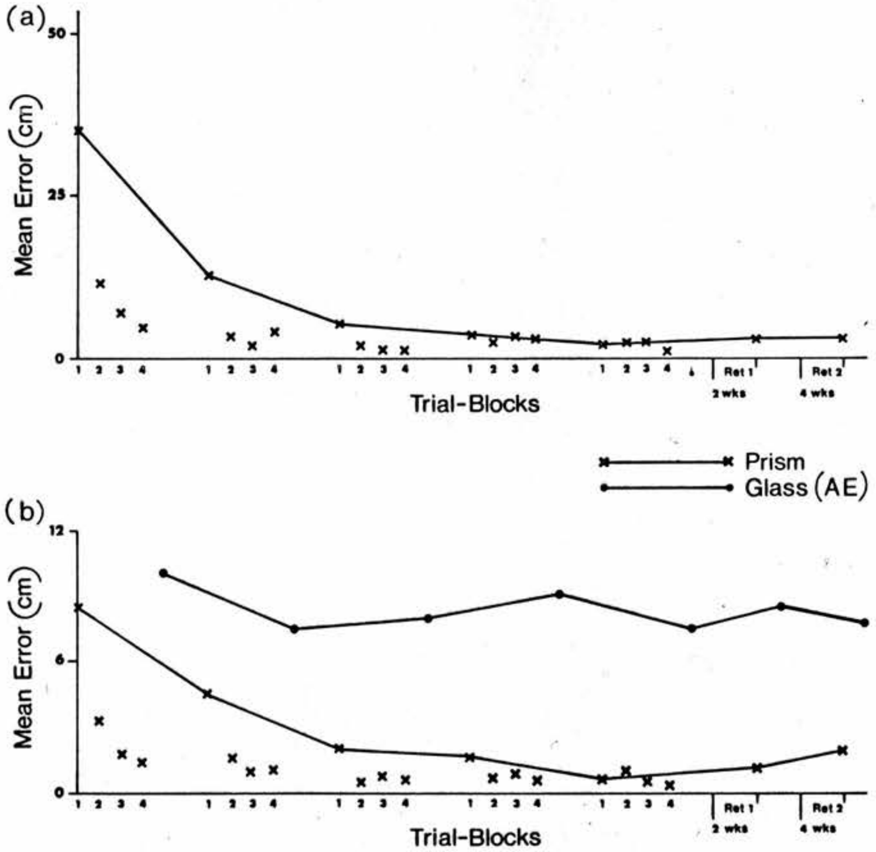


Figure 8

(a) Mean Total Errors in cm (with pretraining (Glass) errors subtracted)
(b) 1st Trial Errors (cm)
per Trial-Block for Group 1 (OT) (N = 6) for five training sessions (of four Trial-Blocks each) and two Retention tests (after 2 weeks and 4 weeks). The mean 1st Trial Errors for the aftereffect (AE) tests are also shown for the two subjects.



The long-term effect is not restricted to the three-day interval but persists, as the results of the retention tests reveal, for at least as long as four weeks (see Figure 8). The profile of First Trial errors, essentially similar to the overall performance profile, suggests that the adaptation responses are stored in the nervous system and may be conserved over considerable periods of time despite intervening periods of normal reaching. It is clear that, once established, the adaptation responses may be evoked where appropriate without need of further feedback.

This interpretation is supported by the aftereffect (AE and AE Ret) scores (see Figures 7 and 8). These errors show no change <u>within</u> each of the five sessions, i.e. the errors are constant over ten trials with no visual feedback. The mean AE error per trial is also constant over the five sessions, equal in magnitude to the initial error on the prism on the first session (first point on Figure 7 (a)). By contrast, the AE Ret scores <u>increase</u> over the five sessions to the point where very little difference between AE and AE Ret errors is recorded on the final session. Thus the conventional measures of "adaptation", i.e. the shifts in pre- to post-exposure scores, <u>decrease</u> to a non-significant level on the fifth session, although the behaviour of the subjects under rearrangement conditions becomes progressively more accurate. These trends are recorded in Table 7, where the "adaptation" profile in terms of this "pre-post shift" may be seen to be similar to the results obtained recently by Lackner in a study of repeated exposure to prismatic rearrangement using the conventional paradigm (Yachzel and Lackner, 1977). The apparent <u>decrease</u> in adaptation over the five sessions in Lackner's experiment is also attributable to an increase in errors on the pre-exposure tests, i.e. to the conservation of progressively more accurate adaptation responses evoked by the experimental context. Thus the use of this conventional measure of adaptation as the "shift" between pre- and post-exposure tests would not give an accurate measure of adaptation in subjects who are not "naive", i.e. those participating in within-subject experimental designs (e.g. Held and Bossom, 1961; Mikaelian and Malatesta, 1974). By contrast, the direct measure of the increase in accuracy in the presence of the rearrangement device would seem to provide a more faithful representation of adaptation.

Table 7

Mean errors per trial for five successive exposure sessions. The first three columns refer to this study (Experiment 2), with errors measured in cm and a 30 diopter prism; the data from Yachzel and Lackner's experiment show errors in degrees with a 20 diopter prism.

	AE Ret	AE	Difference	Yachzel & Lackner (1977)	
Session	'Pre'	'Post'	'Adaptation'	Single step	Stepwise
1	0.6	7.1	6.4	4.35	2.02
2	5.1	8.7	3.6	2.22	2.61
3	3.4	6.6	3.2	1.77	1.48
4	4.8	8.2	3.4	1.17	1.77
5	6.4	7.3	0.9	1.64	1.94

In conclusion, the first part of this experiment demonstrates the existence of long-term adaptation effects in human adults using a single prism. In the second part "learning to learn" effects similar to those shown by squirrel monkeys are investigated.

PART 2: Multiple Adaptation

Design

A single group (Group 2) of twenty-eight subjects were given training over ten sessions separated by three days each. These sessions consisted of three Trial-Blocks of ten trials, one block for each of the three conditions (prisms base right and left, and glass). To ensure that sufficient adaptation occurred to each condition initially, two Trial-Blocks of each condition were given for the first two sessions.(1)

In order to investigate the effects of the order of presentation of these conditions on the adaptations, one group of twelve subjects (Group 2a) was presented with the three conditions in a random order, while another group of sixteen subjects (Group 2b) received a regular order of presentation. Group 2b was further subdivided such that half of the subjects (Group 2b1) received the conditions in the order Prism A, Prism B, Glass; the other half (Group 2b2) were given the order Prism A, Glass, Prism B. Half of the subjects from each subgroup of Group 2 were given the base right prism, half the base left, as the first prism (Prism A for Group 2b) on Session 1. Since the errors induced by these two prisms are in opposite directions, the error analysis reflects the absolute values only, to permit direct comparison between the relative accuracy of all subjects on the different conditions.

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(1) In the preliminary study, under similar conditions, it was found that adaptation occurred within twenty trials for both prism conditions.

Results and Discussion

The error profiles from this group of subjects show inter-prismatic improvements over the ten training sessions. This improvement involves: (1) reduction in negative transfer from the previous prism condition, (2) increased rate of adaptation within each condition, and (3) improvement on the first trials of each prism condition.

These findings are supported by the results of statistical analysis in the form of two analyses of variance: (a) on the Total Errors for each condition per session for each subject (corrected for their normal pointing accuracy), (b) on the First Trial errors per condition (uncorrected). The results of these analyses are shown in Table 8. The sources of the significant differences were revealed by further analysis on the significant main effects and interactions using Scheffé's test for multiple comparisons (Edwards, 1960). The details of these analyses are presented in Appendix B.

The main finding is that repeated exposure to the prismatic conditions produces overall improvement in adaptation performance over the ten sessions ($p < .001$ (1)). This improvement was achieved regardless of the order of presentation of the three conditions (i.e. random, regular Pa Pb G or Pa G Pb, see Figure 9 (b)). Further details of this "learning to learn" profile are as follows:

(1) The exposure condition, i.e. glass, prism base-right or base-left, is a significant factor ($p < .001$, see Figure 10 (a)) with the

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(1) The p-values reported here refer to the analysis using the Total Errors per condition.

Table 8

Analysis of Variance (including repeated measures) with three factors: Group (three levels, fixed); Condition (three levels, fixed); Session (ten levels, fixed).

(a) Total Errors per Session

Source	MSerror	F	df	p
Group	520.94	1.36	2,25	ns
Condition	307.92	58.72	2,50	<.001
Session	80.77	33.57	9,225	<.001
Group x Cond	307.92	4.89	4,50	<.01
Group x Sess	80.77	1.69	18,225	ns
Cond x Sess	73.88	5.05	18,450	<.001
Group x Cond x Sess	73.88	1.71	36,450	<.01

(b) First Trial Errors

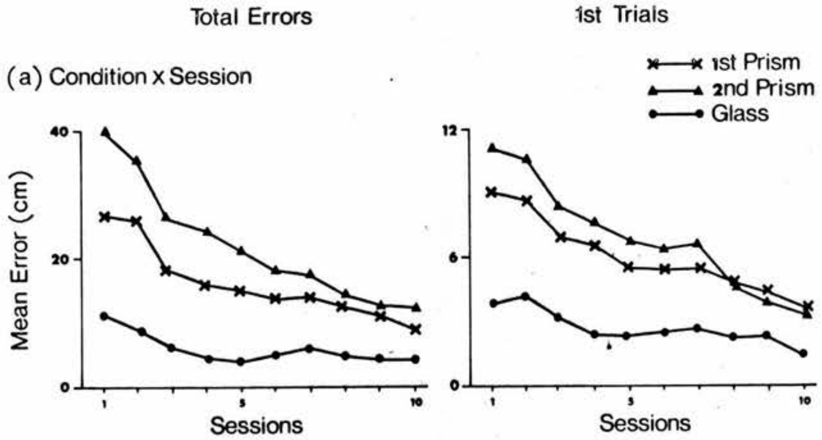
Source	MSerror	F	df	p
Group	49.37	2.73	2,25	ns
Condition	28.21	46.19	2,50	<.001
Session	10.72	23.55	9,225	<.001
Group x Cond	28.21	1.58	4,50	ns
Group x Sess	10.72	1.25	18,225	ns
Cond x Sess	10.05	2.73	18,450	<.001
Group x Cond x Sess	10.05	1.60	36,450	<.01

Figure 9

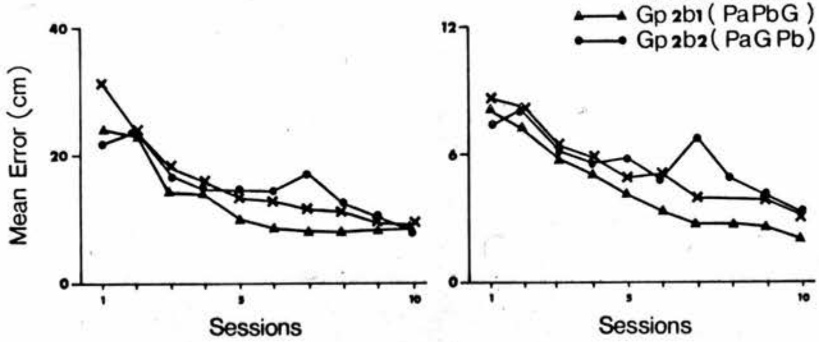
(a) Condition x Session interaction (b) Group x Session interaction

Mean Total Errors and 1st Trial Errors (cm) (a) for each condition, (b) for each Group per session.

(a) Condition x Session



(b) Group x Session



glass condition producing smaller errors than the two prisms ($p < .01$). The significant improvement is therefore attributable for the most part to improvement on the two prismatic conditions over the ten sessions rather than to a reduction in aftereffect errors on the glass condition ($p < .01$).

(2) The learning profiles for the two prisms differ according to the *order of presentation* of the three conditions. Group 2b2 (Pa G Pb) show no significant difference between the two prisms, whereas significantly larger errors were recorded with the second prism for both the random order of presentation (Group 2a) and the regular order Pa Pb G (Group 2b1) ($p < .01$, see Figure 10). This suggests that the *interference* between the different prism conditions depends on whether the glass condition intervened. Thus the order Pa Pb G produces negative transfer from the first to the second prism, whereas the order Pa G Pb produces no interference on the second prism, instead "aftereffect" errors on the glass are recorded (see Figure 11). The interference between prisms presented in immediate succession is significantly reduced, however, over the ten sessions ($p < .01$).

(3) The similarity between the performance profiles derived from the Total Error scores and from the First Trial scores (see Figure 9 and Table 8) suggests that the changes in adaptation performance involve a *predictive* component similar to that shown in the monkeys' performance. This is substantiated by a further analysis of the proportion of first trial errors which might be regarded as predictive, i.e. within the range of normal accuracy (less than 1.5 cm). As inspection of Table 9 reveals, a considerable number of subjects attained predictive performance within the ten sessions. Since individual differences were

recorded, with some subjects showing consistently better performance than others ($p < .001$), it seems reasonable to conclude that multiple adaptation of this predictive type can be achieved by human adults following repeated exposure to such rearrangement condition.

Table 9

Percentage of subjects predicting the correct response for each condition as defined by an error on the first trial within the normal range of accuracy ($\leqslant 1.5$ cm)

	Group 2a			Group 2b1			Group 2b2		
Session	1st	2nd	Glass	1st	2nd	Glass	1st	2nd	Glass
1	0	0	8	0	0	50	0	0	0
2	0	0	25	12	0	38	0	12	25
3	17	0	33	12	12	50	12	12	0
4	17	17	33	12	0	50	12	25	12
5	8	8	50	38	25	88	0	12	25
6	25	8	33	25	25	75	12	25	25
7	17	42	33	50	25	88	0	0	25
8	17	33	50	62	25	62	12	12	38
9	33	33	42	50	25	62	0	25	38
10	25	50	83	50	50	75	12	12	50

The results from this group, therefore, demonstrate that long-term effects in the form of "learning to learn" influences operate in adaptation in human adults. The predictive nature of the performance indicates that subjects were using some form of cue to signal which adaptation response was appropriate. The preliminary study with human subjects showed that spatial dissociation facilitates serial reversal improvement in human adaptation as well as with squirrel monkeys. In this study, however, no such contextual cue was provided. Subjects given the regular orders of presentation reported that the prisms always appeared in the same order. This suggests that they may have used the order of presentation as a cue. However, this form of identification did not seem to be necessarily beneficial, as the second prism (Prism B) was frequently referred to as "the one I can't do!" by subjects in Group 2b1 (Pa Pb G). The different profiles recorded from the two groups given regular orders of presentation indicate that the order Pa Pb G is more conducive to multiple adaptation. A possible interpretation of this effect is that the consecutive presentation of the two prisms, resulting in negative transfer initially, provided greater contrast between the conditions and hence easier identification.

For subjects who could not use the order of presentation as a cue, i.e. those experiencing the random order of presentation (Group 2a), the contrast between the two conditions provides a potential means of identification. An indication that such information was used comes from the fact that subjects in this group did succeed in attaining predictive performance. These subjects were able to identify the glass condition fairly readily, showing high levels of predictive performance on this condition, i.e. suppressing aftereffect errors. This was also substantiated by verbal reports from subjects indicating that they used the colour fringes produced by the prisms as a form of identification. Discrimination between the two prisms appeared to be more difficult, although some subjects reported that the calibration lines on the target board were distorted, with compression in opposite directions by the two prisms. The fact that the subjects presented with the three conditions in a regular order did not appear to use such information for identification suggests that the mere presence of the visual distortions is not sufficient for this to be used for identification. (Subjects in Group 2b2 (Pa G Pb) were under the impression, at least initially, that <u>three</u> prisms were involved.) The contrast between successive presentations provided further information, drawing attention not only to the compression effect but also to its <u>direction</u>. Such an effect of contrast in the "structuring" of visual stimuli has been reported by McGonigle and Jones (1975). Thus it seems reasonable to conclude that sufficient information for the identification of the two prisms is provided by their repeated <u>successive</u> presentation when no other cue (e.g. spatial as in the previous experiment) is available.

Figure 10

Group x Condition interaction

Mean Total Errors and 1st Trial Errors (cm) per condition (1st Prism, 2nd Prism, Glass) for each group.

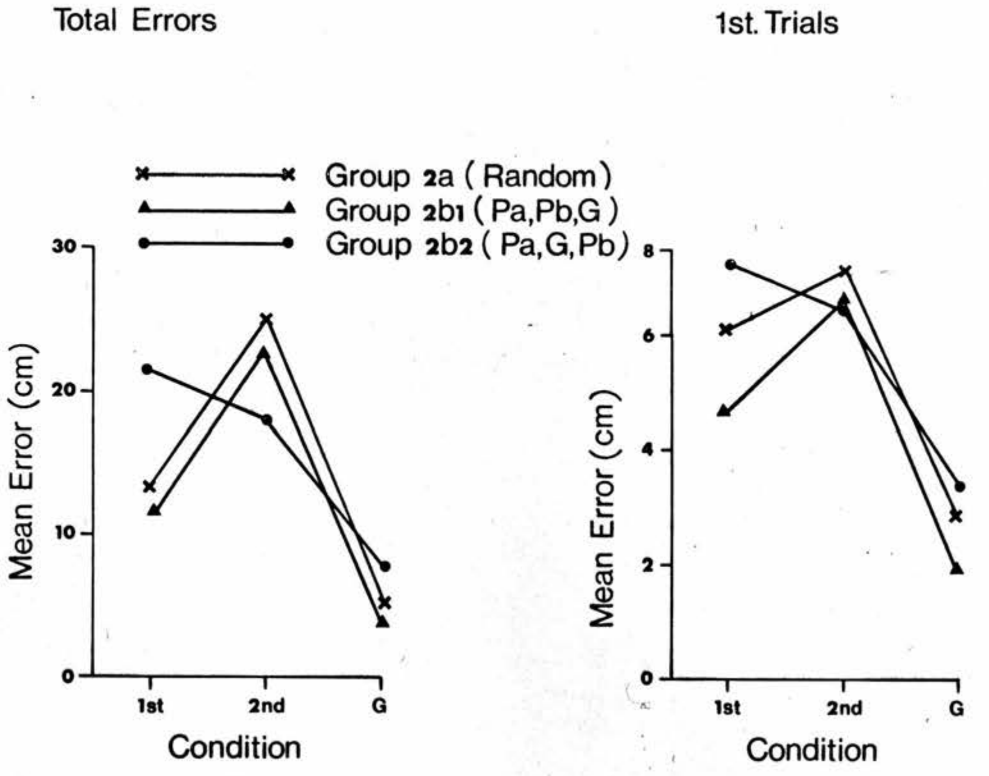
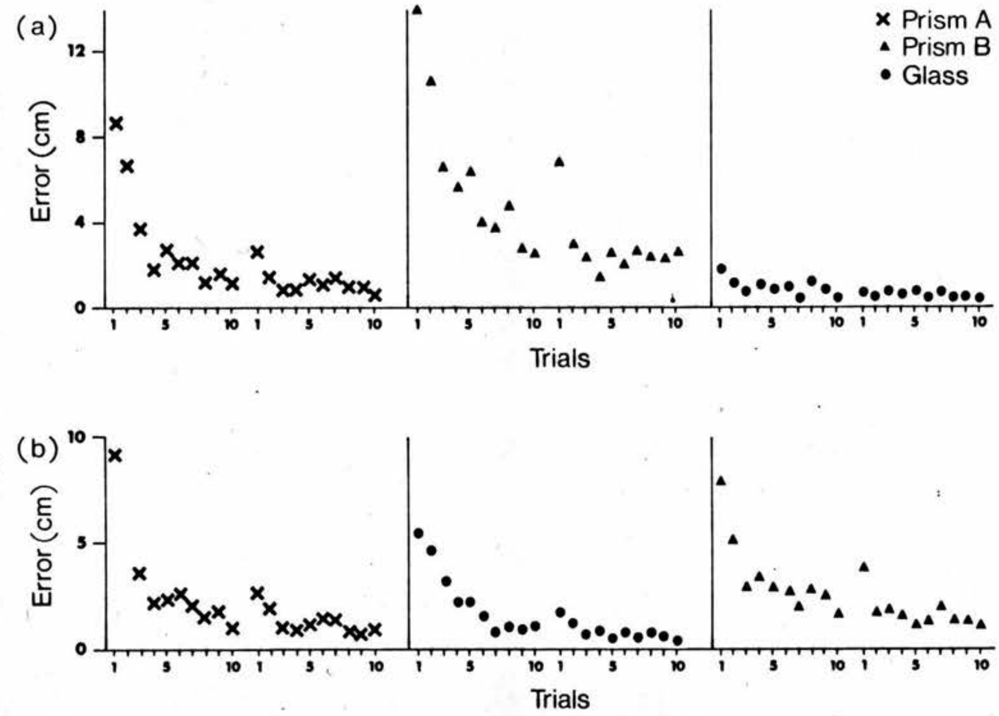


Figure 11

Mean Errors (cm) per trial for Group 2 on Session 1 for (a) order Pa Pb G (N = 14), (b) order Pa G Pb (N = 14).



GENERAL DISCUSSION

The two experiments reported here demonstrate that adaptation is a process with long-term influences as indicated by savings effects on re-adaptation to the same prism and "learning to learn" effects following repeated exposure to different prisms. These findings, therefore, provide the empirical basis for a challenge to the established paradigm in adaptation research. Before discussing the more detailed features of the process, an important question must be answered: does the adaptation performance of these subjects take the same form as adaptation defined conventionally?

As far as the exposure conditions are concerned, it was noted previously that these satisfy the stringent criteria for adaptation research outlined by Howard (Howard, 1968; see page 53). The measures of adaptation, however, differ from those normally employed, i.e. the use of aftereffects following removal of the prism. The long-term adaptation effects recorded in both studies suggest that the "pre-post shift" measure is not valid for repeated exposure conditions (cf Yachzel and Lackner, 1977). Thus the use of measures of accuracy in the presence of the prism, plus any negative transfer (a form of aftereffect) on the following prism presentation, seems justified. It should be noted, also, that when the glass condition was presented without visual feedback (as in the standard aftereffect test) following prismatic exposure, aftereffect errors were recorded.

The presence of such aftereffect errors is usually taken as evidence that "true" adaptation, as opposed to the use of a "conscious correction" strategy, has occurred. In these experiments there are several other reasons for believing that conscious correction cannot explain the subject's performance:

(1) In the first experiment the subjects are squirrel monkeys who would not be expected to use such strategies! The fact that the profile of human adaptation is essentially similar to that produced by monkeys suggests that similar processes are involved.

(2) Conscious correction is a notoriously inefficient means of compensating for the effects of rearrangements, as the report of one of Kohler's (1964) subjects (mentioned in Chapter 3, page 39) illustrates. This is because "true" adaptation occurs unconsciously and so the subject must continuously change his conscious adjustment to correspond to the shifting baseline of error he experiences.

(3) The displacement induced by wedge prisms varies in magnitude over the different target positions. Analysis of the errors recorded over the five target positions by the human subjects revealed that the errors on the initial sessions reflect these differences. On the later sessions, however, no such differences were found (see Appendix B), indicating that the subjects learnt to compensate accurately for the different displacements. A <u>conscious</u> strategy for this would be difficult and presumably take considerable time.

It is clear, therefore, that the profiles recorded in these two experiments reflect <u>adaptation</u> of the sort under investigation in conventional research. The results obtained in these studies, however, indicate that the process underlying adaptation is considerably different from that assumed by those adopting the established paradigm: adaptation has a <u>long-term</u> component with influences which closely resemble conventional learning effects. The specific effect paralleled in these experiments is the complex, and imperfectly understood, process of "learning to learn". At this point, therefore, it seems reasonable to conclude that adaptation can be <u>learnt</u>, although <u>what</u> is learnt is still unclear. In the following chapter a preliminary attempt is made to answer this question.

CHAPTER 5

WHAT IS LEARNT DURING ADAPTATION?

The empirical work reported in the previous chapter established that learning is involved in the adaptation process, thus achieving the principal aim of this thesis. In this chapter a preliminary consideration of the nature of what is learnt is undertaken as a secondary question. This question has been generally ignored in adaptation research since the conventional view of adaptation does not include learning processes. It is from the field of learning itself, therefore, that possible answers must be sought. A problem is immediately apparent, however, namely that adaptation involves the development of a new correlation between visual stimulation and very precise motor responses. Conventional learning theorists (e.g. Hull, 1934; Skinner, 1938), however, have been concerned with acts, defined by outcome,(1) and hold to the notion of motor equivalence in what is learnt: "a variability of specific responses, with circumstance, in such a way as to produce a single result" (Hebb, 1949, p 153).

The adaptation process, however, requires accurate response differentiation on the part of the subject. For the precise patterns of muscle efference required to bring the pointing limb to the spatial position specified by the distorted visual stimulation must be learnt. And, as the findings reported in Chapter 4 show, several conflicting

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(1) "If workers in operant conditioning had started by proposing that they study the responses of the experimental apparatus and not the responses of the animal, it would have seemed an approach unlikely to pay off. But in practice it seems to work." (Dallett, 1969, p 119).

reaching strategies for use in the same stimulus situation can be acquired and maintained in progressively more accurate forms. Such a process, if it were based on motor-response learning, would clearly require excellent motoric memory⁽¹⁾ on the part of the subject. Conventional learning theories, however, have little to say about motoric memory. For it is not the specific muscular responses which are under investigation when a rat learns to depress a lever a certain number of times for a food reward, but rather the "behaviour of the apparatus":

> "It is usual, and in practice necessary, to define an animal's response in terms of its end effect: the rat reaches and enters the food box, the chimpanzee's hand makes contact with a stimulus plaque and moves it ...... A rat trained to depress a lever to get food may do so from any of several positions, in each of which the muscular pattern is different ..... Very often, all that can be predicted after the response is learned is that the lever will be moved downward."
> (Hebb, 1949, p 154).

Exceptions to this paradigm do exist, however, Notterman (1966), for example, trained rats to regulate the force with which they pressed a lever on the basis of response-produced feedback. In addition, the rats learnt to use different forces to press the same lever on

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(1) As Russell (1976), in a discussion of the possible mechanisms of motor control, pointed out:

> "... open-loop control requires the storage in memory of an infinite number of learned movements in the form of some representation of the motor commands (Henry and Rogers, 1960). Similarly, closed-loop control requires some representation of the sensory consequences of these movements (Adams, 1971). The memory requirements in either case, in terms of the storage and subsequent retrieval, are enormous."
> (Russell, 1976, p 68).

different occasions signalled by the level of illumination in the experimental context (Notterman and Mintz, 1966). These results, suggesting that response differentiation may be based on mechanisms similar to those involved in stimulus discrimination, indicate that it is possible to bridge the gap between the requirements of a theory of adaptation and the conventional learning paradigm. It is proposed, therefore, that adaptation is a process governed by conventional learning principles which operate to produce accurate response differentiation on the basis of response-produced feedback. The following experiment is a preliminary attempt to substantiate this proposal.

EXPERIMENT 3 - HAND DIFFERENTIATION IN THE SQUIRREL MONKEY

Subjects

The subjects were six adult squirrel monkeys (*Saimiri scuireus*) approximately seven years old. Five were male and one female. They had had previous experience in test situations involving the Wisconsin General Testing Apparatus (WGTA) where they had undergone investigations of sensory discrimination and object permanence. One monkey had been used earlier as a 'prototype' in a preliminary feasibility study for training hand use. The others were completely naive in this respect and had no prior laboratory experience of any specialised motoric 'shaping'. They were maintained on MRC diet 2 on which they were fed *ad libitum*.

Experimental Design

This study (reported by McGonigle and Flook, 1978a, see Appendix F) was carried out in two phases. The first involved the initial reversal of the spontaneous hand preference for the manipulation of a stimulus object in order to retrieve a food reward.

Phase 2 involved the conditioning of the use of the two hands to different external stimuli. Tests of durability and transfer to other contexts were planned for both phases.

The task was a relatively simple one in that the monkeys were already familiar with the experimental apparatus - a Wisconsin General Testing Apparatus (WGTA) - in which they had experienced previous training on sensory discrimination tasks. Their previous experience had not, however, involved the use of any specialised motor responses, as they were free to manipulate stimuli in any way they chose to obtain the food reward situated in a foodwell beneath the object. In this task the response was more constrained. The stimulus object had to be pushed so that it swivelled round to reveal the foodwell. Pretraining was therefore given to all subjects to enable them to acquire reasonable proficiency at this manipulation.

PHASE 1: Reversal of spontaneous hand preferences

Apparatus

The training apparatus was a WGTA painted mid-grey. Round tobacco tins painted blue or yellow were used as stimuli. One tin was mounted in the centre of the test-tray (painted white) on a brass pivot. When pushed, it swivelled aside revealing a foodwell. The tin could be locked in position over the foodwell, and a pulley cord under the test-tray enabled the experimenter to free the lock so that the monkey could push aside the tin and gain access to the foodwell.

Procedure

In general the procedure was similar to that used in sensory discrimination tasks. Training involved a maximum of forty trials per session and conditions of massed practice with an interval between trials (ITI) of 15 sec. A correct response was rewarded with a half peanut. A correction method was employed which allowed the monkey freedom to manipulate the tin on any one trial until the hand selected by the experimenter was used. The experimenter unlocked the tin only when force was exerted on the tin by the appropriate hand.

Design

Stage A

All subjects were allowed free choice of hand (i.e. the experimenter unlocked the tin whichever hand was used) in manipulating the tin (colour X) in the WGTA for four sessions (160 trials). The experimenter recorded both the hand used to manipulate (M) the tin and the hand used to retrieve (R) the peanut.

Stage B

The non-preferred hand for manipulation was determined for each subject from the results of Stage A(1). All subjects showed a significant preference(2). Subjects then received training in the WGTA with a different tin (colour Y) for five sessions (200 trials) during which responses by the non-preferred hand only were reinforced. The experimenter again recorded the retrieval (R) hand for each trial.

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(1) The 'prototype' monkey showed no preference for either hand at this stage, having received training on the use of both hands in this situation. This subject had shown a significant preference before training, and so this was used to determine which hand was trained in Stage B.

(2) For the first three subjects (Brown, Orange, Beardie) the position of the brass pivot was such that right-handed manipulation was easier than left-handed. This was corrected after the first two sessions with these subjects. However their original preferences for this task may reflect the design of the equipment rather than a preference for right-hand use per se.

Stage C

Retention tests (using tin Y) of 80,40 and 80 trials respectively were carried out at intervals of 1, 3 and 7 weeks following Stage B. These tests were given with no differential reinforcement of hands (i.e. free choice).

Results and Discussion

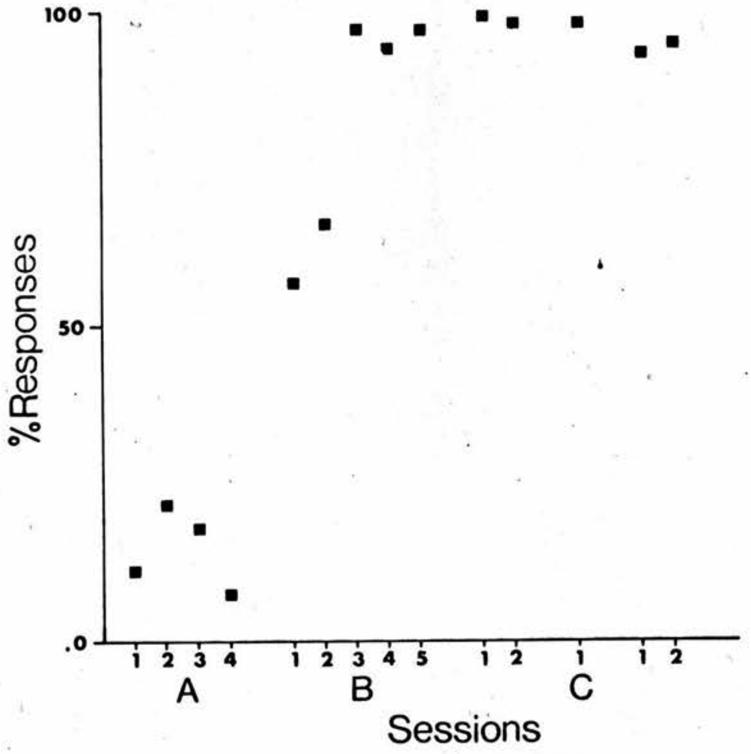
All subjects attained a level of performance of above ninety percent correct over two successive sessions within the training period (Stage B). The results of the retention tests (Stage C) show that this reversed hand preference remained stable over several weeks without further differential reinforcement. Figure 12 records the mean scores for the originally non-preferred hand on each of these stages. (The scores for the individual subjects are presented in Appendix C.)

This part of the experiment, therefore, demonstrates that spontaneous hand preferences can be reversed by adjusting the reward contingency in a procedure analogous to sensory discrimination tasks. The successful reversal of stable hand preferences (see Appendix C for a more detailed analysis of the hand preferences expressed by these monkeys), without involving the physical obstruction of the use of the preferred limb employed by other investigators (Peterson, 1951; Warren et al, 1967), suggests that it is the contingency between response (by a particular forelimb) and external consequence that determines preference, rather than the relative physical efficiency of the two limbs (Warren et al, 1967). Following the establishment of differentiation in the use of the two limbs on the basis of differential reinforcement, the question of selective conditioning of these responses to external cues could be investigated.

Figure 12

Percentage of responses per session (mean for six subjects) using the Trained hand under the following conditions:

A: Free choice (colour X)
B: Training - non-preferred (Trained) hand reinforced (colour Y)
C: Retention after 1, 3 and 7 weeks - free choice (colour Y)



PHASE 2: Selective conditioning of hand use

Subjects

As in Phase 1.

Apparatus

The training situation (WGTA) was the same as for Phase 1. Transfer tests were carried out in the Home Cage and in a U-shaped apparatus. For tests in the Home Cage a portable version of the tray and lockable tin device was used. Subjects were tested alone in their Home Cages. The U-shaped apparatus consisted of three wooden chambers arranged to form the sides of a U. In the centre was a wooden board on which test-trays could be placed. The sides of each chamber facing inwards to the board were made of perspex (transparent), with a horizontal slit through which the monkey could reach to manipulate stimuli presented on the tray. Occluding screens could be lowered between trials. Access to each chamber was controlled by sliding doors between the chambers. A similar test-tray with a pulley system to lock the tin was used in this apparatus. Testing was carried out only in the two side chambers (A and B), which looked onto the test-tray from opposite directions.

Procedure

As for Phase 1.

Design

Stage A

All subjects were first given retraining in the WGTA (with tin Y) on the hand (H1) trained in Phase 1. They were then given training (with tin X) to use the originally preferred hand (H2) to a criterion of 18/20 successive correct responses for two successive sessions. During this stage the 'prototype' monkey showed persistent instability in responding with his originally preferred hand and was withdrawn from the rest of the study.

The remaining five successful animals were then given eight further sessions of training, with alternate sessions requiring appropriate responses to tin X (H2) or tin Y (H1) analogous to "serial-reversal" training. Thus sessions 1, 3, 5 and 7 involved reinforcing the trained hand (H1), with tin Y being used as the stimulus; sessions 2, 4, 6 and 8 involved presentation of tin X and the originally preferred hand (H2) being reinforced.

Training then proceeded with the presentation of the two stimuli (X and Y) successively within each session in a quasi-random (Gellermann, 1933) sequence. The correction procedure was used and extended to include the provision that no change in the stimulus should occur until three successive correct responses, following the error, had been made to it. This greatly increased the number of correction trials at first, thus reducing the number of 'Gellermann' trials to thirty per session on average. Training continued until the performance criterion of 18/20 successive correct trials over two sessions was reached.

Following successful acquisition of this cued hand discrimination, two further stages in the experiment could becarried out. The first of these was simply to test for the durability of this learning over a period of several weeks. The second was to study the effects of different contexts on the discrimination. The colour cues had become effective as 'triggers' or 'releasers' (see Tinbergen, 1951) of appropriate behaviour, but their effectiveness might depend on the conservation of the test situation (WGTA).

Stage B

Retention tests were given in the WGTA 3, 6, 11 and 13 weeks after training was completed. These each consisted of 100 'Gellermann' trials as in the training sessions, but only a single correct response was required on the correction trials.

Stage C

Transfer tests under the same conditions as the retention tests were carried out in each of the three situations: Home Cage, sides A and B of the U-shaped apparatus. These tests were given during the weeks between the Stage B retention tests.

Results and Discussion

Stage A

All five subjects learnt to use their originally preferred hand (H2) to manipulate tin X within two sessions (80 trials) with the mean number of errors recorded equal to 12. On the "serial-reversal" training sessions the monkeys learnt to use the appropriate hand within each session, with the number of errors recorded on each reversal remaining constant (between 6 and 9 errors). Thus, although "serial-reversal" improvement was recorded in terms of the reduction of the number of errors from that incurred in the original training of the non-preferred hand (see Figure 13), this improvement does not extend to the level of the spontaneous hand preferences recorded in Phase 1. This training procedure, therefore, failed to produce accurate hand differentiation involving the use of the colour cue to *predict* the correct response. The difficulty experienced by these monkeys on this task is attributable to the response differentiation, i.e. the selective use of their two forelimbs, rather than to any difficulty in discriminating between the two colours: similar two-choice colour discriminations are learnt by squirrel monkeys with little difficulty (e.g. McGonigle and Chalmers, 1977). Training on the quasi-random (Gellermann) sequences, however, proved successful, with all subjects attaining the performance criterion of 18 out of 20 correct responses for two successive sessions, within ten sessions (see Table 10). The experience of rapid switching between the two conditions, therefore, may serve to establish the differential use of the two forelimbs as alternative response classes. The contingency relationship between the use of the particular limbs in the presence of the two colours may then be learnt. Terminal performance on this stage, therefore, paralleled that on a "conditional discrimination" task and the predictive performance of subjects in the adaptation situation in Experiments 1 and 2.

Stage B

This cued hand differentiation was shown to be durable, as retention tests (with differential reinforcement) showed no decrement in performance over intervals of several weeks. Table 10 records both the acquisition and performance scores expressed as the mean numbers of trials to criterion and the mean numbers of errors per 100 trials for the group of five subjects. It can be seen that there was no asymmetry in the use of the two hands.

Stage C

The transfer tests showed clearly that there was no transfer to the Home Cage situation. However, some transfer was recorded for the U-shaped apparatus, and between sides of this box. The means for these tests are shown in Table 10. Inspection of the scores for individual subjects (see Appendix C) reveals that no subject reached criterion in 100 trials in the Home Cage test, whereas four out of five succeeded in both sides of the U-shaped box. The subject who failed to reach criterion showed perseveration of responses by one hand, Hand 1, in the U-shaped box, but by the other hand, Hand 2, in the Home Cage. The other subjects showed perseveration of whichever response was rewarded on the previous trial in the Home Cage tests. Thus it seems that all subjects treated the Home Cage differently from the other contexts.

Table 10

Mean acquisition and performance scores (N = 5) on Gellermann sequence presentation of cued hand discrimination: colour Y - Hand 1; colour X - Hand 2.

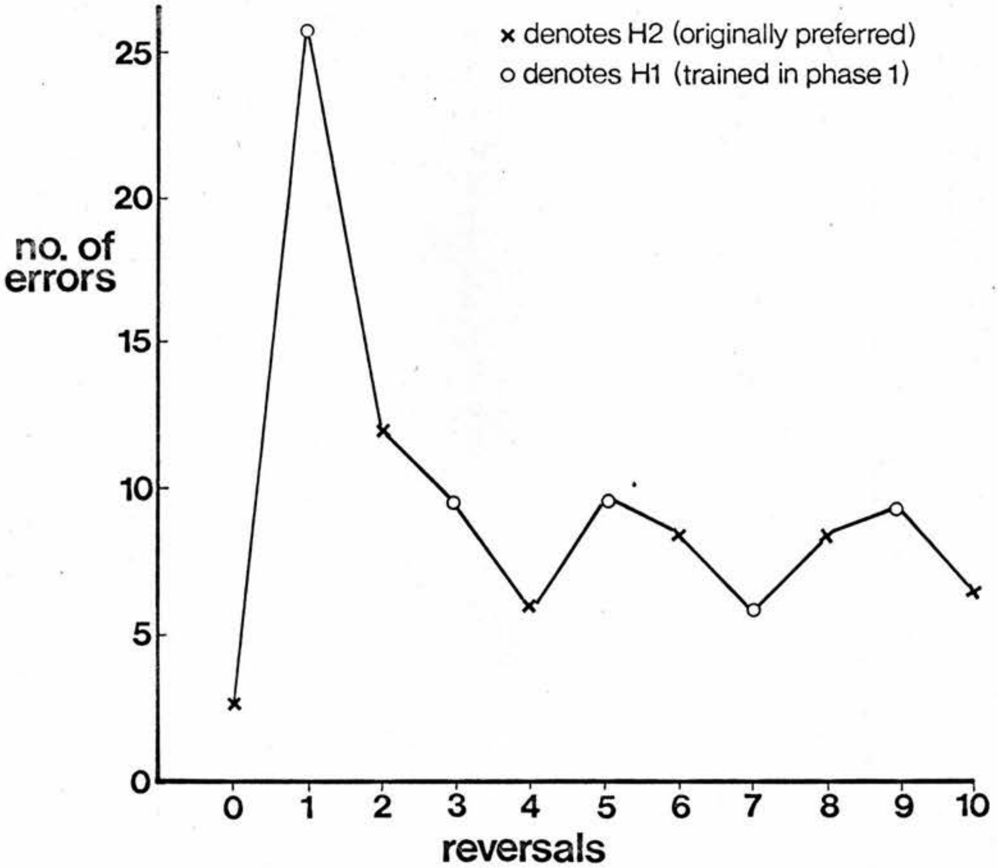
	Total No of Trials	Mean No of Errors Hand 1	Hand 2	Trials to Criterion
Acquisition				
Training to Criterion	350	37.6	37.2	270
Training (1st 100)	100	17.6	18.6	-
Performance				
Training (last 100)	100	5.2	6.8	50
Retention (3 wks)	100	5.5	4.8	44
(6 wks)	100	2.8	3.2	44
(11 wks)	100	2.4	2.6	42
(13 wks)	100	1.6	1.8	43
Transfer				
Home Cage	100	16.0	22.8	-
U-box Side A *	100	8.0	4.7	60
Side B *	100	5.0	3.5	44

* Means excluding subject who failed to reach criterion

Figure 13

Mean number of errors for five subjects per session (40 trials) on successive "reversals" of hand use:

0: spontaneous hand preference (Phase 1, Stage A)
1: first reversal of this preference (Phase 1, Stage B)
2-10: reversal training (Phase 2, Stage A)



Conclusions

This experiment demonstrates that response differentiation, in this case the use of different forelimbs to manipulate a stimulus object, can be achieved on the basis of differential reinforcement. The retention of this response differentiation over periods of several weeks in the absence of further differential reinforcement indicates that motor-response learning of this form has sufficient durability to sustain long-term effects such as those reported in the adaptation experiments. The further finding that these differentiated motor responses may be selectively conditioned to different external cues which were previously neutral with respect to the responses - the colour of the stimulus in this case - provides a parallel with "conditional discrimination" and the predictive performance in the adaptation situation. The performance of these squirrel monkeys, therefore, suggests that specific motor responses can be acquired through the operation of conventional learning processes. Thus, the concept of "motor equivalence" (Lashley, 1933), although appropriate in some contexts (e.g. MacFarlane, 1930), should not be applied to all learning situations(1).

The results of this experiment, while lacking the depth to be definitive, suggest, nevertheless, that the process of response

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(1) Hand preferences per se suggest that motor equivalence may not apply in situations requiring manipulation of the stimulus as opposed to those involving spatial location.

differentiation operates according to conventional learning processes. The similarity between the profiles obtained from this study and those from the adaptation experiments reported in Chapter 4 provides support for the conclusion that motor learning mechanisms may underlie adaptation to visuo-motor rearrangement.

CHAPTER 6

A "MOTOR-SENSORY" APPROACH

The empirical work presented in this thesis has practical as well as theoretical implications for adaptation research. The practical implications, which will be discussed first, stem primarily from the finding that adaptation has long-term influences. These effects invalidate the use of within-subject designs in which several exposure conditions are presented to each subject following intervals of perhaps one or two days. Such designs assume that once normal coordination is restored the subject returns to a "naive" state. Long-term adaptation, causing subsequent exposure to produce effects which differ from the original adaptation, implies that the effects of different exposure conditions cannot be compared using the same subjects. Counter-balancing the order of presentation may be effective in that the profiles for successive presentations will be obscured, but any comparison between absolute magnitudes of adaptation recorded by subjects with different rearrangement experiences must be meaningless.

The conventional measure of adaptation in terms of aftereffects is also invalidated by the work reported in this thesis. The learning view of adaptation implies that the post-exposure test should be considered as a "transfer of learning" situation. Held's claim (Held and Bossom, 1961) that "under properly controlled conditions" the aftereffects recorded equal the adaptation obtained during the exposure phase is tenable if and only if the exposure and post-test conditions are identical(1) - a condition he fails to satisfy in his own experiments (e.g. Held and Gottlieb, 1958).

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(1) This dependence of aftereffect measures on the conditions under which the test is carried out is confirmed by the reports of several investigators who found variations according to the activities involved (Baily, 1972; Freedman et al, 1965), and the presence or absence of the goggles which housed the prisms (Uhlarik and Canon, 1970; Welch, 1971; Kravitz, 1972).

The rationale for the use of aftereffects includes controlling against "conscious correction", i.e. the use of deliberate corrective strategies by subjects as a result of seeing their errors of localisation(1). Although one would wish to avoid results attributable to such behaviour, one should also wish to obtain a fair assessment of the adaptation. To achieve such a fair measure the adaptation must be recorded during the exposure, or training, phase. As a check against conscious correction, the prism may be removed for a few trials at the end of the session. Alternatively, a different prism may be substituted and any negative transfer recorded will indicate the extent of the aftereffect. This latter technique, employed in the experiments reported in this thesis, provides the test conditions which are closest to the exposure situation. However, some differences endemic to the rearrangement device, such as colour fringes and compression effects in the visual field, may provide sufficient information to the experienced subject that the prism has been changed. (The predictive performance recorded by subjects in Experiments 1 and 2 in the absence of any external cues may depend on such effects.) The use of mirror arrangements as an alternative to wedge prisms to avoid such extraneous distortions is therefore advisable.

The implication of the above discussion is that comparisons between the magnitudes of adaptation obtained using different techniques must be considered invalid. Thus the recent controversies,

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(1) "If it had to be maintained by a deliberate redirection of movement, the whole subject of visuo-motor adaptation would be trivial."
(Howard and Templeton, 1966, p 386).

concerning intermanual transfer for example (e.g. Cohen, 1973; Prablanc et al, 1975), may have been confused rather than clarified by the use of different measurement and exposure techniques. The dispute concerning the necessity for active movement in adaptation (e.g. Weinstein et al, 1964; Held and Mikaelian, 1964) may also reflect the different techniques employed: Held's failure to obtain any adaptation under passive conditions (Held and Hein, 1958) may reflect the generally low scores obtained using his technique (approximately thirty percent of the displacement following active exposure). Meaningful comparisons between active and passive exposure conditions can be achieved only when fair measures of adaptation are recorded in both cases. As the preceding discussion indicates, these take the form of measures of accuracy in the presence of the prism rather than aftereffect measures which, as Pick and Hay (1965) noted, involve active movements for both conditions in Held's experiments.

The theoretical implications of this thesis are based on the finding that adaptation can be learnt. The conventional model of adaptation (Held, 1961) has no capacity for the storage of alternative visuo-motor correlations as separate entities. Held's "Correlation Storage" contains only the component parts of each correlation, temporarily in co-existence, with no identification other than temporal:

> "The proposed system neither selects nor filters the incoming signals it receives on the basis of special functional relations (other than temporal) between the efferent and afferent signals."
> (Held, 1961, p 31).

In order to account for the long-term effects reported in this thesis the adaptation responses must be stored in a form that can be reactivated when the situation demands. Thus Held's (1961) model must be rejected on the basis of its failure to deal with long-term adaptation. The involvement of action in the development of visuo-motor coordination, however, is not challenged by this thesis. On the contrary, active movement is implicated in a fundamental way in any motor-response learning account of adaptation. Thus, the motor-sensory approach advocated in this thesis regards the development of associations between self-produced movement and the consequent transformations of visual stimulation as the basis of visuo-motor coordination. The particular class of visual transformation depends on the type of movement involved. Gibson (1968) has described several classes of transformation following movements of the observer or external objects. These are as follows:

> "... (a) when a figure in the array transforms with occlusion effects the motion of an object is specified. (b) When the total array transforms with occlusion effects the movement (locomotion) of the observer is specified. (c) When a certain familiar elastic protrusion enters the array the movement of a limb is specified. These optical motions are registered by exploratory adjustments of the head-eye-retina system. (d) When the borders of the ocular orbits sweep across the array head turning is specified. (e) When the retina sweeps over the potential image in one of the several ways possible for the oculomotor system an eye movement is specified."
> (Gibson, 1968).

It can be seen that these fall into two groups: (1) <u>action-contingent</u> transformations, (2) transformations due to movement in the external world. Thus it is possible that an organism can distinguish between his own movement and that of the external world on the basis of the type of transformation produced. Gibson suggests that the information regarding the type of motion can be directly "picked up" from the transformations of the visual array (Gibson, 1966), thus providing no difficulty for the neonatal organism (or adult under rearrangement conditions) in distinguishing between his own movement and motion in the external world. Even without such direct translation of the visual stimulation into sensations of movement, however, the organism should have little difficulty in making associations between movements and their visual consequences since there is a one-to-one correspondence between movements and visual transformations. Provided the young organism is aware of these contingency relationships, repeated experience with them should result in identification of the action-contingent, as opposed to externally produced, visual transformations. To develop such associations between self-produced movement and its visual consequences, the organism must have the following capacities: (1) It must be able to identify the particular movement performed and so be able to repeat it. (2) It must be able to discriminate between different types of visual transformation. (3) It must be able to pick up the contingency relationship between movement and visual transformation. Evidence for all such capacities in the human newborn is available.

(1) The first requirement, identification of a particular movement for the purposes of repetition, is essentially the mechanism described by Piaget (1953) as the "primary circular reaction". This capacity for repeating a movement involving part, or all, of the body, is seen by Piaget to follow from the initial stage of reflexes, in which,

for example, the infant turns its head in response to pressure on its cheek - the "rooting" reflex. The stage of primary circular reactions involves the repeated performance of such responses in the absence of the eliciting stimulus. This repetition, or practice, of such actions paves the way for the "secondary circular reaction" in which the action is repeated with the effect of maintaining the occurrence of a consequence, for example repeatedly hitting balls suspended above the cot to make them bounce up and down. Experimental work with infants involving conditioning techniques provides further evidence for their ability to identify and repeat particular actions. For example, head-turning has been successfully conditioned in newborns (e.g. Bower, 1966; Papousek, 1967; Siqueland and Lipsett, 1966). Such studies demonstrate not only the discrimination of head movements from other patterns of behaviour, but also discrmination between movements to the left and to the right. Thus the human infant appears to have the required capacity of identifying and repeating specific actions.

(2) The second requirement of discrimination between different types of visual transformation also appears to be present at an early stage. Bower (1974) has carried out several studies with young infants showing that they respond differently to different patterns of visual transformation. Thus the human infant is indeed capable of identifying motor movements and visual transformations. However, is he able to form associations between such related events?

(3) Watson proposes that young organisms are indeed aware of such contingencies:

> "... 'contingency awareness' refers to an organism's functional knowledge that the nature of the stimuli

> received is sometimes affected by the nature of the behaviour the organism is emitting. More specifically, contingency awareness refers to an organism's readiness to react adaptively in a contingency situation and to an organism's sensitivity in the perception of contingency situations when they occur."
> (Watson, 1966).

Support for such contingency awareness has come from Watson's own work (Watson, 1966) in which infants learnt to play "contingency games". For example, infants learnt to fixate one of the experimenter's fists, resulting in the hand being opened; should the infant fixate the other fist, it remained closed. The experimenter then changed his choice of fist and the infant rapidly adjusted to the new contingency. Other work on learning in infants has also suggested that what is important is not the actual reward (food, light, etc.) but the relationship between a given behaviour and a given event in the external world (Papousek, 1969). It was also noticed that once the infants had detected the contingency they would stop responding, and only start again if the contingency were changed. It may be concluded, therefore, that young organisms have the necessary capacities for developing associations between self-produced movements and their visual consequences through learning processes.

The contingencies operating between actions and visual consequences involve one-to-one relationships. For every time the organism makes a particular movement there is a <u>unique</u> visual consequence, and conversely every visual transformation is the result of a unique action. It is possible, therefore, that the visual consequences of observer movement, once associated with a particular action, subsequently come to signify the occurrence of that action. The investiture of visual stimulation with such signalling properties provides an interpretation (McGonigle, 1976) of the apparent primacy of vision in the control of action. Experiments reported by Lee, for example, show that human adults (Lishman and Lee, 1973) and young children (Lee and Aronson, 1974), exposed to visual stimulation from an environment moving towards them (the "swinging room"), respond by swaying, or even falling backwards, i.e. by attempting to counteract their supposed forward movement. Such findings may be taken as showing that subjects interpret visual transformation normally consequent to their own movement as indicative of such movement.

Once such associations between the perceiver's own movements and their visual consequences have been established, it is possible that similar associations may be developed between visual transformations and the motions of objects in relation to the perceiver. Thus the mature subject may be able to predict the point of contact of an object moving towards him, a rod approaching his face for example. The disconfirmation of such predictions under rearrangement conditions would then provide information concerning the nature of the distortion. Thus, subjects given "passive" exposure to familiar situations in which they expect certain relationships between visual stimulation and movement to hold, may be able to use any disconfirmed expectancies as a basis for adjusting their behaviour. This motor-sensory account, therefore, is consistent with the reports of adaptation by (adult) subjects following exposure to such "passive" conditions (Wallach et al, 1963; Templeton et al, 1965; Howard et al, 1966). Held's (1961) model, however, requiring reafferent feedback for adaptation, is unable to account for such findings. This analysis suggests, therefore, that active, self-produced movement is not the critical factor in adaptation. Rather, the vital feature is the association, derived from the subject's previous experience involving response-produced feedback, between action and visual transformation in a reversible relationship.

This interpretation suggests that there is a fundamental difference between adaptation in the mature organism and the development of visuo-motor coordination in the neonate, two processes which have been interpreted as involving the same underlying mechanism (e.g. Held, 1961). For the adult subjected to visuo-motor rearrangement is in a situation where his previously accurate, well-rehearsed actions suddenly become inappropriate when paired with the distorted visual stimulation. The adult, therefore, is in possession of a set of associations between action and visual transformation. The neonate, by contrast, has no such correlation which can be subjected to sudden interference(1). Thus there is no possibility that the neonate could establish an <u>alternative</u> correlation which might interfere with a previous one, any "innate" correlation presumably being appropriate though imprecise. Experience for the neonate, therefore, serves to establish associations where none existed previously. For the adult,

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(1) It might be argued that such a change occurs at birth, and that the neonate is then in possession of coordinations which are appropriate to the uterine environment, but not to the outside world. However, it seems unlikely that visuo-motor coordination could develop to any great extent in the uterus, in which no light is present, and, in many animals, the eyes are not open.

however, it permits the development of a new correlation to replace the old, both co-existing in the nervous system without mutual cancellation.

This difference, though important, does not imply that adaptation research has no relevance for the understanding of perceptual development. The implication is merely that one should expect not only similarities but also differences between these two processes - the recovery from disruption cannot be expected to be identical to the original development. One important finding which does appear to be relevant to both adaptation and development is the role of action. As Held and his colleagues (Held and Hein, 1963; Held and Bauer, 1967) claim, active movement in the presence of visual stimulation may be the essential factor in the development of visuo-motor coordination in the neonate. For the associations between action and visual stimulation must be established on the basis of self-produced movement(1), i.e. movement for which there is an "Efference Copy" (von Holst, 1954). "Passive" exposure to visual stimulation would not necessarily provide the neonate with information concerning the result of its own active movements, although the contingency relationship operating between visual transformation and the passive movements might be learnt.

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(1) It should be noted that Konorski concluded that:

"... a passive displacement of the body or limbs followed by drive reduction does not lead to the formation of an instrumental response imitating that displacement. One is forced to conclude that the individual has to perform the given movement by himself in order to reproduce it in instrumental conditioning."
(Conorski, 1967, p 468-9).

An implication of this thesis is that specific classes of active movement will have selective effects. It should be clear from the discussion in this chapter that the crucial associations involve the "action-contingent" transformations. Possibly the most important of these is the whole-field displacement which results from head movement. It should be noted that in neither of the original rearing studies reported by Held (Held and Hein, 1963; Held and Bauer, 1967) was this class of transformation controlled. Both cats and monkeys were free to move their heads in a stimulus-rich environment. Such an important source of information should surely be controlled before the selective impact of restricting sight of particular limbs can be investigated.

In conclusion, the conceptual implication of this motor-sensory approach is that visuo-motor coordination should be regarded as a development within several motor-sensory systems, functionally differentiated on the basis of the various contingency relationships which operate between action classes and sensory consequences. The specification of the response classes involved, coupled with experimental demonstrations of their primary role in perception, constitutes an important problem for further research.

APPENDIX A

Analysis of the results from Experiment 1 (monkey adaptation study, pages 50-66)

The error data shown in Figure 14 were subjected to an analysis of variance (including repeated measures) using the computer program BMD08V - Analysis of variance (BMD, 1971). The mean errors reflect the *magnitudes* only, the directions of the errors being opposite for the two prisms. The analysis included six factors: Order (2 levels, fixed); Condition (2 levels, fixed); Prism (2 levels, fixed); Stage (4 levels, random); Trial (20 levels, fixed); Subject (2 levels nested in Order, random). These factors were defined as follows:

Order: corresponds to Groups 1 and 2 in which the two conditions were presented in Order 1 (AS, SS) and Order 2 (SS,AS)

Condition: Condition 1 (AS) and Condition 2 (SS)

Prism: Prism A and Prism B

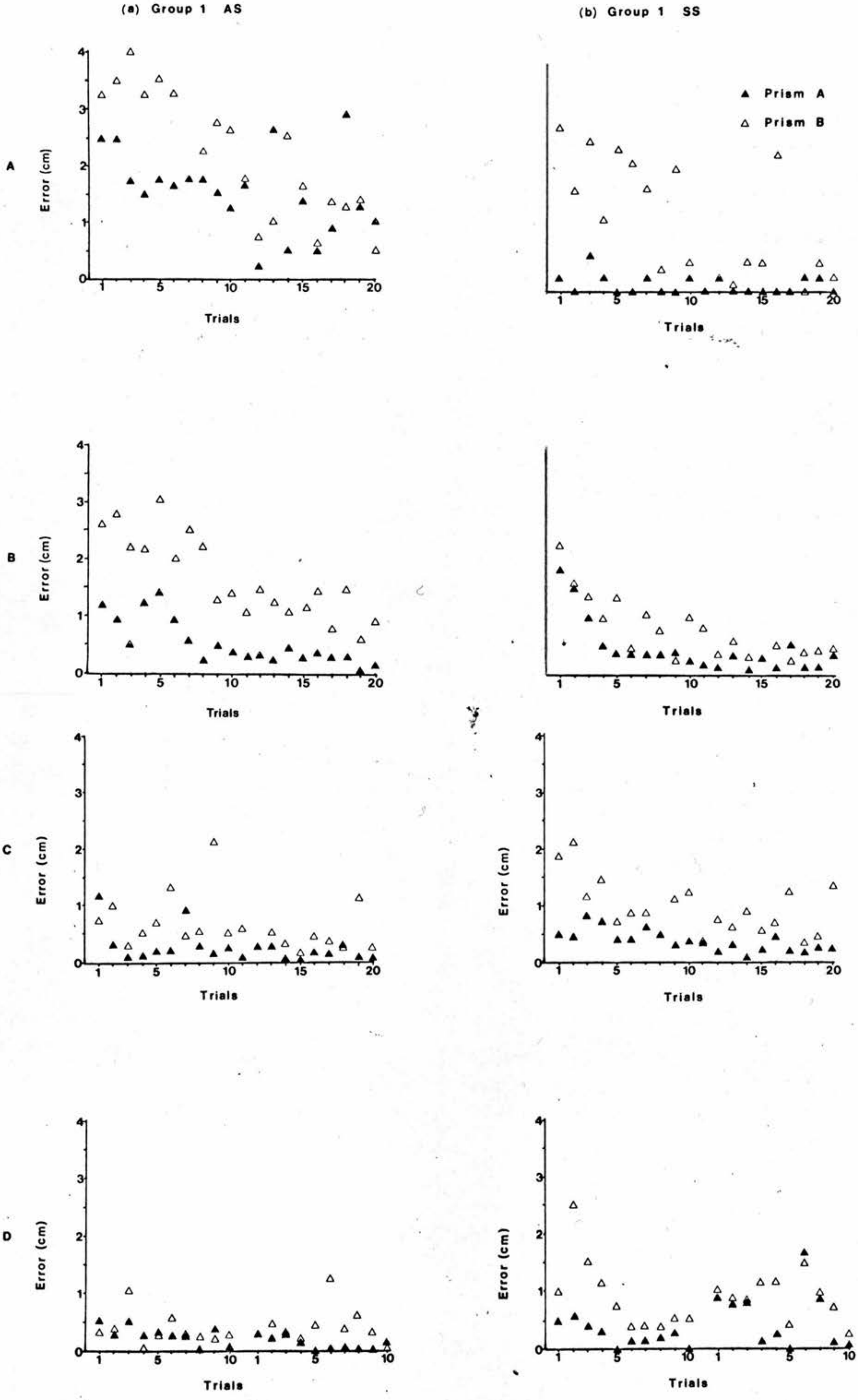
Stage: Stages A, B, C, and D where each value is the mean error for the prism presentations in that stage; these were treated as random since they constitute a sample of the set of possible stages, each with a number of trials which is a proportion of the number of trials per session

Trial: The first 20 trials of each prism presentation (for Stage D, where only ten trials per presentation was given, the second presentation of each prism for the session was treated as trials 11 to 20)

Subject: The two subjects in each group.

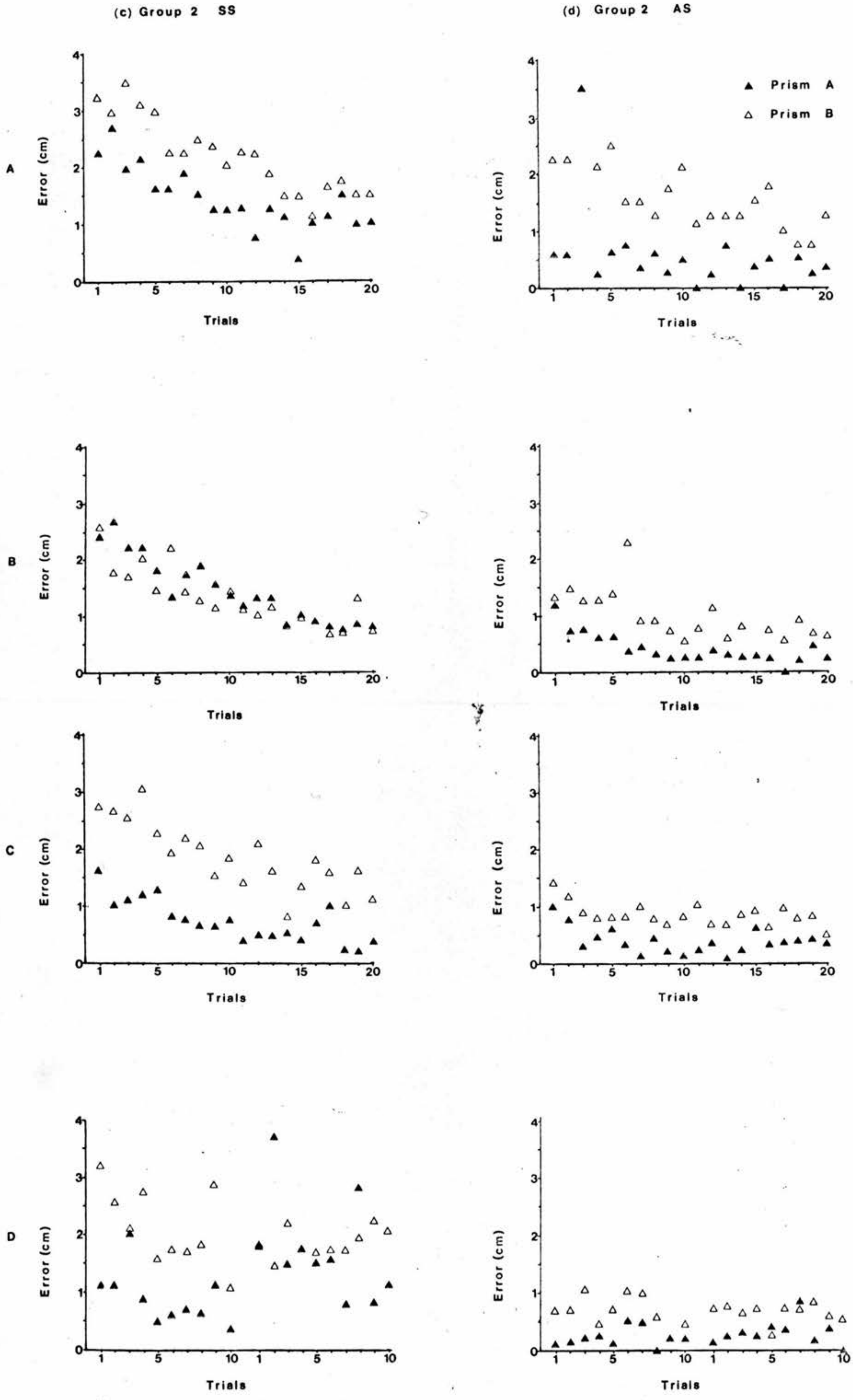
The results of this analysis showing the values for all the testable F ratios are given in Table 11.

Figure 14



Mean Error (cm) per trial for the prism presentations in Stages A, B, C and D for Group 1 (a) AS, (b) SS.conditions.

Figure 14



Mean Error (cm) per trial for the prism presentations in Stages A, B, C and D for Group 2 (c) SS, (d) AS conditions.

Table 11

Analysis of variance (including repeated measures) with six factors: Order (2 levels, fixed); Condition (2 levels, fixed); Prism (2 levels, fixed); Stage (4 levels, random); Trial (20 levels, fixed); Subject (2 levels nested in Order, random).

Source	MSerror	df	F	p
Order *	40.978	1,3	4.293	
Condition *	69.282	1,4	1.678	
Prism *	40.091	1,4	10.460	<.05
Stage	3.983	3,6	24.463	<.01
Trial *	6.012	1,89	4.218	<.05
Subject	3.983	2,6	7.506	<.05
Order x Cond *	41.939	1,4	8.925	<.05
Order x Prism *	33.384	6,3	0.204	
Order x Stage	3.983	3,6	2.783	
Order x Trial *	2.467	89,74	0.924	
Cond x Prism *	20.256	7,3	0.747	
Cond x Stage	5.185	3,6	11.478	<.01
Cond x Trial *	2.380	60,95	1.328	
Cond x Subj			-	
Prism x Stage	4.852	3,6	2.948	
Prism x Trial *	2.562	35,95	1.669	<.05
Prism x Subj	4.852	2,6	5.314	<.05
Stage x Trial	1.374	57,114	3.186	<.01
Stage x Subj			-	
Trial x Subj			-	
Order x Cond x Prism *	5.506	6,5	2.635	
Order x Cond x Stage	5.185	3,6	6.204	<.05
Order x Cond x Trial *	2.532	57,95	1.305	
Order x Prism x Stage	4.852	3,6	1.565	
Order x Prism x Trial			-	
Order x Stage x Trial	1.374	57,114	0.606	

Table 11 (Contd)

Source	MSerror	df	F	p
Cond x Prism x Stage	14.033	3,6	1.344	
Cond x Prism x Trial *	2.119	86,91	0.952	
Cond x Prism x Subj			-	
Cond x Stage x Trial	1.495	57,114	0.950	
Cond x Stage x Subj			-	
Cond x Trial x Subj			-	
Prism x Stage x Trial	1.184	57,114	1.227	
Prism x Stage x Subj			-	
Prism x Trial x Subj			-	
Stage x Trial x Subj			-	
Order x Cond x Prism x Stage	14.033	3,6	0.293	
Order x Cond x Prism x Trial	0.715	19,38	0.680	
Order x Cond x Stage x Trial	1.495	57,114	1.052	
Order x Prism x Stage x Trial	1.184	57,114	1.154	
Cond x Prism x Stage x Trial	1.206	57,114	0.885	
Cond x Prism x Stage x Subj			-	
Cond x Prism x Trial x Subj			-	
Cond x Stage x Trial x Subj			-	
Prism x Stage x Trial x Subj			-	
Order x Cond x Prism x Stage x Trial	1.206	57,114	0.822	
Cond x Prism x Stage x Trial x Subj			-	

* Quasi-F calculated from the expected Mean Squares; each F" is of the form

$$F'' = \frac{MS_1 + MS_2}{MS_3 + MS_4}$$

df estimated as follows: numerator df $= \dfrac{(MS_1 + MS_2)^2}{MS_1{}^2/df_1 + MS_2{}^2/df_2}$

denominator df $= \dfrac{(MS_3 + MS_4)^2}{MS_3{}^2/df_3 + MS_4{}^2/df_4}$

The significant results are as follows:

(1) The highest order significant interaction was that of Order x Cond x Stage (see Figure 6, page 60). This reflects the improvement over the four stages shown on the AS condition by both groups, while performance on the SS condition was either stable at a relatively high level of accuracy (Group 1), or generally poor with the improvement shown on Stage B reversed on Stage D (Group 2). This effect is shown in the Order x Cond interaction, with Order 1 showing better overall performance on Condition 2 (SS) (mean for AS = 1.76, SS = 1.27), whereas Order 2 shows superior performance on Condition 1 (AS) (mean for AS = 1.41, SS = 3.08). The Cond x Stage interaction shows the improvement over Stages A to D for Condition 1 (mean for A = 2.91, B = 1.65, C = 1.05, D = 0.73), whereas Condition 2 shows no such trend (mean for A = 2.44, B = 2.01, C = 1.95, D = 2.30). These effects may be interpreted as showing that although performance was better on the second training condition (i.e. there was positive transfer between conditions), improvement in adaptation performance over all four stages of training occurred on the AS (i.e. spatial dissociation) condition only.

(2) The form of this improvement may be seen in the Stage x Trial interaction which shows increasingly less improvement over trials with the same level of terminal performance for the four stages. This implies that as training proceeds through Stages A to D the initial error is reduced and consequently less improvement need occur to achieve accurate reaching (adaptation). This type of improvement is shown by the performance on the first trial of each prism presentation where the number of correct responses can be seen to increase,

reaching 100 per cent on Stage D for the AS condition (see Table 4, page 62). Thus multiple adaptation in this condition involves not only "savings on re-adaptation" but accurate prediction of the correct response. The performance on Stage E, single trial alternations between the prisms, (see Table 12), reflects this predictive performance as all responses are on "First Trials" with the prisms.

Table 12

Performance on single trial alternations (Stage E)

Group	Condition	% Correct	
		Prism A	Prism B
1	AS	96.2	90.0
	SS	87.5	80.8
2	SS	-	-
	AS	98.8	97.5
3	AS	100.0	97.5
	SS	65.0	87.5

(3) An overall difference between the two prisms was recorded (mean for Pa = 1.31, Pb = 2.45). Although the Cond x Prism x Stage interaction fails to reach significance it can be seen from Figure14 that the difference between the prisms is greater on Stages A and B than C and D for the AS condition, Figure14 (a) and (d), whereas for the SS condition, Figure14 (b) and (c), the two prisms differ on all except Stage B. This reflects an initial asymmetry between prisms for the AS condition, and the selective deterioration in performance with Prism B (Stages C and D) for the SS condition.

(4) The significant Subject and Subj x Prism effects reflect individual differences in the abilities of the squirrel monkeys to adapt to the prisms.

APPENDIX B

Analysis of the results of Experiment 2 (Human Adaptation)
Part 2: Multiple Adaptation (pages 77 - 86)

Two analyses of variance were carried out on the error scores using the computer program BMDP2V - Analysis of variance and covariance including repeated measures (BMD, 1976): (1) the Total Errors (cm) per session (corrected for normal errors for each subject); (2) the First Trial errors (cm) per session (uncorrected). Three factors were involved, with repeated measures on two factors: Group (three levels, fixed); Condition (three levels, fixed); Session (ten levels, fixed). These were defined as follows:

Group: 1: Group 2a (random) n = 12
2: Group 2b1 (Pa Pb G) n = 8
3: Group 2b2 (Pa G Pb) n = 8

Condition: 1st prism, 2nd prism (i.e. Pa and Pb respectively for Group 2b), glass

Session: Sessions 1 to 10

Figure 15 illustrates the three-way interaction, Group x Cond x Sess, graphically. This significant interaction reflects the different effects over the training sessions on the three conditions for the three groups. The sources of these differences were revealed by further analysis involving the use of Scheffé's test for multiple comparisons between cell means, or in this case sums (Edwards, 1960), for the significant effects and interactions. The significant differences (see Table 13) are as follows:

(1) The Glass condition shows significantly smaller errors than the two prism conditions (Table 13 (a)).

(2) Improvement over the ten sessions was found for the two prism conditions (Table 13 (c)). Both linear and quadratic components of

this trend were found to be significant, indicating improvement which is more rapid on the earlier sessions (Table 13 (b)).

(3) No significant difference was found between prisms for Group 2b2 (Pa G Pb), whereas the two prisms show differences in the other two groups (Table 13 (d)).

(4) The difference between the prisms for these groups (random and regular Pa Pb G) was found to decrease over sessions (Table 13 (e)).

Individual differences in performance were analysed by comparing the frequency of scores above the median for subjects who scored above as opposed to below the median on the first session. It was found that some subjects showed consistently better performance than others throughout the experiment ($\chi^2 = 13.74$, df = 1, $p < .001$).

The magnitudes of the errors recorded for each of the five target positions reflected the magnitude of the prism-induced displacement initially, but not on the later sessions (see Table 14). Trend analysis (Edwards, 1960) on the errors for sessions 1 and 2 revealed a significant linear trend, with a positive gradient, for the base-right prism, reflecting the larger displacement on target positions towards the base of the prism (positions 4 and 5), as compared to those viewed through the apex (positions 1 and 2). Although the linear trend fails to reach significance for the base-left prism, the gradient of this trend is negative reflecting the larger displacement on positions 1 and 2 (see Table 15). The same analysis carried out on the errors for sessions 9 and 10 showed no significant linear trends for either prism. However, the quadratic trend was significant for the base-left prism, showing greater accuracy on the central target positions.

Figure 15

Group x Condition x Session interaction

Mean Total Errors and 1st Trial Errors (cm) for (a) Group 2a (Random) (N = 12), (b) Group 2b1 (Pa Pb G) (N = 8), (c) Group 2b2 (Pa G Pb) (N = 8). Each graph shows the errors for each condition per session.

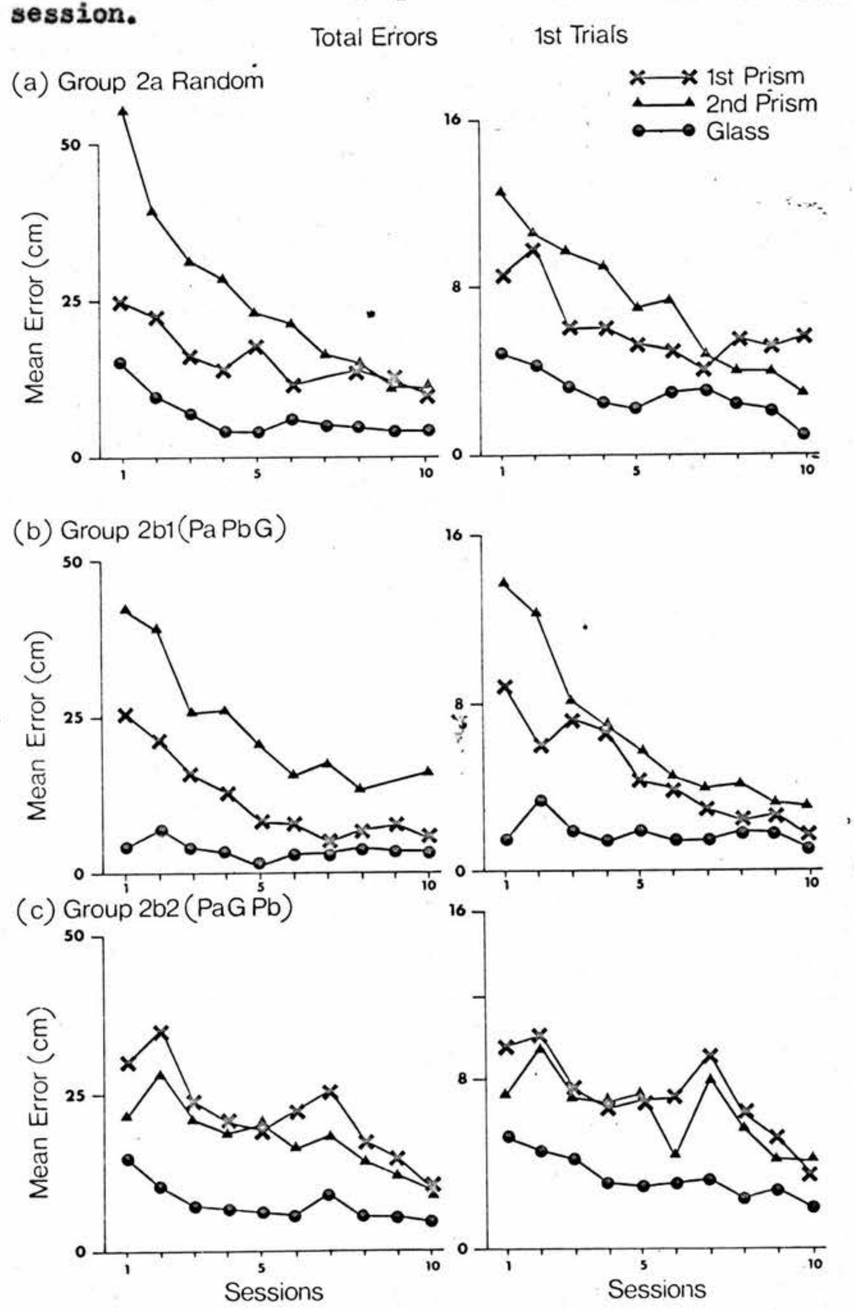


Table 13

Results of Scheffe's test for multiple comparisons.

	Source	Comparison	MSerror	F	df	p
(a)	Condition	Glass vs (P1 + P2)	307.92	106.75	2,837	<.01
(b)	Session	linear trend S1 to S10	184.25	115.64	1,25	<.01
		quadratic trend S1 to S10	159.03	13.08	1,25	<.01
(c)	Cond x Sess	S1 vs S10 (P1)	73.88	61.40	29,810	<.01
		S1 vs S10 (P2)	73.88	140.20	29,810	<.01
(d)	Group x Cond	P1 vs P2 (2a + 2b1)	307.92	35.36	8,900	<.01
		(P1 vs P2) ((2a + 2b1) vs 2b2)	307.92	19.15	8,900	<.05
(e)	Group x Cond x Sess	(S1-5 vs S6-10) (P1 vs P2) (2a + 2b1)	73.88	133.09	89,990	<.01

Table 14

Mean error (cm) per trial for each prism for each of the five target positions (a) Sessions 1 and 2; (b) Sessions 9 and 10.

		Target position				
	Prism	1	2	3	4	5
(a)	R	3.1	3.1	3.5	3.9	4.0
	L	5.0	4.0	4.0	3.7	4.1
(b)	R	1.8	1.6	1.2	1.7	1.7
	L	2.5	1.7	1.6	1.6	2.0

Table 15

Results of trend analysis on the mean error scores for each target position for each prism (a) Sessions 1 and 2; (b) Sessions 9 and 10.

		Linear			Quadratic			
	Prism	F	gradient	p	F	p	MSerror	df
(a)	R	6.444	+ve	<.05	1	ns	45.02	1,108
	L	3.168	-ve	ns	3.532	ns	54.82	1,108
(b)	R	1	-ve	ns	3.284	ns	14.00	1,108
	L	3.361	-ve	ns	10.100	<.01	15.63	1,108

APPENDIX C

Results from Experiment 3 (monkey hand differentiation study, Chapter 5)

Phase 1: Reversal of hand preference

Table 16 records the performance of each subject in Phase 1 where the spontaneous hand preferences(Stage A) were reversed by the use of differential reinforcement (Stage B). Stage C involves retention tests, without differential reinforcement, of this trained hand preference.

Table 16

% responses by Trained hand

Stage	Session	Subject					
		Brown	Orange	Beardie	Female	Small	Male
A	1	0	0	7.5	5	20	35
	2	0	0	0	37.5	7.5	85
	3	0	0	0	20	0	87.5
	4	0	0	0	10	2.5	27.5
B	1	52.5	65	45	85	72.5	82.5
	2	87.5	77.5	65	100	87.5	36.7
	3	100	92.5	95	97.5	97.5	100
	4	100	90	92.5	100	100	100
	5	95	92.5	97.5	100	100	100
C 1 wk	1	97.5	95	100	100	100	100
	2	95	95	100	100	100	100
3 wks	1	100	92.5	95	100	100	100
7 wks	1	100	90	70	100	100	100
	2	100	95	72.5	100	100	100

Phase 2: Selective hand use

Table 17 records the performance of each subject on Stage C (transfer to other contexts) following the attainment of differential hand use according to the colour of the stimulus.

Table 17

Individual scores on transfer tests to other contexts

(a) Number of trials to criterion

	WGTA	Home Cage	U-shaped box	
			Side A	Side B
Brown	64	-	44	41
Orange	40	-	64	40
Female	64	-	74	40
Small	40	-	-	-
Beardie	40	-	60	56
Mean	50	-	60*	44*

(b) Number of errors per 100 trials (50 trials per hand)

	WGTA		Home Cage		Side A		Side B	
	Hand 1	Hand 2	Hand 1	Hand 2	Hand 1	Hand 2	Hand 1	Hand 2
Brown	8	10	14	21	9	0	4	3
Orange	5	4	20	25	11	4	3	5
Female	3	10	21	20	4	10	1	5
Small	3	5	0	36	46	3	32	12
Beardie	7	5	25	12	8	7	12	1
Mean	5.2	6.8	16.0	22.8	17.5 8.0*	4.2 4.7*	10.4 5.0*	5.2 3.5*

* Means excluding subject (Small) who failed to reach criterion.

A more detailed analysis of the hand preferences recorded

Spontaneous hand preferences were recorded for these subjects on the simpler task of retrieving a peanut from the foodwell of the test-tray. These tests were carried out in the four "contexts" used in Experiment 3, i.e. WGTA, Home Cage (HC), and the two sides of the U-shaped apparatus (Side A and Side B). Test-retest and inter-test correlations (see Table 18) reveal that hand preferences within each context are stable over the three-month interval between administrations of the same test, and that preferences recorded in the U-shaped apparatus do not correlate with those recorded in the more familiar WGTA and Home Cage situations. (It should be noted that these tests were the first experience the monkeys received in the U-shaped apparatus.) Thus it appears that these squirrel monkeys show consistent preferences on successive administrations of the same test in the same context, but that these preferences do not generalise to other tests, findings which parallel work with rhesus monkeys (e.g. Kounin, 1938; Brookshire and Warren, 1962). For the purpose of this study, however, intra-test consistency is the necessary feature and this was shown in the performance of these squirrel monkeys.

Table 18

Spearman Rank Correlations for spontaneous hand use in retrieving a peanut from the foodwell of the test-tray in four different contexts.

	HC	WGTA	Side A	Side B
HC	.90**	.50**	-.13	.30
WGTA		.96**	.11	.16
Side A			.77**	.75**
Side B				.59*

For test/retest correlations (diagonal) N = 12

For inter-test correlations N = 30

** $p < .01$ * $p < .05$

The task used in Experiment 3 comes under the rather ambiguous classification of tasks which could involve the use of two hands (i.e. bimanual), since subjects were free to use different hands to manipulate the stimulus object and to retrieve the food reward. No direct influence was brought to bear on the retrieval hand in this experiment: the monkeys were free to touch the stimulus object and the food reward with either hand once the initial manipulation had been performed by the appropriate hand. Analysis of the use of the hands used for manipulation and retrieval (see Table 19) reveals a significant positive correlation, in the form of scores which differ significantly from fifty percent (Binomial test, Siegel, 1956). It is clear from the individual scores, however, that only some subjects changed their preference for the retrieval hand to accord with the reversed preference for manipulation. It should also be noted that two subjects (Orange and Male) did not spontaneously use the same hand for these two activities (Stage A). Thus it appears that hand preferences may be expressed on either or both of the activities and that these preferences may or may not be the same. Following Bresson's analysis (Bresson et al, 1977) it seems that the coordinated or complementary activity of the two hands in bimanual tasks may also be an expression of handedness, implying that the procedure of scoring preference as the use of the same hand on both parts of the task (e.g. Brookshire and Warren, 1962; Ettlinger and Moffett, 1964) may be misconceived.

Table 19

% Manipulations and Retrievals made by the same hand

Stage	No. of Trials	Subject						Mean
		Brown	Orange	Beardie	Female	Small	Male	
A	160	100**	60	86.2**	63.1*	93.1**	45	74.6**
B	200	58.5	73.5**	73**	93**	59	17.7**	62.4**
C 1 wk	80	55	93.5**	91.2**	100**	12.5**	7.5**	60**
3 wks	40	85**	90**	95**	100**	32.5*	10**	68.8**
7 wks	80	55	93.8**	71.2**	100**	23.8**	3.8**	57.9**

** $p < .001$ Binomial test (2 tailed)

* $p < .01$

APPENDIX D

Manuscript submitted to Perception in 1974, and later incorporated into the more extensive paper published in Perception (Flook and McGonigle, 1977, see Appendix E).

SIMULTANEOUS MULTIPLE ADAPTATION TO SENSORY DISTORTION IN SQUIRREL MONKEY: A PRELIMINARY REPORT

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ABSTRACT

Two squirrel monkeys were first trained on a series of successive adaptations to left and right displacing prisms (30 diopters). Subsequently it was found that they were capable of responding under both distortion conditions without the need for readaptation.

Acknowledgements

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1. INTRODUCTION

Recently, in response to a claim by Ettlinger and Blakemore (1967) that monkeys do not cross modally match, we decided to develop some new ways to test monkeys in this sphere. In particular, we aimed to provide for a test which did not depend on (special) learning, but which allowed, nevertheless, for adequate and repeated quantification of cross-modal transfer (the 'virtual object' test of Bower *et al*, 1970, fails on possibly both these criteria) and which did *not* involve a spatial separation between the 'sample' stimulus and the stimulus to be matched. (This is, we feel, a vital feature as monkeys may succumb to the operation of a rule of perceptual 'necessity' which would demand two separate identities for any (2) objects, however otherwise similar, which co-exist in time and occupy different positions in space).

One method, which we devised, seemed to cater for most of the above criteria. Basically it required a monkey to reach for an object e.g. a peanut which was embedded in an assortment of other (inedible) objects. Normally, of course, this would be no problem for the animal - preliminary tests showed that our squirrel monkeys (addicted to peanuts) quickly and accurately retrieve a peanut as a first priority. But under the conditions envisaged by us - those involving sensory distortion - the task was more difficult. Specifically, the question was this: if a monkey, in reaching for a peanut, grasped something else instead (due to the influence of the distorting prisms) would the object grasped in error be recognized haptically such that (a) it would not be retrieved and (b) a correcting response to the position of the nut would be effected?

Clearly, these tests could only be carried out if the monkey did not see its hand at the terminus of its reach. The success of the tests would also depend on how well it had attended to the other objects in the field so that it remembered their location relative to the position of the nut. Furthermore, the monkey would need to have some training on adaptation to lateral distortion (both to left and right displacement) such that it would - at least under more conventional conditions of adaptation testing - correct very quickly once a pointing mistake was recorded.

With a sophisticated monkey of this sort, we argued, it should be possible to shift prisms randomly from left to right displacements and then see if S̲ could use haptic information to locate the position of its pointing limb and thus correct its error.

There was, however, one further problem with this plan - we didn't know if squirrel monkeys could adapt to prismatic distortion effects.

Our experimental strategy was thus as follows:

2. EXPERIMENT 1

2.1. <u>Subjects</u>. Two male squirrel monkeys (<u>Saimiri scuireus</u>) approximately five years old. They were experimentally sophisticated in test situations involving the WGTA where they had undergone extensive investigations using size, brightness, and pattern stimuli. They were naive, however, with respect to the apparatus described below, and had never previously taken part in any sensory distortion experiment. They were maintained on MRC diet 2 on which they were fed <u>ad lib</u>.

2.2. <u>Apparatus</u>. Subjects were placed in a metal chamber ($21\frac{1}{2}$" L x $15\frac{1}{2}$" B x $21\frac{1}{2}$" H) which had a small circular window at one end of it (1¼" diameter). Through this window the monkey could see a ledge protruding from below it (3" deep and 7½" long) with four foodwells countersunk into its surface (1" apart). The ledge was matte black with white strips 1/5" apart showing on its upper surface. Immediately below the ledge we cut an aperture 7½" long and 1¼" deep through which the monkey could reach to the upper side of the ledge. Outside the window was fitted a wedge prism holder which could slide in front of it either of two 30 diopter prisms (base left and base right) or a clear glass pane.

On the monkeys' side of the window we installed a fairly rudimentary form of head holder which also housed a photo-relay. Thus when S̲ peered through the window it broke a photo beam which turned on two lamps outside the apparatus. These illuminated the ledge and provided the sole lighting available.

A click generator gave the cue for the commencement of a reaching trial.

Above the apparatus, we installed a TV camera which recorded the reaches of the subject at their termini.

2.3. Procedure. (a) Pretraining. The monkeys were pretrained to look through the window, locate the position of the nut, and reach for it through the slit aperture located below the window. The ledge occluded the S̲'s view of its pointing limb until it appeared at the terminus of its reach. As our squirrel monkeys were found loath to reach to places where they would not see their arm, they required plenty of encouragement to reach through the slit and around the edge of the ledge. They also had a (competing) tendency to attempt to reach at the nut through the clear glass window present throughout pretraining.

(b) Testing. Ss were required to reach for a peanut which was located at any one of four positions on the ledge as per a predetermined random sequence. They were permitted to correct their mistakes in the course of any given 'trial'. The inter-trial interval (ITI) was 10 secs. during which time the monkey was kept in darkness and the photocells controlling the lamps were rendered inoperative. At the end of a 10 sec. period, a click generator provided the monkey with a cue (lasting 5 secs.) indicating that the lighting circuit was again operative. A new trial began when the monkey put his head in the holder.

During the ITI, the experimenter occluded the window of the test chamber and replaced the nut.

2.4. Experimental Design. One monkey began adaptation trials with a base-left, the other with a base-right 30 diopter prism. Each was trained to a performance criterion of 10 successively correct ballistic reaches. After each successful adaptation the prisms were 'reversed', i.e. shifted from base left to base right. The object of training was to make the monkeys proficient in switching from one lateral adaptation to the other with a minimum of error as in a 'serial reversal' learning task. In the absence of appropriate guidelines, however, as to which procedure would be most effective, each monkey was tested under slightly different conditions of prismatic 'reversal'. One Subject (M1) was given multiple reversal training in the context of a single experimental session, whilst the other (M2) was given adaptation training to only one prism per session.

2.5. Results. Errors were measured using a Video tape recorder and a TV monitor with a screen size of 26". An error was calculated in 1/5" as the distance between the middle finger of the pointing hand (when it first appeared at the edge of the ledge) and the mid point of the foodwell. Both monkeys were observed to keep their fingers close together and move them in unison (as in a palmar grasp) when reaching for the nut.

The monkeys were found to adapt to the distortion conditions, although M1 stopped responding during the first session of adaptation and was only induced to proceed with reaching on the following session. M2, however, was successful in adaptation in the course of a single session and Graph I records his performance there.

Insert Graph I about here

It is noteworthy that in both cases, adaptation to SD seemed to be almost an all or none affair - either the monkey made a pointing error of almost constant magnitude, or it hit the target. However, two further effects should also be noted (a) correcting movements under visual control often resulted in the pointing limb being moved away from the target; and (b) the number of correcting movements declined with the increasing sophistication of the subject.

It was found further that 'serial-reversal' prismatic reversal learning occurred for M2 who experienced only one reversal per day (see Graph II). M1, on the other hand, did not show improvement with multiple reversal shifts within sessions (an average of 4 shifts was given per session for 5 successive sessions). In fact, disimprovement was recorded and it did not seem too promising at this stage to continue training using these conditions. Furthermore, this disimprovement was also recorded by M2 when it too was tested during multiple-reversal sessions as Graph III indicates.

Insert Graph II and IIIabout here

Parenthetically, we record the dramatic improvements which occurred in M1's performance after rest periods of 10 mins; following these 'time outs', highly accurate reaching under the same SD conditions was observed to occur without further training (see Graph IV).

Insert Graph IV about here

2.6. Discussion. Our first attempts in the study of adaptation to lateral distortion in squirrel monkey clearly indicate, we submit, that the two subjects of our investigation adapt to the sensory distortion conditions as described earlier.

Furthermore, it would seem - although more intensive training could well change the picture - that multiple intra-sessional prismatic L-R shifts cause confusion and disimprovement in adaptation performance. On the other hand, as the performance of M2 shows, there is a dramatic savings effect recorded when such shifts occur across, as opposed to within, sessions.

The dramatic savings effects (virtually one-error adaptations at the end of training) provoked a further question: Could the squirrel monkey maintain two or more states of adaptation in its response repertoire at the same time?

To help answer this question we ran a second experiment.

3. EXPERIMENT II

3.1. Subjects. As in Experiment I.

3.2. Apparatus. This was modified to include a new 'distortion' window at the opposite side of the apparatus. A second TV camera was mounted on this side and synchronized with the first. Lighting was provided by a 60 watt red bulb which burned continuously as did (on Experiment II only) the (white light) lamps on the original side of the apparatus.

3.3. Experimental Design and Procedure. The two monkeys were given retraining to a prism on the original side of the apparatus. Following this, alternation training was given between the original side of the apparatus and the new side of the box. At this stage the new window was fitted with clear glass only. When the monkeys were adjusted to these new requirements, a prism was fitted to the new side of the apparatus which displaced in the opposite direction to the prism in the original window. Training on both prisms began on a 20-trial block-per-prism basis with three such blocks per session, for eight sessions in all. At this point the trial blocks gave way to single trial alternation for 2 sessions of 60 trials per session.

Finally, the prisms were switched from one side to the other for one block of 60 alternation trials. The procedure was similar to that for Experiment I.

3.4. Results. As Graph V and Table I show, both monkeys succeeded in simultaneous adaptation to prisms which displaced in opposite directions. This conclusion is supported by the accuracy of Trial 1 (per trial block) responding together with the profile of intra-sessional responding provided by Graph V.

Insert Graph V and Table I about here

The additional finding, that transposition of prisms proved disruptive, is also contained in Table I.

4. DISCUSSION

It is only too clear that we have strayed somewhat from our original purpose in seeking a new method to study cross-modal matching! In our view, however, several interesting questions concerning the nature of adaptation to sensory distortion per se have arisen to justify an experimental diversion.

Clearly, we have only a prototypic investigation to report at this stage. Nevertheless we feel secure in the claim that our subjects (who are in no way atypical of our colony as measured by other learning tests) (i) adapt quickly to distortion of considerable magnitude; (ii) show considerable savings during readaptation trials, and (iii) appear capable of sustaining a state of multiple adaptation at least so long as the conditions involved in one adaptation are discriminable from one another.

At this stage of investigation it is not possible to say with any confidence whether extrinsic (e.g. contextual) or intrinsic factors are mainly responsible for the dissociation of adaptation states observed. It is possible for example that the monkeys used different eyes for each adaptation - although this seems unlikely in view of the multiple-reversal session findings. We have checked and eliminated the possibility that different hands were used.

On the other hand, Graybiel and Held (1970), and Hein and Diamond (1971) have argued for a possible dissociation between adaptation obtained under scotopic and photopic levels of illumination.

This factor may well be implicated in our own study as a bright white light was the illuminant on one side of the apparatus and a

'Red' light on the other; a special set of tests will have to be run to check this possibility. However, there are already grounds for believing that this explanation is not appropriate here.

Firstly, the monkeys were in a darkened chamber at all times and could have easily maintained dark adaptation when viewing the bait on the well lit side of the apparatus. Secondly, the short interval between reaching trials in the final stages of the experiment (15 secs) would hardly be sufficient to permit a change of (dark) adaptation; and thirdly, M2 showed a high level of proficiency on the <u>same</u> side of the apparatus where the lighting was identical for both distortion conditions.

In our view, the results obtained here suggest that context, which has previously been implicated in dissociation effects in both ethological (cf. Tinbergen, 1951) and laboratory situations (Logan, 1961, and McGonigle and Jones, 1974) may be implicated.

The concept of "context" will not of course explain <u>how</u> adaptation takes place - it suggests instead how it might be possible for <u>S</u> to maintain what would otherwise appear to be contradictory reaching strategies without reciprocal interference effects being in evidence. On this view, therefore, it should be possible to train an animal to perform competently in many further situations where other adaptations are required, e.g. adaptation to displacement along the vertical axis without affecting the integrity of previously established ones to lateral distortion only.

Insofar, however, as all adaptive responses involved 'active' movement of the pointing limb by <u>S</u>, we have no reason to seek a modification of Held's (1965) account of the mechanism of adaptation.

Nevertheless, we would submit that our results - if confirmed by subsequent experiment as evidence for multiple adaptation without readaptation - might suggest some further elaboration of Held's theory in terms of how space is constructed or represented by the subject as a function of the context in which it operates. For the 'represented' position of a target is not necessarily synonymous with its currently viewed location. Squirrel monkeys are adept at catching insects on the wing whose location they can only extrapolate from information provided through tracking their flight path. Furthermore, monkeys, like humans, can point or reach towards the location which a target <u>once</u> occupied even though it is currently displaced from that position (the 'position habit', well known in animal discrimination learning could be taken as an instance of the role of 'represented' position; and a recent study of object permanence by squirrel monkeys completed in our laboratory suggests a strong tendency by these subjects to determine their choices more by the 'represented location' of the bait than by the currently viewed one (McGonigle and Loudon, 1974)).

Observations such as these suggest to us that the process of adaptation requires a new mapping of the 'represented' or known location of the object on the position of the object given by the 'current view'. The role of context would then be to indicate to the subject which schema of (spatial) representation is appropriate to the pointing strategy required as in, e.g. reaching into a water from an air medium. Informal lab tests done with a large water jar show that squirrel monkeys quickly make a distinction between the pointing requirements involved in reaching into a water jar for a peanut and snatching one from the hand of the experimenter.

Finally, although we hate to have to say so, more experiments are necessary to investigate in much greater depth several of the clearly complex phenomena which we report in this very preliminary fashion.

References

Bower, T.G.R., Broughton, J.M., and Moore, M.K., 1970. The coordination of vision and touch in infancy. Perception and Psychophysics, 8.

Ettlinger, G. and Blakemore, C.B., 1967. Cross modal matching in the monkey. Neuropsychologia, 5, 147-54.

Graybiel, Ann M. and Held, R., 1970. Prismatic adaptation under scotopic and photopic conditions. Journal of Experimental Psychology, 85, No. 1, 16-22.

Hein, Alan, and Diamond, R.M., 1971. Independence of the cat's scotopic and photopic systems in acquiring control of visually guided behavior. Journal of Comparative and Physiological Psychology, 76, No. 1, 31-38.

Held, R., 1965. Plasticity in sensory-motor systems. Scientific American, 213, 84-94.

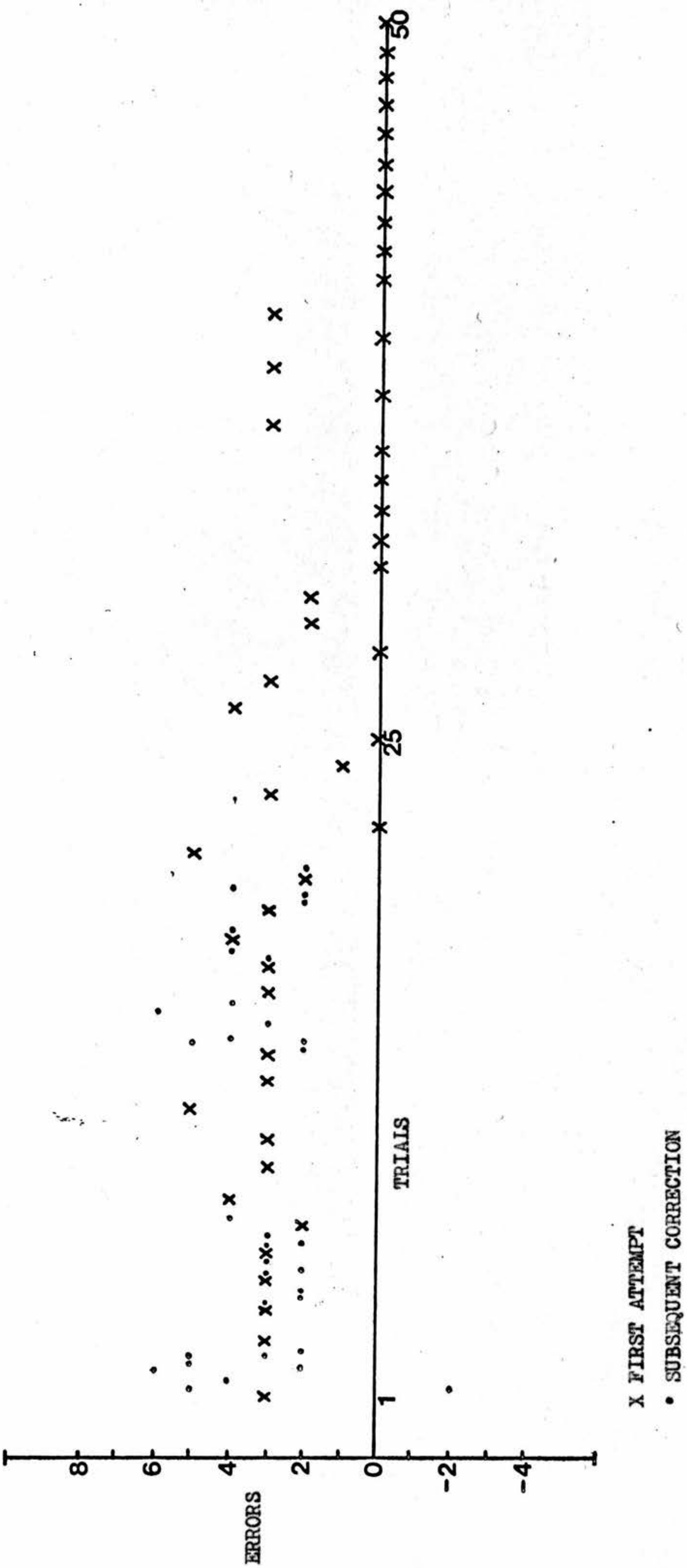
Logan, F.A., 1961. Specificity of discrimination learning to the original context. Science, 133, 1355-1356.

McGonigle, B.O. and Jones, B.T., 1974. Rules of relation in size discrimination by squirrel monkeys I. (Ms. in preparation).

McGonigle, B.O. and Loudon, B., 1974. Object permanence in squirrel monkeys and the delayed response problem. (Ms. in preparation)

Tinbergen, N., 1951. The study of instinct. Oxford University Press.

Graph I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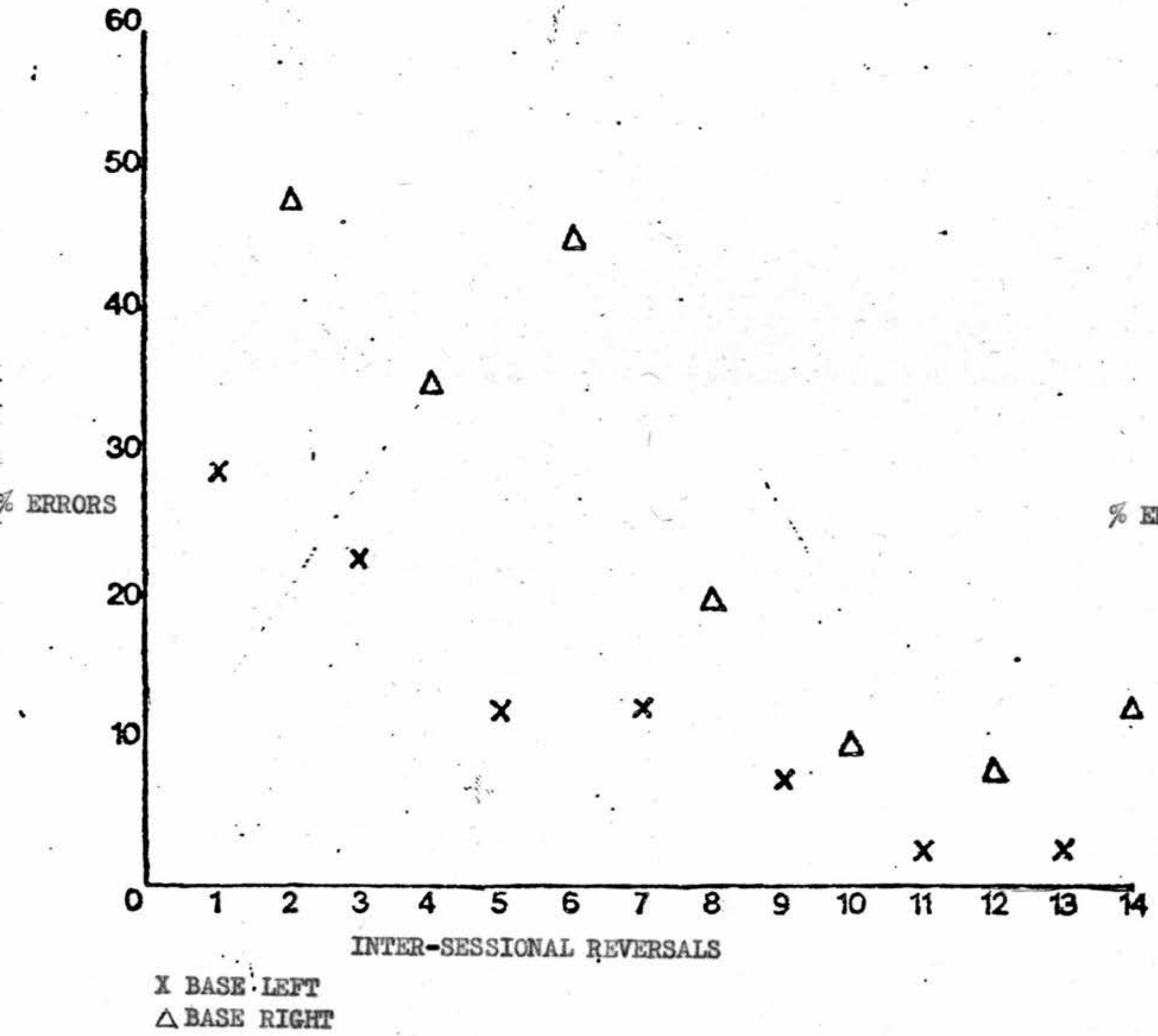
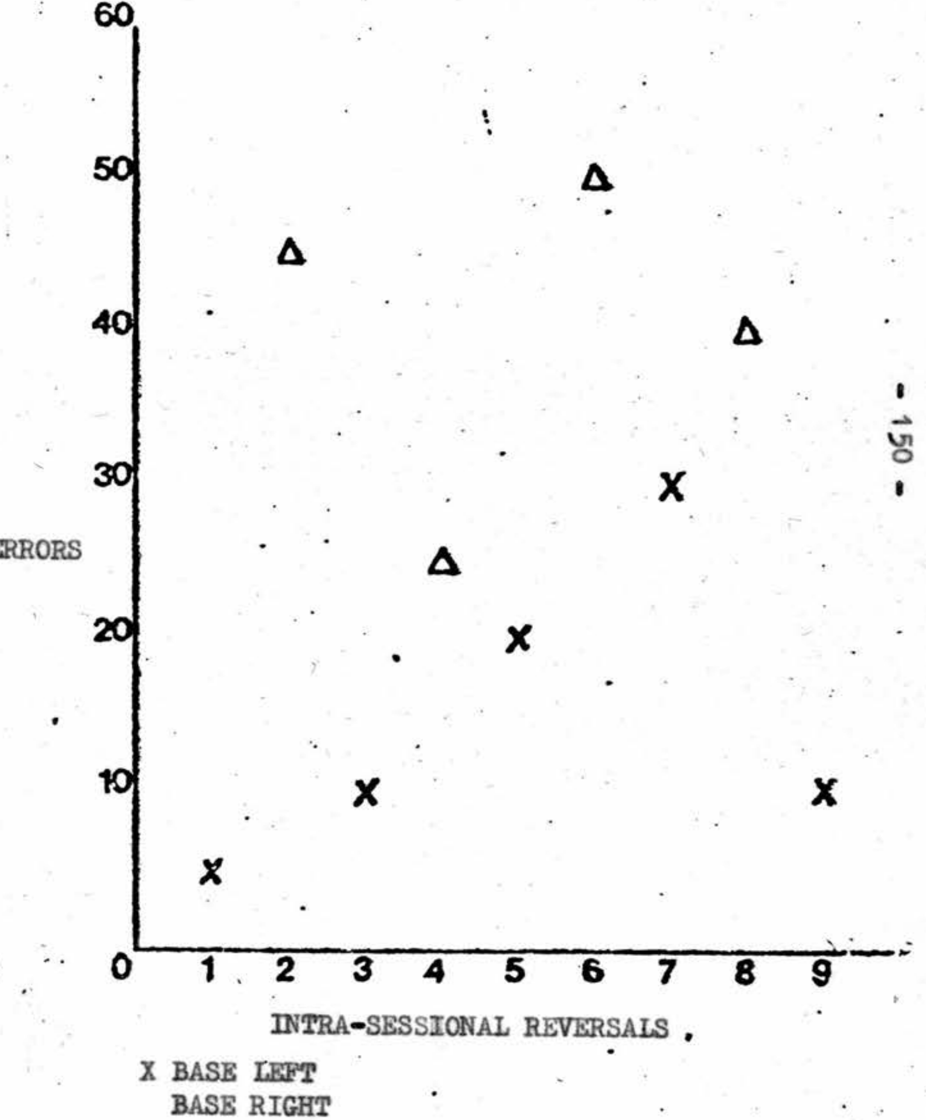
6
4
2
0
-2
-4
TRIALS
1
25
50
X FIRST ATTEMPT
• SUBSEQUENT CORRECTION

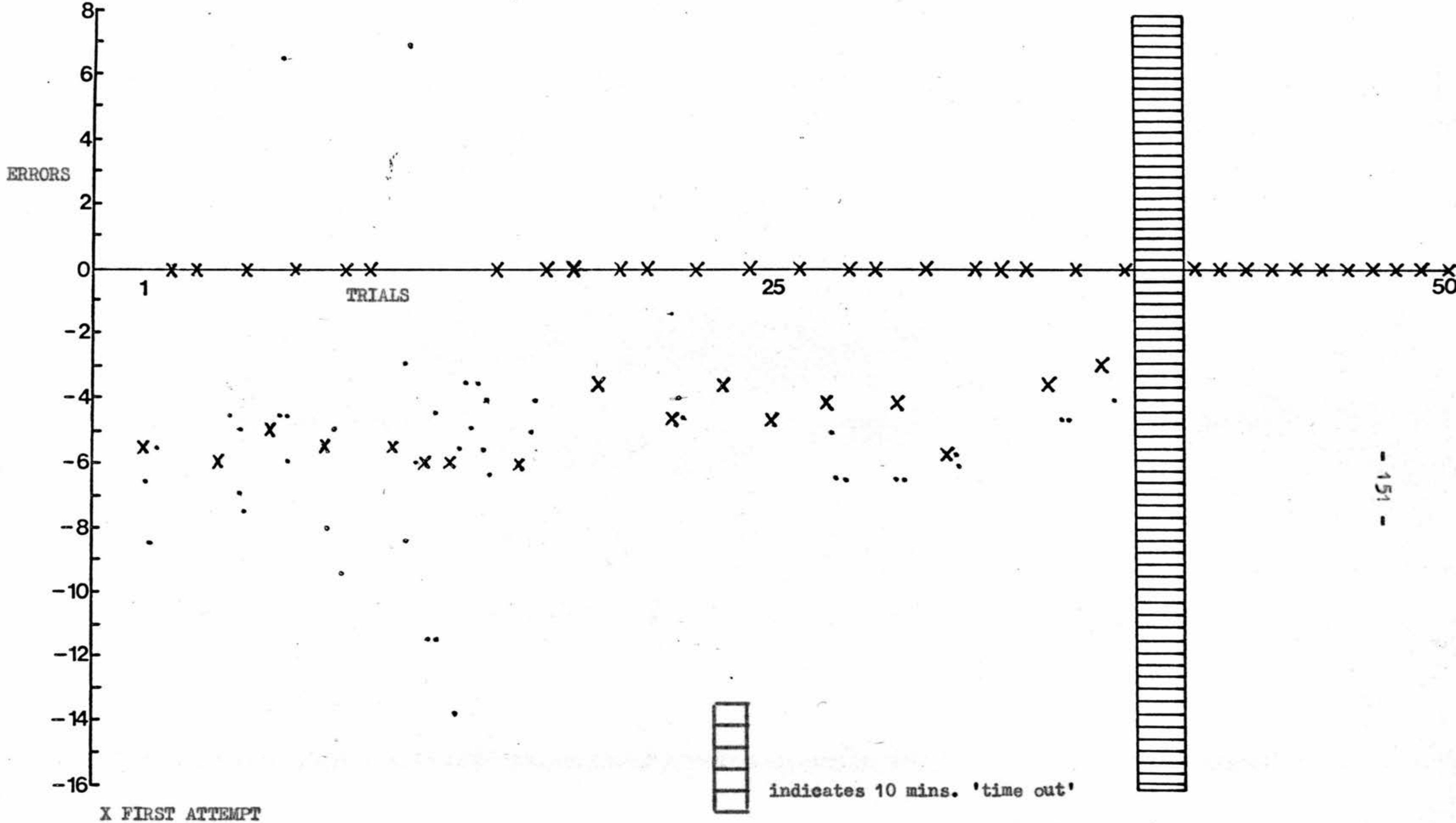
Graph II



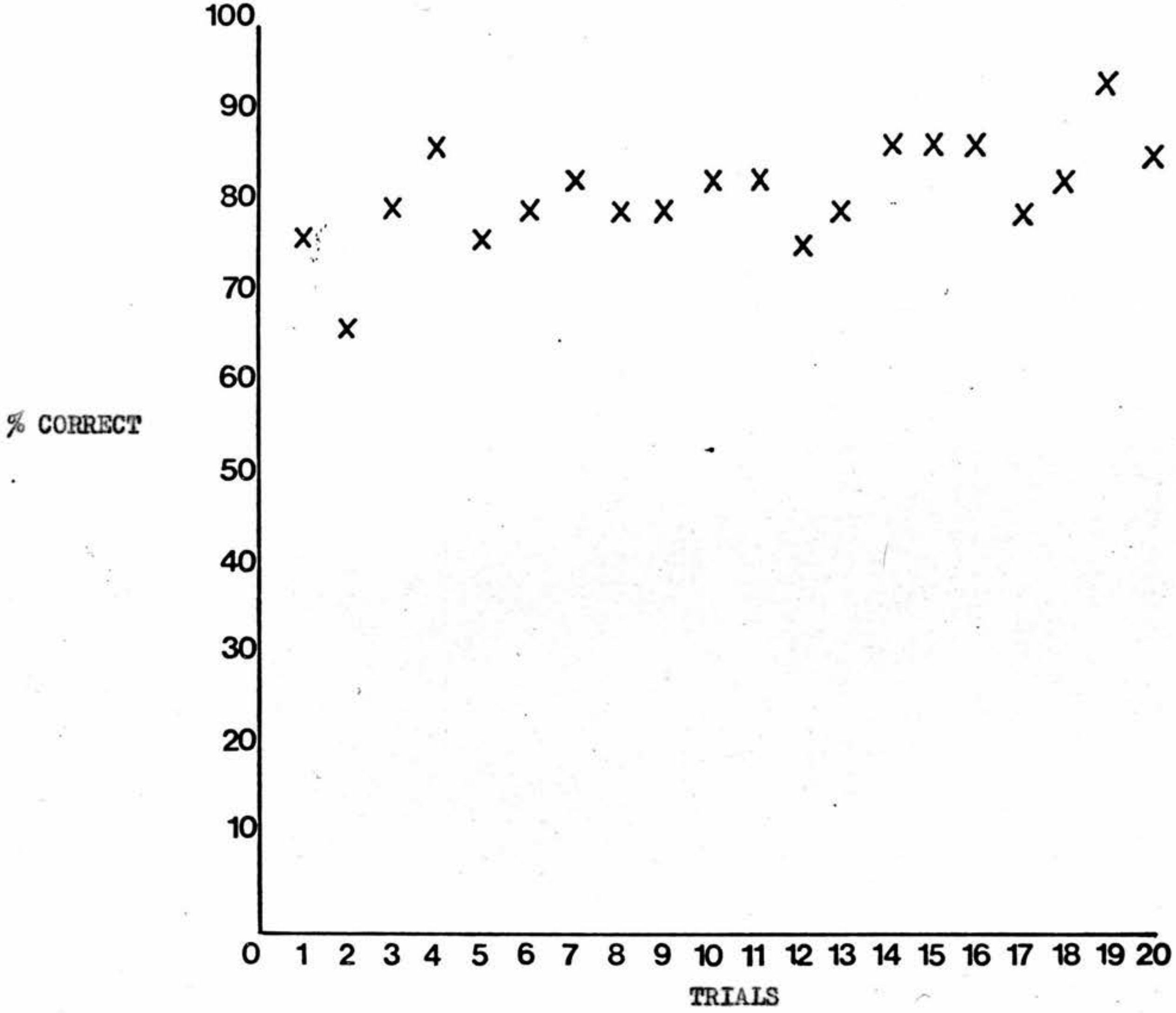
Graph III



Graph IV



X FIRST ATTEMPT
• SUBSEQUENT CORRECTION



LEGEND INTRA-SESSION AVERAGE PERFORMANCE FOR M1 + M2.

Table I

Reaching Trials: Percent Correct

Subject	M1		M2	
Side	A	B	A	B
First Trials of 20 Trial Block	75	62	100	100
Alternations	91	76	98	91
Alternations with prisms transposed	17	0	63	53

Perception, 1977, volume 6, pages 15-29

APPENDIX E

Serial adaptation to conflicting prismatic rearrangement effects in monkey and man

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Abstract. Seven adult male squirrel monkeys adapted successfully to prisms displacing in equal and opposite directions. After protracted training under certain conditions, they succeeded in conserving adaptation to both prisms without benefit of readaptation trials. Results obtained with thirty-six undergraduates under similar conditions of test (although for a much shorter period) are also reported.

1 Introduction

The subject of this report was suggested to us by a serendipitous finding encountered in the course of an attempt to develop new cross-modal techniques for research on the squirrel monkey(1). We discovered that two subjects who were first allowed to adapt to the distorting effects of a laterally displacing prism were subsequently able to conserve that adaptation following intervals of forty-eight hours or more spent in the context of their home cages; furthermore, when required subsequently to adapt to the distortion produced by a prism displacing in an equal but opposite direction to the original one, we found that, if they were given adequate opportunity to switch (serially) from one prismatic condition to the other, and if the 'fields' viewed by the prisms were spatially dissociated, both monkeys finally achieved conservation of *both* states of adaptation without mutual interference and without the need for readaptation trials.

In the paper which follows, we shall review the salient points of procedure and the main results obtained in that first investigation. However, the major part of this report will be devoted to a much more extensive record of the performance of five additional squirrel monkeys, tested subsequently to check these effects more rigorously. A short study with human subjects is included for comparison.

2 Experiment 1 (first investigation)

2.1 *Subjects*

Two male squirrel monkeys (*Saimiri scuireus*) approximately five years old served as subjects. They were experimentally sophisticated in test situations involving the Wisconsin general testing apparatus where they had undergone extensive investigations in which size, brightness, and pattern stimuli were used (see McGonigle and Jones 1975). They were naive, however, with respect to the apparatus described below, and had never previously taken part in any sensory distortion experiment. They were maintained on MRC diet 2 on which they were fed *ad libitum.*

2.2 *Apparatus*

Subjects were placed in a metal chamber (55 cm long × 40 cm wide × 55 cm high) which had a small circular window at one end (3·2 cm in diameter). Through this

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¶ Author to whom requests for reprints should be sent.

(1) Our object was to produce a prism-sophisticated monkey, trained to correct any pointing mistake (in either direction) after only one error; then to test him and see if he could use haptic information to correct mistakes incurred under conditions of visually elicited reaching.

window the monkey could see a ledge (7·5 cm deep x 19 cm long) protruding from below it with four foodwells countersunk into its surface (2·5 cm apart). The ledge was matte black with white strips (0·5 cm apart) showing on its upper surface. Immediately below the ledge was an aperture (19 cm long x 3·2 cm deep) through which the monkey could reach to the upper side of the ledge. Outside the window was fitted a wedge prism holder which could slide into position either of two 30-diopter prisms (base-left and base-right) or a clear glass pane.

On the monkey's side of the window was installed a fairly rudimentary form of head holder, which also housed a photorelay. Thus when a subject peered through the window it broke a photobeam, which turned on two lamps outside the apparatus. These illuminated the ledge and provided the sole lighting available. A click generator gave the cue for the commencement of a reaching trial. Above the apparatus, was installed a television camera which recorded the reaches of the subject at their termini.

2.3 *Procedure* (2)

(a) Pretraining. The monkeys were pretrained to look through the window, locate the position of the nut, and reach for it through the slit aperture located below the window. The ledge occluded the subject's view of its pointing limb until it appeared at the terminus of its reach.
(b) Testing. Subjects were required to reach for a peanut which was located at any one of four positions on the ledge as per a 'predetermined' random sequence. They were permitted to correct their mistakes in the course of any given 'trial'. The intertrial interval (ITI) was ten seconds, during which time the monkey was kept in darkness and the photocells controlling the lamps rendered inoperative. At the end of a ten-second period, a click generator provided the monkey with a cue (lasting five seconds) indicating that the lighting circuit was again operative. A new trial began when the monkey put his head in the holder. During the ITI, the experimenter occluded the window of the test chamber and replaced the nut.'

2.4 *Experimental design*

The object of training was to make the monkeys proficient in switching from one lateral adaptation (P1) to the other (P2) with a minimum of error as in a 'serial-reversal' learning task. One monkey began adaptation trials with a base-left, the other with a base-right 30-diopter prism. Each was trained to a performance criterion of ten successively correct ballistic reaches. After each successful adaptation the prisms were 'reversed', i.e. shifted from base-left to base-right. In the absence of appropriate guidelines as to which procedure would be most effective, however, each monkey was tested under slightly different conditions of prismatic 'reversal'. One subject (M1) was given multiple-reversal training in the context of a single experimental session, whilst the other (M2) was given adaptation training to only one prism per session.

2.5 *Results*

Errors were measured using a videotape recorder and a television monitor with a screen size of 66 cm. An error was calculated in units of 0·5 cm as the distance between the middle finger of the pointing hand (when it first appeared at the edge of the ledge) and the midpoint of the foodwell. Both monkeys were observed to keep their fingers close together and move them in unison (as in a palmar grasp) when reaching for the nut.

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(2) It should be noted that this procedure conforms to most of the requirements set out by Howard (1968).

The monkeys were found to adapt to the distortion conditions, although M1 stopped responding during the first session of adaptation and was only induced to proceed with reaching on the following session. M2 was successful in adapting during the course of a single session.

It was also found that 'serial-reversal' prismatic-reversal learning occurred for M2, who experienced only one reversal per day (see figure 1a). M1, on the other hand, did not show improvement with multiple reversal shifts within sessions (an average of four shifts was given per session for five successive sessions). In fact, disimprovement was recorded and it did not seem too promising at this stage to continue training under these conditions. Furthermore, this disimprovement was also recorded by M2 when it too was tested during multiple-reversal sessions, as figure 1b indicates.

Two further effects should also be noted: (i) correcting movements under *visual* control sometimes resulted in the pointing limb being moved away from the target; and (ii) the number of such correcting movements declined with the growing sophistication of the subjects(3).

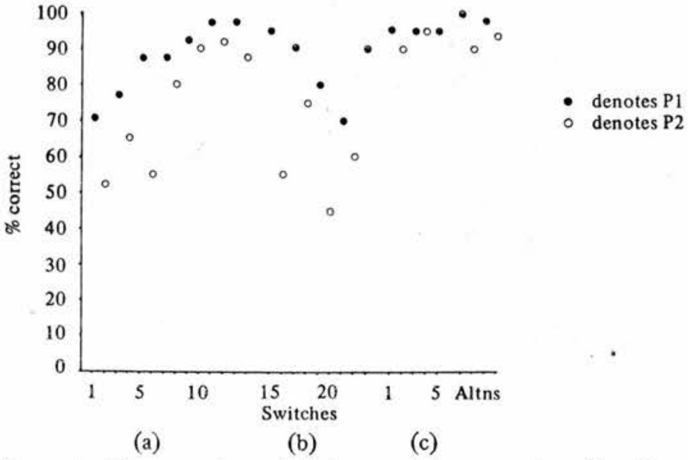

Figure 1. The percentage of trials correct for successive prismatic switches for subject M2: (a) one switch per session (switches 1-14); (b) three switches per session (switches 15-24); (c) three switches per session followed by one trial per prism, labelled 'Altns'. This last condition is described in experiment 2.

2.6 *Discussion*

Our first attempts in the study of adaptation to lateral distortion in squirrel monkeys clearly indicate, we submit, that the two subjects of our investigation adapted to the sensory distortion conditions as described earlier.

Furthermore, it would seem that multiple intrasessional prismatic left-right shifts cause confusion and disimprovement in adaptation performance. On the other hand, as the performance of M2 shows, there is a dramatic savings effect recorded when such shifts occur across, as opposed to within, sessions. These savings effects resemble those reported by Taylor (1962), who found that lines which at first appeared curved when he wore contact wedge prisms looked straight after an hour; in a later session, however, he observed 'straightening' after only twenty seconds of exposure.

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(3) It should be stated here that conventional 'aftereffects' were also recorded in the course of these pilot investigations when a clear glass window replaced a prismatic one. The procedure was not continued as we did not wish to confuse the monkey with too many reaching conditions in the same experiment. Furthermore, with two prism conditions, we felt we already had a measure of 'aftereffect' in any (mutual) interference we might record during (re)adaptation training.

The dramatic savings effects (virtually one-error adaptations at the end of training) provoked a further question: could the squirrel monkey maintain simultaneously two or more states of 'adaptation' in its response repertoire? To help answer this question we ran a second experiment.

3 Experiment 2 (first investigation)

3.1 *Subjects and apparatus*

Subjects were as in experiment 1. The apparatus was modified to include a new 'distortion' window at the opposite side of the apparatus. A second television camera was mounted on this side and synchronized with the first. Lighting was provided by a 60-W red bulb which burned continuously, as did (in experiment 2 only) the (white light) lamps on the original side of the apparatus.

3.2 *Experimental design and procedure*

The two monkeys were given retraining to a prism on the original side of the apparatus. Following this, alternation training was given between the original side of the apparatus and the new side of the box. At this stage the new window was fitted with clear glass only. When the monkeys were adjusted to these new requirements, a prism which displaced in the *direction opposite* to the prism in the original window was fitted to the new side of the apparatus. Training on *both* prisms began on a twenty-trial-block-per-prism basis with three such blocks per session, for up to eight sessions in all. At this point the trial blocks gave way to single trial alternation for two sessions of sixty trials per session.

Finally, the prisms were transposed from one side of the apparatus to the other for one block of sixty alternation trials. The procedure was similar to that for experiment 1.

3.3 *Results*

Both monkeys succeeded in simultaneous adaptations to prisms which displaced in opposite directions. This is shown by table 1, which records the accuracy of 'first trial' responses. A correct 'hit' was defined as hand contact with any part of the nut. We have checked and eliminated the possibility that different arms were used for each prism. Figure 1c records the alternation profile of M2.

Table 1. Reaching trials: the percentage of correct responses for subjects M1 and M2.

	M1		M2	
	original side	new side	original side	new side
First trials of twenty trial blocks	75	62	100	100
Alternations	91	76	98	91
Alternations with prisms transposed	17	0	63	53

3.4 *Discussion*

Although several interesting effects were observed in the course of these preliminary investigations, we concentrated further experimental effort on two principal findings. Our experimental questions were now as follows:

(1) How different are the performances of monkeys trained to adapt serially to two different prisms as a function of the spatial location of the prisms? Is spatial disjuncture between prism sites necessary to learning but not to performance, i.e. can monkeys who learn both adaptations under conditions of spatial dissociation *perform* adequately when subsequently exposed to both prisms in the same spatial locus?

(2) How reliably does the squirrel monkey conserve visuomotor adaptation over long periods of exposure to a context demanding quite a different 'hand–eye' correlation?

4 Experiment 3 (second investigation)

4.1 *Subjects*

Five additional male squirrel monkeys with laboratory histories similar to those of the pair employed in experiments 1 and 2. They had no previous laboratory experience of prism-induced distortion effects.

4.2 *Apparatus*

This was similar in most respects to that described in experiment 1. However, the head holders were no longer instrumental in turning on the lighting for the test fields. Instead each field was illuminated constantly by equivalent pairs of shaded 5 W bulbs. Note that we now began to use a Sanyo Slow Playback machine to analyze the records, which were kept on HD tape.

4.3 *Procedure*

In general the procedure was similar to that which prevailed in the preliminary experiments. There was one important change, however, which should be noted. From the onset of training, forty trials were given to each subject per session. From information about the rate of adaptation provided by experiment 1, a *fixed trial* replaced a *performance* criterion. This method, we felt, allowed for greater comparability of adaptation rate across subjects.

4.4 *Design*

A counterbalanced and much more formal interpretation of the essential features of the first experiments formed the core of the investigation. Basically two monkeys (Group 1) were first trained to alternate between prisms 1 and 2 located at opposite ends of the box (AS); following this training, they were then given prism-alternation training on the same side of the apparatus (SS). Two subjects (Group 2) began with alternation training on the same side of the apparatus (SS) which was followed by alternation across the apparatus (AS). One monkey (Group 3) was simply overtrained (OT) on one prism at one end of the apparatus to record the degree of conservation of adaptation over successive sessions (separated by twenty-four hours). Later he was given AS and SS training. The design is summarized by table 2 below.

Table 2. Scheme of experimental design.

	Phase 1	Phase 2	Phase 3
Group 1	AS	SS	
Group 2	SS	AS	
Group 3	OT	AS	SS

4.5 *Results*

Figure 2 shows the original adaptation performance of all monkeys tested in experiment 2. Table 3 gives a profile of the frequency of occasions, subjects corrected under visual control during the course of the first two adaptations. As in experiment 1, we observed the tendency for some 'corrections' under visual control to go in the wrong direction (see column 3, table 3).

However, the main presentation of the data is provided by figures 3–8. These are best understood as forming two distinct populations. The 'main effects' are recorded in the graphs illustrating interprismatic transfer effects (figures 3–5), whilst the results of statistical tests are included in table 4(4). These data indicate that (i) a

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(4) We use the words (prism) 'reversal', 'switch', and 'shift' interchangeably.

serial improvement effect occurred in group 1 (AS) after initial disimprovement caused by interference (figure 3a); (ii) there was a marked asymmetry in the learning of the original versus the second prism shown by this group, reflecting (negative) adaptation transfer (figure 3a); (iii) 'multiple' adaptation eventually occurred in the

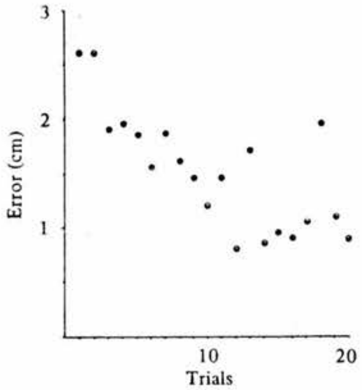

Figure 2. Mean error per trial for the first prismatic adaptation ($N = 5$).

Table 3. Direction of corrective movements under visual control (first twenty adaptation trials per prism).

		Original adaptation (P1)			Adaptation on first prism shift (P2)		
		+	0	−	+	0	−
SS	Bill	12	1	0	26	26	13
	Bump	12	4	3	15	26	9
AS	Red	16	8	5	26	31	14
	Mick	20	9	5	29	10	2
OT	Green	20	17	4	-	-	-
	Total	80	39	17	96	93	38
	%	59	29	12	42	41	17

Key: + indicates limb translation towards target
0 indicates 'corrective' movements with no directional bias
− indicates arm movement away from target whilst subject's hand is in full view

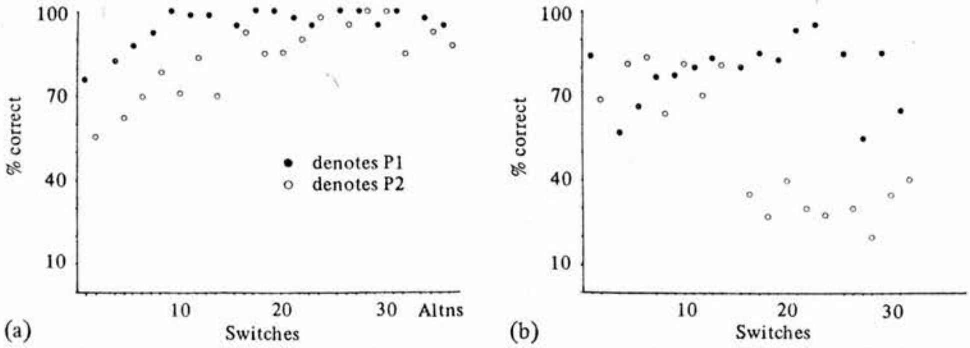

Figure 3. Percentage of trials correct for successive prismatic switches: (a) group 1 (AS); (b) group 2 (SS). Note that eighty trials per prism were given for switches 1 and 2; forty trials for switches 3-14; twenty trials for switches 15-24; and ten trials for switches 25-32. In figure 3a one trial per prism was then given, labelled 'Altns'.

AS condition. This is suggested by figure 3a but demonstrated explicitly by table 5, which records the percentage of first-trial hits following each switch of prisms.

If the monkeys were to transfer their adaptation responses from one prism to another, as they do initially (see first switch of figure 3), then no hits whatever would be recorded on the first reach following prism shift. However, the results of table 5 show that, when test-sophisticated, the monkeys' reaches are 'on target' in the majority of cases following prism shift.

Further results of experiment 3 are: (iv) Group 2 (SS) registered a (selective) disintegration of adaptation performance when the rate of prism switching reaches two or more shifts per session (figure 3b). (v) Group 2 transferred successfully to the AS condition and recapitulated the original performance of group 1 (figure 4b). (vi) Group 1 succeeded in maintaining a high level of *performance* during their subsequent SS testing phase (figure 4a). (vii) The OT monkey (group 3) showed a high degree of conservation of adaptation when required to operate with only one prism (figure 5a). Figures 5b and 5c record the performance of this monkey on subsequent AS and SS phases, as does table 5.

The second population of graphs (figures 6–8) records the *intra*sessional performance of all subjects over the entire range of training. These provide a fine-grain analysis of the adaptation transfer, which confirms the main effects already demonstrated.

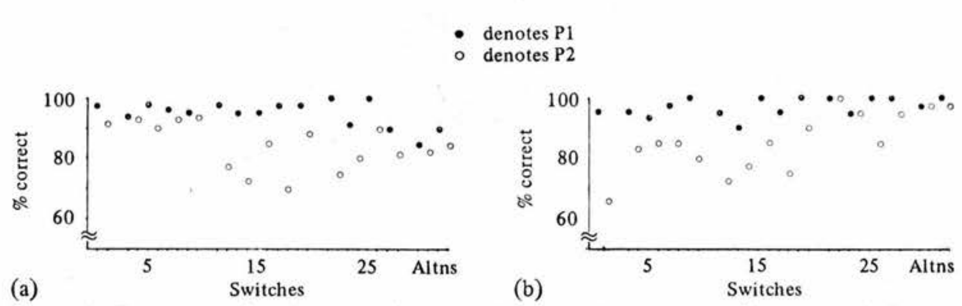

Figure 4. Percentage of trials correct for successive prismatic switches: (a) group 1 (SS); (b) group 2 (AS). Note that eighty trials per prism were given for switches 1 and 2; forty trials for switches 3-10; twenty trials for switches 11-20; ten trials for switches 21-28; and one trial per prism, labelled 'Altns'.

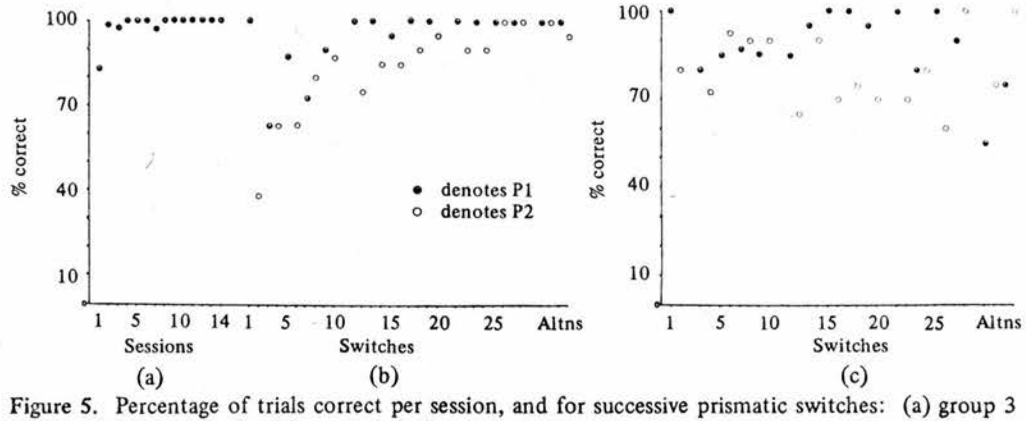

Figure 5. Percentage of trials correct per session, and for successive prismatic switches: (a) group 3 (OT); (b) group 3 (AS); (c) group 3 (SS). Note that eighty trials per prism were given for switches 1 and 2; forty trials for switches 3-10; twenty trials for switches 11-20; ten trials for switches 21-28; and one trial per prism, labelled 'Altns'.

Table 4. Results of statistical tests on data from experiment 3. (a) Intershift error analysis of variance (group 1 vs group 2); (b) intrashift error analysis of variance (group 1 vs group 2).

	p	F	d.f.		p	F	d.f.
(a)							
Phase 1 (AS vs SS)				**Phase 2 (SS vs AS)**			
Group effect	<0·01	76·38	1, 112	Prism effect	<0·01	69·35	1, 96
Prism effect	<0·01	44·82	1, 112	Group x shift	<0·01	4·83	3, 96
Group x shift	<0·01	15·04	3, 112				
(b)							
Reversals 1-2 (AS vs SS)				**Reversals 1-2 (SS vs AS)**			
Prism effect	<0·01	23·54	1, 16	Prism effect	<0·01	22·85	1, 16
Trials effect (four blocks of five trials)	<0·01	20·61	3, 16	Trials effect	<0·05	4·66	3, 16
Reversals 3-14				**Reversals 3-10**			
Group effect	<0·01	25·61	1, 176	Prism effect	<0·01	35·08	1, 112
Prism effect	<0·01	24·90	1, 176	Trials effect	<0·01	31·53	3, 112
Trials effect	<0·01	47·71	3, 176	Group x prism	<0·05	4·15	1, 112
Group x prism	<0·01	43·09	1, 176				
Reversals 15-24				**Reversals 11-20**			
Group effect	<0·01	151·15	1, 144	Prism effect	<0·01	58·97	1, 144
Prism effect	<0·01	115·00	1, 144	Trials effect	<0·01	9·23	3, 144
Trials effect	<0·01	17·07	3, 144	**Reversals 21-28**			
Group x prism	<0·01	30·20	1, 144	Group effect	<0·05	5·07	1, 48
Group x trials	<0·01	6·91	3, 144	Prism effect	<0·01	31·57	1, 48
Reversals 25-32				Trials effect	<0·05	4·55	1, 48
Group effect	<0·01	71·28	1, 48	Group x trials	<0·05	6·78	1, 48
Prism effect	<0·01	8·06	1, 48	Prism x trials	<0·05	4·55	1, 48

Table 5. Percentage of first trials correct. The number of the group is given in brackets. P1 was first used during original adaptation. P2 was first used on the original prism-prism shift.

Switches	AS (1)		SS (2)	
	P1	P2	P1	P2
1-2	0	0	0	0
3-14	58	26	0	17
15-24	80	90	50	0
25-32[a]	100	100	75	0
[b]	100	100	25	50

Switches	SS (1)		AS (2)		AS (3)		SS (3)	
	P1	P2	P1	P2	P1	P2	P1	P2
1-2	100	0	100	0	100	0	100	0
3-10	38	38	65	50	0	25	0	50
11-20	80	40	60	50	100	20	80	20
21-28[a]	100	75	100	100	100	50	100	0
[b]	75	50	100	100	100	100	0	100

[a] Where first presented during a single session.

[b] Where presented subsequently during a single session.

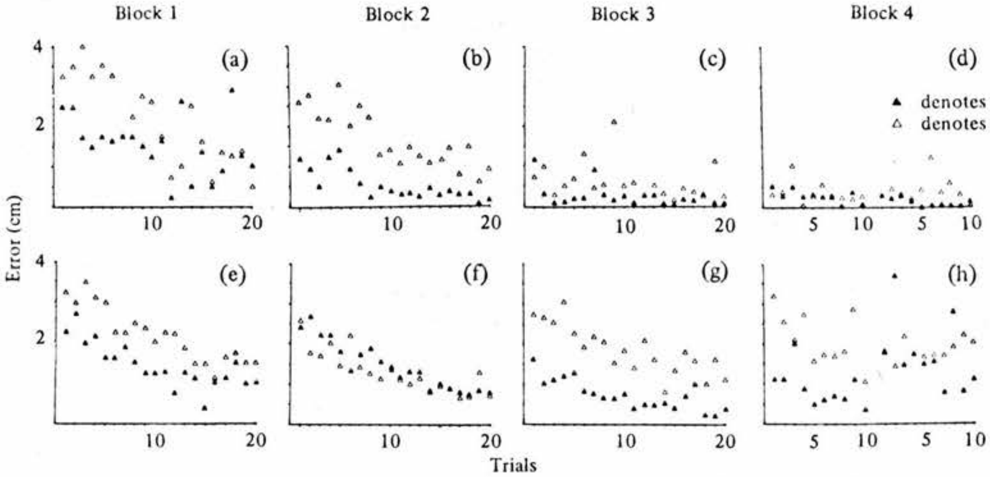

Figure 6. Mean error per trial for blocks of prismatic switches: (a)-(d) group 1 (AS); (e)-(h) group 2 (SS). Block 1 consists of switches 1 and 2; block 2 of switches 3-14; block 3 of switches 15-24; block 4 of switches 25-32.

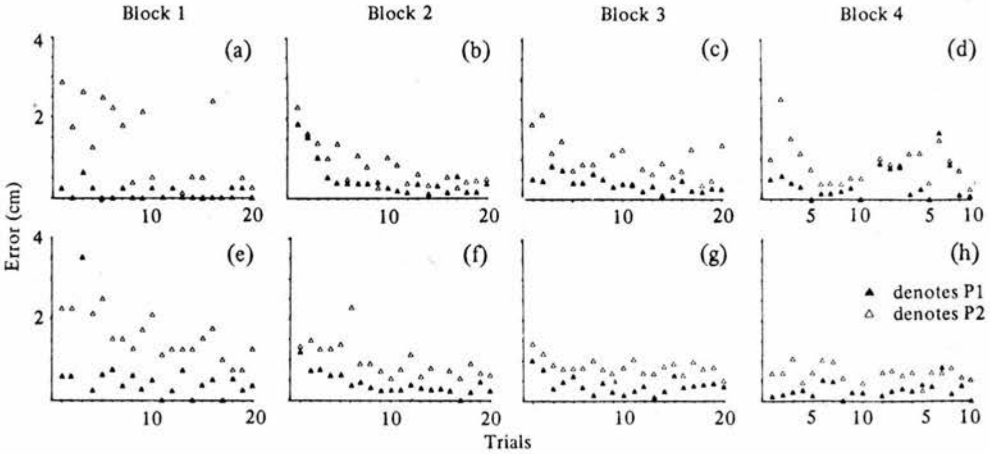

Figure 7. Mean error per trial for blocks of prismatic switches: (a)-(d) group 1 (SS); (e)-(h) group 2 (AS). Block 1 consists of switches 1 and 2; block 2 of switches 3-10; block 3 of switches 11-20; block 4 of switches 21-28.

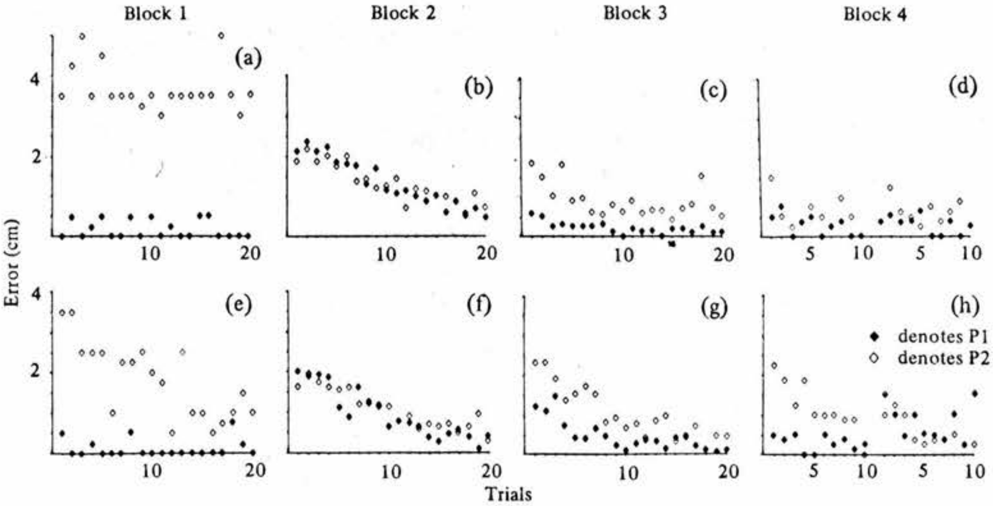

Figure 8. Mean error per trial for blocks of prismatic switches: (a)-(d) group 3 (AS); (e)-(h) group 3 (SS); blocks are as in figure 7.

4.6 *Discussion*

The data presented above appear to be clear, consistent, and 'robust'. However, before discussing their implications, in terms usually reserved for research on human subjects, we should first like to demonstrate similar trends with human subjects tested under roughly comparable conditions. Owing to severe limitations on their availability—they were taking part in second year practical classes—and because we had no means of anticipating the length of training that might be required, the study falls tantalizingly short of a full confirmation of our monkey data. However, we believe the results sufficiently suggestive to cast doubt on any hypothesis which might implicate species differences in accounting for the findings we report.

5 Experiment 4

5.1 *Subjects*

Thirty-six undergraduates taken as volunteers from the second-year practical classes run by the Department of Psychology, University of Edinburgh, served as subjects.

5.2 *Apparatus*

Two Imhof stands were used to support aluminium panels, each of which housed a small circular window (3·3 cm in diameter). When subjects looked through the window, they could see the edge of a second panel, 40 cm away, which extended obliquely from the bottom of the upright panel and which occluded the subject's pointing limb from view until the terminus of his reach. The target board was 50-cm wide and calibrated in units of 2·54 cm. A slide holder at the back of the window (on the upright panel) held two 30-diopter wedge prisms and a clear glass block. The stands were parallel to each other and subjects sat between them on a swivel chair.

5.3 *Procedure*

Subjects pointed at a total of ten different target positions in a 'predetermined' random sequence. The pointing finger of each subject was marked with a dyed stripe for ease of measurement. The experimenter (who was invariably the first author—the second author was usually in attendance) called out the target number to begin a trial. The subject responded by pointing towards the target under the occluding panel, only seeing his finger at the terminus of a reach. No corrections under visual guidance were permitted. The subject returned his hand to his lap after a reach had been recorded, and any error had been computed. The intertrial interval was approximately ten seconds.

5.4 *Experimental design*

We used a serial-training design similar to that employed with squirrel monkeys. However, each subject was tested for one session of approximately thirty minutes only. The session began with ten practice trials where the subject viewed the target through clear glass. These trials were followed by ten blocks each of twenty adaptation training trials to prisms alternating between base-left and base-right. For their first prism adaptation exposure, subjects were divided equally between base-left and base-right prisms.

Otherwise subjects were distributed equally amongst three experimental groups. The first two groups comprised group A, who had serial adaptation training involving alternation from one stand to the other (a 180° rotation, which provided an analogue of the AS condition); group B, who had serial adaptation training on the same stand (the SS analogue); and group C, who alternated between a prism and a clear glass block on the same stand. As subjects could not be relied upon to present themselves for further testing, we were unable to include a condition which was the direct analogue of that encountered by the OT monkey. However, condition C was provided to measure any serial improvement which might occur under recurrent adaptation conditions with a single prism, and to compare the results with the interference effects expected of the 'contradictory' prism conditions (A and B).

5.5 *Results*

The human data are presented in figures 9 and 10. Figure 9 is a record of the original adaptation performance for all subjects combined. Figure 10a shows the AS group (A). Although adaptation performance for the second prism was significantly inferior to that of original adaptation ($p < 0\cdot001$; $t = 7\cdot427$; d.f. = 11), there was a steady trend towards progressive error elimination with subsequent prism shifts (gradient = $-0\cdot258$, $r = 0\cdot855$, $t = 4\cdot362$, d.f. = 7, $p < 0\cdot01$). (However, the

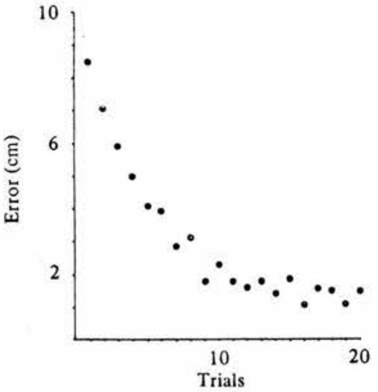

Figure 9. Mean error per trial for the first prismatic adaptation ($N = 36$).

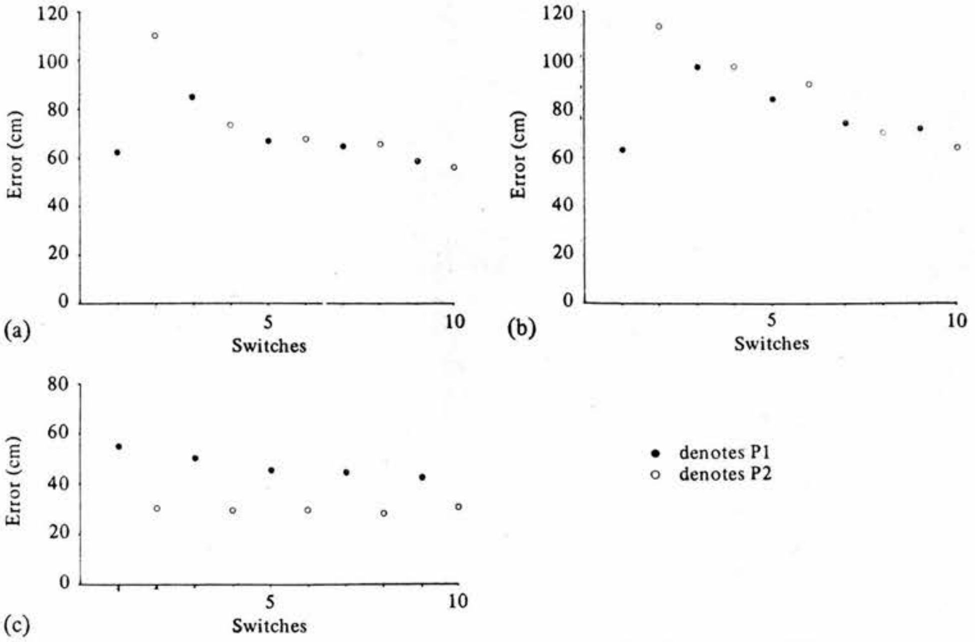

Figure 10. Mean error per prismatic switch: (a) group A (AS); (b) group B (SS); (c) group C (control).

gradient for shifts two to five, which visual inspection of figure 10a reveals to constitute the main component of the overall improvement recorded during successive readaptation performance, is $-0\cdot711$, $r = 0\cdot956$, $t = 4\cdot622$, d.f. = 2, $p < 0\cdot05$.) This was also the case with the SS group (B), whose rate of 'second adaptation' was significantly inferior to the original one ($p < 0\cdot01$, $t = 4\cdot134$, d.f. = 11); thereafter, they too showed a progressive elimination of error with successive shifts (gradient = $-0\cdot312$, $r = 0\cdot964$, $t = 9\cdot628$, d.f. = 7, $p < 0\cdot001$). On all points from shift 2 to shift 10, however, the SS group were inferior to the AS group ($p < 0\cdot002$ on a one-tailed sign test). The third group (C) recorded a 'cumulative' adaptation effect, i.e. they improved their adaptation rate over successive readaptation sessions (prism errors for switches 1, 3, 5, 7, 9, gradient = $-0\cdot153$, $r = 0\cdot957$, $t = 0\cdot677$, d.f. = 3, $p < 0\cdot05$; glass errors for switches 2, 4, 6, 8, 10, gradient = $-0\cdot002$, $r = 0\cdot061$, $t = 0\cdot105$, d.f. = 3, not significant). In this condition we took conventional measures of aftereffect during 'clear glass' exposure. Table 6 records the mean subject total error for each prism condition separately.

Table 6. Aftereffects (cm) following prism exposure.

Switch number	Prism base-right	Prism base-left
2	+34·1	−20·9
4	+28·6	−23·5
6	+30·3	−22·4
8	+20·5	−23·7
10	+27·9	−21·6

Key: + indicates error to the right
− indicates error to the left

5.6 *Discussion*

Although this study with human subjects fell short of a full replication of the monkey data, similar trends were nevertheless revealed. With human subjects, also, it would seem that spatial separation of prisms is beneficial in helping reduce negative 'aftereffects'. Whilst neither graph (of AS and SS) reveal performance which even at the terminus of training is superior to original adaptation performance, we are confident, on the basis of group C results, that given more training time, long-term cumulative adaptation effects to both prisms should emerge. For any evaluation of the human data in this respect must be measured against the short duration of the study as compared with the monkey experiment. In this respect we find ourselves in a position somewhat analogous with that of Lazar and van Laer (1968), who, although failing to demonstrate a 'learning set' effect with human subjects exposed to three (successive) prismatic conditions, nevertheless concluded that "more time ... might yield results comparable to those found in most discrimination learning and transfer of training experiments".

6 General discussion

We now feel bound to deal with a possible query which may have troubled the reader since the beginning of this report. It is this: what kind of adaptation has the monkey shown? Is it a case of 'learning to point crookedly at a target' rather than 'genuine' adaptation? Have the 'usual' criteria for determining adaptation been met?

As far as the exposure conditions are concerned, we appear to have met most, if not all of Howard's stringent criteria (Howard 1968)⁽⁵⁾. But what of the criteria governing postexposure tests? How might the sceptic distinguish 'true' from 'pseudo' adaptation in our experiments? By means of intermanual transfer or adaptation aftereffect measures? Clearly intermanual transfer cannot be criterial for such a distinction as the above one, otherwise Harris (1963), Bossom and Hamilton (1963), Hamilton (1967), Templeton et al (1974), for example, have been studying something other than 'true' adaptation in the experiments they have reported, which show adaptation that is selective to the trained limb. On these criteria also, Prablanc et al (1975), reporting, as they do, adaptation of the two arms to opposite prism displacements, would be clearly disqualified⁽⁶⁾.

Although short-term aftereffects are often used as a postexposure measure of adaptation, and we had observed and measured similar effects in the course of preliminary investigations, we decided against using such measures in the long-term investigation of adaptation we report here. One reason for this is that the work of Kohler (1964) shows that aftereffects become progressively reduced under conditions of long-term exposure. Yet it would be difficult to deny that 'adaptation' (albeit selective to one half-field) had occurred and did not diminish as negative aftereffects disappeared. Long-term (conditioned) effects were, however, recorded in Kohler's experiment and it is this type of adaptation which we exploit as an *'aftereffect'* in the monkey investigation reported here. Thus the mutual, if somewhat asymmetrical, interference effects of prisms (as a function of test order) are taken by us as measures of adaptation—an assumption fully supported by the performance record of the OT animal, who showed the kind of conditioned adaptation effect observed by Taylor (1962). In this context it is interesting to note that using conventional 'aftereffect' measures, Klapp et al (1974) reported long-lasting effects of up to four weeks following brief exposure to prism conditions.

Given then, that some form of adaptation occurred during the course of the experiments we describe, the question arises as to what sort of compensation it is and what determines it. For it now seems well-established that there are many different kinds of adaptation. As Prablanc et al (1975) remark, "It is probably more fruitful to consider prism adaptation as a process aimed at resolving the visuomotor conflict by using *any* available cue [our emphasis] rather than as a process relying on a single specific mechanism".

(5) These are in summary: (i) the use of different targets in random order to avoid stereotyping movements; (ii) the adoption of a 'terminal display with target' procedure rather than any of those Howard criticizes; (iii) the reduction of 'accidental' features of prism use by (a) the deployment of simple visual targets in the region of the median plane and (b) the use of a prismatic window rather than spectacle frames attached to the head, which induce rubbery transformations, parallax effects, and other contaminations following head movement; (iv) by preventing subjects from getting a distorted view of their own bodies, the elimination of visual asymmetry, which itself may "induce behavioural changes in the subject quite apart from any effect due to sensorimotor discordance" (Howard 1968, p 22); (v) placing the targets at eye level, the only plane where tilt distortion does not occur with vertical prisms.

(6) Unlike the subjects described by the French investigators cited above, however, the monkeys in our experiment did not need to use different pointing limbs to maintain 'contrary' adaptations. And in one subject where we attempted to force a change of pointing limb through the use of a slide arrangement similar to that reported by Sperry, we found evidence of bimanual adaptation. A second animal became upset by this procedure, which we then abandoned for the duration of the investigation on the grounds that it was more important to see if contrary adaptations could be conserved with the same pointing limb than to determine the extent of intermanual transfer or bimanual adaptation.

Confronted by this range of possibilities, we might begin by eliminating any proprioceptive change as causal to the monkey data, for Hay and Pick (1966) have shown it to be a transient factor in adaptation and unlikely therefore to be implicated in long-term studies such as our own. However, to judge by Harris's heroic attempts to prise predictions out of various theories seeking to account for adaptation (Harris 1965, p 422), even under conditions far more restricted than those obtaining in this and the more conventional adaptation experiments (i.e. Harris's interpretation of various adaptation theories assumes that the subject is adapting by pointing with one arm at a single target and using a stereotyped arm movement), it does not seem at all a simple matter to distinguish operationally between several other alternatives on offer with respect to those criteria which we might usefully employ in animal studies, e.g. 'intermanual transfer' and 'aftereffect'. (We beg to be excused consideration of 'conscious correction' as a possible strategy with squirrel monkeys!)

Following Kohler's lead, however, emphasizing the primacy of *behavioural* compensation in 'reversed field' experiments, we currently favour the idea that some form of motor adjustment, triggered selectively by exteroceptive cues, provides the causal mechanism. As reaching under an occluding screen involves a novel underarm reach for the monkey (if not also for the human subject), it may serve to isolate these (this class of) responses from home cage and other activity which could, conceivably, compete with them.

However, response novelty, or response isolation, will scarcely be sufficient to account for the multiple adaptation results we recorded with the same pointing limb and with (ostensibly at least) the same sort of reaching response in both cases. Clearly it would require (additionally) an excellent motoric memory (e.g. for context specific adjustments) to sustain (conflicting) reaching strategies over the long term, and a current experiment of ours on precisely this question already gives some clue to the potential of the 'action engram' in squirrel monkey. In this experiment, monkeys are trained to discriminate their pointing limbs on the basis of reward contingencies only. Thus for example reaching for a yellow tin with the 'preferred' hand is not reinforced (tin locked in position by the experimenter), whereas reaching with the 'nonpreferred' hand is rewarded (the experimenter unlocks the tin and monkey retrieves the peanut). We have discovered that monkeys quickly learn to

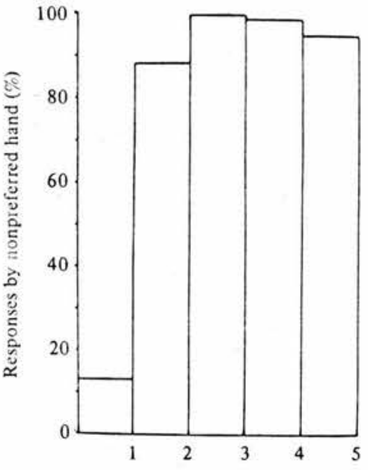

Figure 11. Percentage of responses made by the nonpreferred hand for the conditions: (1) pretraining (free choice); (2) training (nonpreferred hand reinforced); (3)-(5) retention 1, 3, and 7 weeks after training (free choice).

select the appropriate hand and transfer this learning to a variety of contexts, e.g. the home cage so long as the appropriate cue (i.e. a coloured tin) is available. Furthermore, the 'memory' for hand discrimination seems very durable; when retested without further training over intervals of one, three and seven weeks following original learning, monkeys show excellent retention, as figure 11 shows.

Although we do not yet know how precisely the monkey can learn to regulate his action in relation to exteroceptive cueing—or even if exteroceptive cues are always necessary (monkeys may need them more than humans), the suggestion arises that adaptation which occurs when the error provoked by prisms is well outside the normal range of error for comparable (nondistortion) tasks affords the subject an opportunity not only to compensate for any error so induced, by means of feedback information, but additionally to link such exteroceptive information which happens to coincide with the occasion of error as the basis of a feed-forward system which can put the organism in a state of readiness for future compensatory demands should these conditions recur. As Pribram (1971) points out, "these feed-forward processes are ubiquitous in the motor system ...".

Research on prismatic adaptation appears to have placed a heavy emphasis on the feedback aspects of servocontrol. Perhaps the time has come to emphasize more strongly those aspects of adaptation (including compensation to load and other compensations) which constitute the transition phase linking feedback to feedforward achievements.

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References

Bossom J, Hamilton C R, 1963 "Interocular transfer of prism-altered coordinations in split-brain monkeys" *Journal of Comparative and Physiological Psychology* 56 (4) 769-774

Freedman S J, 1968 "Perceptual compensation and learning" in *The Neuropsychology of Spatially Oriented Behavior* Ed. S J Freedman (Homewood, Ill.: Dorsey Press)

Hamilton C R, 1967 "Effects of brain bisection on eye-hand coordination in monkeys wearing prisms" *Journal of Comparative and Physiological Psychology* 64 (3) 434-443

Harris C S, 1963 "Adaptation to displaced vision: visual, motor, or proprioceptive change?" *Science* 140 812-813

Harris C W, 1965 "Perceptual adaptation to inverted, reversed, and displaced vision" *Psychological Review* 72 (6) 419-444

Hay J C, Pick H L, 1966 "Visual and proprioceptive adaptation to optical displacement of the visual stimulus" *Journal of Experimental Psychology* 71 (1) 150-158

Howard I P, 1968 "Displacing the optical array" in *The Neuropsychology of Spatially Oriented Behavior* Ed. S J Freedman (Homewood, Ill.: Dorsey Press)

Klapp S T, Nordell S A, Hoekenga K C, Patton C B, 1974 "Long-lasting after effect of brief prism exposure" *Perception and Psychophysics* 15 399-400

Kohler I, 1964 "The formation and transformation of the perceptual world" translated by H Fiss *Psychological Issues* 3 (4) 1-173

Lazar G, Laer J van, 1968 "Adaptation to displaced vision after experience with lesser displacements" *Perceptual and Motor Skills* 26 579-582

McGonigle B O, Jones B T, 1975 "The perception of linear Gestalten by rat and monkey: sensory sensitivity or the perception of structure" *Perception* 4 419-429

Prablanc C, Tzavaras A, Jeannerod M, 1975 "Adaptation of the two arms to opposite prism displacements" *Quarterly Journal of Experimental Psychology* 27 667-671

Pribram K, 1971 *Languages of the Brain: Experimental Paradoxes and Principles in Neuropsychology* (Englewood Cliffs, NJ: Prentice-Hall)

Rock I, 1966 *The Nature of Perceptual Adaptation* (New York: Basic Books)

Taylor J G, 1962 *The Behavioral Basis of Perception* (New Haven: Yale University Press)

Templeton W B, Howard I P, Wilkinson D A, 1974 "Additivity of components of prismatic adaptation" *Perception and Psychophysics* 15 249-257

Research
Nr. 330 Beitrag...........

APPENDIX F

Short Communication

The Learning of Hand Preferences by Squirrel Monkey

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Summary. In a reaching task with Squirrel Monkeys stable hand preferences were established by reward training. The use of a particular hand was brought under the control of a colour cue.

Introduction

Although monkeys are generally regarded as lacking in cerebral dominance, they frequently express strong hand preferences (Kounin, 1938; Ettlinger and Moffett, 1964; Brookshire and Warren, 1962), particularly in tasks demanding some degree of manipulative skill (Kounin, 1938). Unlike the majority of humans, however, they are not predominantly right-handed; if anything, the evidence would suggest instead a trend towards a greater incidence of left than right lateral preferences (Ettlinger and Moffett, 1964).

Given that strong individual hand preferences do occur, however, it is still far from clear as to what the major determinants of this type of forelimb specialization might be in monkeys. Although many possibilities suggest themselves, we consider here but two of them: (i) that 'handedness' is a further example of response preparedness (Seligman, 1970) and reflects an asymmetry in the rate and / or extent to which both response contingent events and what Bernstein (1967) would describe as the structuration of unknown movements may be learnt by monkeys as a function of which hand is in use. Alternatively, (ii) 'handedness' in monkeys is an example of idiosyncratic motor learning and can be modified experimentally by adjusting the 'pay off' associated with the use of either limb. If this latter alternative is on the right lines, there should be no significant asymmetry in the rate of learning with either limb.

We report here two experiments designed to bear on these (by no means eshaustive) set of possibilities.

Experiment I

Six adult squirrel monkeys were tested. Five of these were male and one was female, all approximately seven years old. They had previous experience gained from sensory

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discrimination and object permanence studies (McGonigle and Jones, 1975). One monkey had been used earlier as a 'prototype' in a preliminary feasibility study of the training conditions we report here. The others were, however, completely naive in this respect and had no prior laboratory experience of any sort in specialized motoric 'shaping'.

The training apparatus was a WGTA. The stimulus was a painted circular tin mounted on a brass pivot at the centre of the test-tray. When pushed, it swivelled away from the foodwell and could be locked in position over it. A pulley cord under the test-tray enabled the experimenter to free the lock and permitted the monkey to push back the tin and gain access to the foodwell. A portable version of the above device was used to test for transfer of hand discrimination to the context of the monkeys' home cages. During home cage trials, only the test monkey remained in the cage.

In general the procedure was similar to that used in conventional sensory discrimination tasks. Training involved a maximum of 40 trials per session and conditions of mass practice with an interval between trials of 15 s. A correct choice was rewarded with a half peanut. A correction method was used which allowed the monkey freedom to manipulate the tin on any one trial until the hand selected by the experimenter as the 'reinforced' hand was used. The experimenter did not unlock the tin, however, until definite, unimanually produced force was exerted on it by the monkey using the appropriate limb.

The experimental conditions and findings of the first investigation are summarized below.

Stage A. All subjects were allowed free choice of hand in manipulating a single tin (X) for four sessions (160 trials). Results for condition A are given in Figure 1. As inspection of it reveals, all but one monkey (the prototype) showed a preference for one hand.

Stage B. The experimenter selected the non-preferred hand (the originally non-preferred hand in the case of the prototype) and reinforced manipulative responses with that hand only. For this condition a new tin of colour (Y) was used. After five sessions all monkeys had reached (minimally) a performance criterion based on using the reinforced limb 90% of the time or more for two successive sessions. This is shown in condition B, Figure 1.

Stage C. To test for the durability of this reversed hand preference, all subjects were retested without differential reinforcement at intervals of 1, 3 and 7 weeks. The results indicate retention to be excellent, as condition C, D, E (Fig. 1) shows. Condition F records the transfer obtained when similar tests (without retaining) were carried out at the animal's home cage.

Following this successful demonstration of hand discrimination training, we asked a second question: Can limb-specific manipulative responses become selectively conditioned to exteroceptive cues?

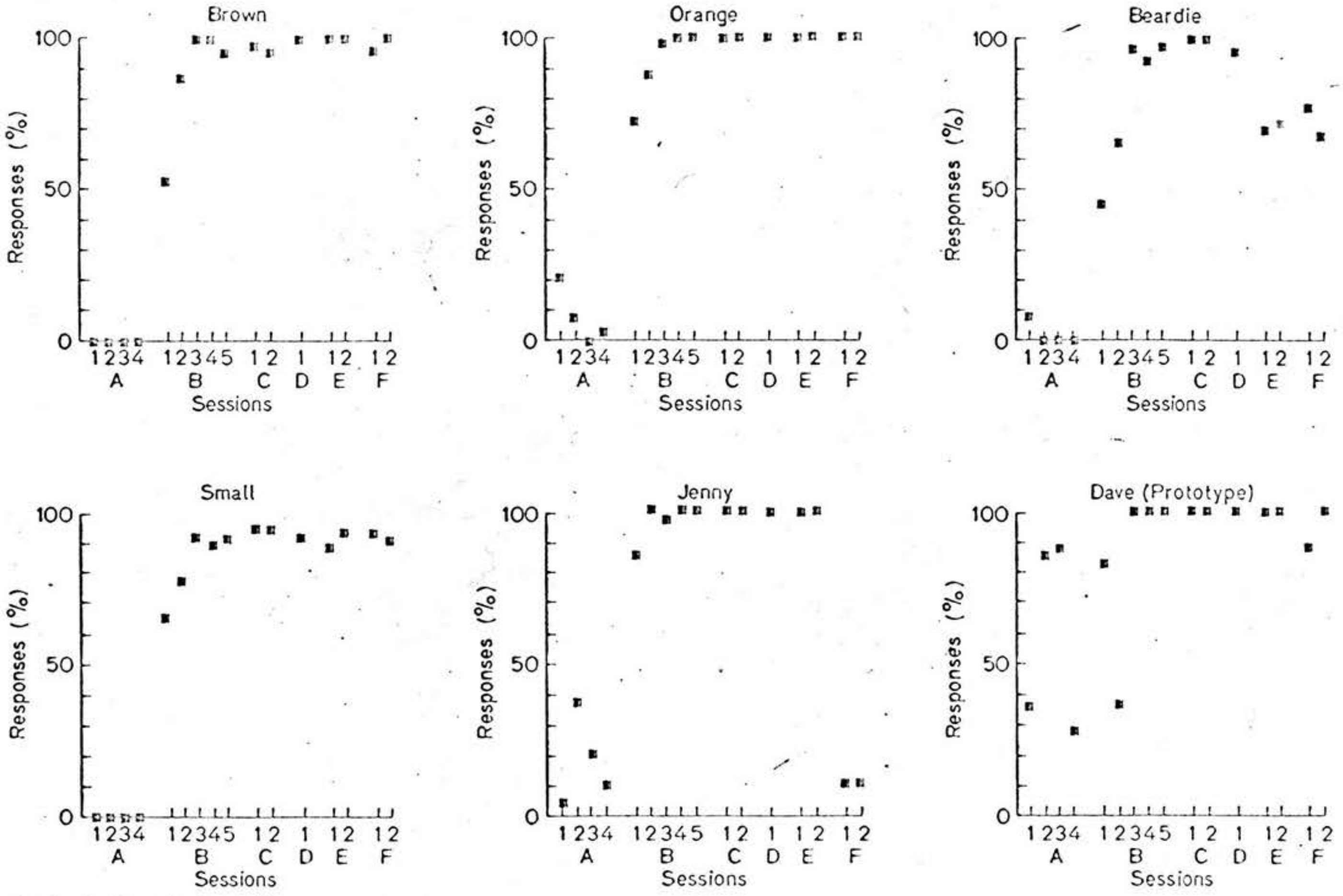

Fig. 1. Percent responses per session using the Trained hand made by six subjects under the following six conditions: *A:* Free choice (colour X). *B:* Training-non-preferred (Trained) hand reinforced (colour Y). *CDE:* Retention after 1, 3, 7 weeks - free choice (colour Y). *F:* Transfer to Home Cage - free choice (colour Y)

Experiment II

As a first step, all monkeys from Experiment I were given retraining on the hand discrimination established in that experiment. Using colour (X), they were then trained to use the originally preferred hand (Hand 2) to a criterion of 18/20 correct choices for two successive sessions. The mean number of trials required to learn this discrimination was 80, and the mean error 12. During this stage the 'prototype' monkey showed persistent instability in choosing with his originally preferred hand and was withdrawn from the rest of the study. The remaining five successful animals were then given eight further sessions of training, each session alternating between reinforced reaching with, e.g., the left hand to tin colour (X) and reinforced reaching with the right hand to colour (Y). Although the monkeys learnt each hand discrimination within a single session, there did not seem to be any overall improvement in the rate at which they acquired a particular discrimination. No significant asymmetry in the learning rates for respective hands was recorded (see Table 1). In an attempt to improve discrimination performance, therefore, monkeys were shifted to a condition where both tins (X and Y) were presented successively in a quasi-random (Gellermann) sequence within the same session. The correction procedure was extended to include the provision that no change in the colour cue could occur until the monkey had made three successively 'correct' responses to it. (This last proviso greatly increased at first the number of correction trials, thus reducing the (average) number of 'Gellermann' trials per session to 30. The performance criterion remained at 18/20 correct over two successive sessions.)

This modified procedure proved successful. As Table 2 illustrates, all five monkeys learnt to reach with one hand for colour (X) and use the other hand for colour (Y). In addition, retention tests carried out three and six weeks later show the discrimination to be highly stable. Unlike the 'simple' case in hand discrimination recorded during Experiment I, however, no positive transfer of this two-handed discrimination to the home cage test was recorded. (Some retention with the originally trained limb was observed, however.)

Overall, the results show clearly that hand preference by monkeys is learnable, and that each limb is capable of 'triggering' by a specific exteroceptive cue which can, in some cases, continue to be an effective 'releaser' in a different context. There is

Table 1. Mean number of errors per session (40 trials) for the five subjects over the eight training sessions.

Session	*Colour*	*Response*	*No. of Errors*
1	Y	H1	9.4
2	X	H2	6.0
3	Y	H1	9.6
4	X	H2	8.4
5	Y	H1	5.8
6	X	H2	7.2
7	Y	H1	9.2
8	X	H2	6.2

Table 2. Mean acquisition and performance scores (N = 5) on the Gellermann sequence presentation of cued hand discrimination: colour Y - Hand 1; colour X - Hand 2.

	Total No. of trials	*Mean errors*		*Trials to criterion*
		Hand 1	*Hand 2*	
Acquisition				
Training to criterion	350	37.6	37.2	270
Training (first 100 trials)	100	17.6	18.6	–
Performance				
Training (last 100 trials)	100	5.2	6.8	50
Retention (3 weeks)	100	5.5	4.8	44
Transfer (home cage)	100	16.0	22.8	–
Retest (WGTA, 6 weeks)	100	2.8	3.2	44

no evidence at this stage, moreover, to suggest that for any monkey one limb is more difficult to associate with these cues than the other.

This finding should not obscure the fact, however, that the squirrel monkey is capable of learning limb-localized action schemes, of elaborating those differential roles for each limb which Bresson et al. (1977) believe (on the basis of studies of human children) to be the precursor of complementary activity between the hands found later (ontogenetically speaking) in tasks which require bimanual activity. And it is from this 'complementarity', *and not from the establishment of a mere right hand preference,* that these French investigators conceive the development of right hand dominance in man.[1] If this analysis is correct, it would imply that the search for the homologue of cerebral dominance in man as expressed by a right hand preference in monkey is misconceived. Instead it would suggest the need to expand our knowledge of the ability of primates, both human and infra-human, to develop both specialized yet complementary roles for each forelimb.

We offer our experiments, therefore, as a small step in that direction.

References

Bernstein, N.: The co-ordination and regulation of movements. Oxford: Pergamon Press (1967)

Bresson, F., Maury, L., Pieraut-Le Bonniec, G., Schonen, S. de: Organization and lateralization of reaching in infants: An instance of asymmetric functions in hands collaboration. Neuropsychol. 15, 311–20 (1977)

Brookshire, K.H. Warren, J.M.: The generality and consistency of handedness in monkeys. Animal Behav. 10, 222–227 (1962)

Ettlinger, G., Moffett, A.: Lateral preferences in the monkey. Nature 204, 606 (1964)

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[1] Of additional interest, given Ettlinger and Moffett's (1964) finding of a left-hand trend in rhesus monkeys, is Bresson et al's (1977) finding that the left hand of 17 - 40 day old infants serves a locative function, as it could well be argued that lateral preference tests for monkeys generally implicate spatial, and particularly locative abilities rather strongly.

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Kounin, J.S.: Laterality in monkeys. J. Gen. Psychol. 52, 375–393 (1938)
McGonigle, B.O. Jones, B.T.: The perception of linear Gestalten by rat and monkey: sensory sensitivity or the perception of structure? Perception 4, 419–429 (1975)
Seligman, M.E.R.: On the generality of the laws of learning. Psychol. Rev. 77, 406 (1970)

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APPENDIX G

Paper to appear in Nature (1978)

Long Term Retention of Single and Multistate Prismatic Adaptation by Humans

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How primates reach accurately for objects has frequently been investigated by sensory rearrangement techniques. When an object is viewed through wedge prisms, for example, reaching is disrupted but corrected rapidly when the subject is given immediate feedback concerning the position of his pointing limb relative to the target(4). Such adaptation to distorted input is conventionally regarded as a process of minimizing the discrepancy between two or more sensory channels (for example vision and proprioception) with the neglected or non-dominant channel conforming to the position information provided by the other. The role of learning in this process is unclear. When the prisms are removed, the effects of such adaptation disappear rapidly - unlike most learning phenomena - and after an interval of 24 h during which the subject reaches "normally", most investigators assume(3) that all traces of adaptation have been eliminated from the nervous system. This view has been challenged recently by results we obtained with squirrel monkeys(1) who retained their adaptation over periods often considerably longer than 48 h spent in their home cages. We also found that they could adapt to two prisms displacing in equal and opposite directions, and eventually conserve both adaptations together with their normal reaching behaviour. Their progressive elimination of error (due to prismatic distortion) as a function of the number of occasions they had exposure to prism conditions suggests, furthermore, powerful motor learning mechanisms at work in the adaptation process. We now report similar findings with human subjects.

Our subjects were 34 students at Edinburgh University. Those with corrected vision continued to wear spectacles or contact lenses throughout the experiment. The subjects looked through a wedge prism with their dominant eye and pointed at the target with their preferred hand. The apparatus was an Imhof stand with a circular window at eye level through which the subject could see a target board calibrated in units for 1 cm but with no numbers visible to the subject. A prism holder, mounted at the rear of the window allowed the experimenter to slide either of two wedge prisms of 30 diopters or a glass block into position across it or occlude it altogether. A white plastic target 1.5 cm high was used with a magnetic base which allowed it to be easily transposed by the experimenter. A panel prevented subjects from seeing their pointing limb until the terminus of their reach. An additional panel could also be fitted which eliminated all visual feedback. Subjects pointed at a total of five different target positions in a sequence determined at random. The index finger of each subject was marked with a dyed stripe to permit easy measurement of error. Following a ballistic response to the target, no corrections under visual guidance were permitted. Instead the subject returned his hand to his lap. The intertrial interval was 10 s. All subjects were given a practice session with the glass condition before the experiment proper. This 'pre-exposure' test provided a record of their pointing accuracy under normal conditions measured by their <u>absolute</u> errors. Subjects were divided into two main groups. In group 1 (six subjects), training was given on one prism only for five separate training sessions each of 40 trials. Each session was separated by an interval of three days. At the end of training, retention tests were given after a first interval of two weeks and then of four weeks. Apart from tests of reaching with the prism in position, tests were also conducted with a clear glass window to measure "after effects".

During these tests no visual feedback was given. All six subjects were given such tests at the end of each retention test period. By way of "probe" tests, two of the subjects were also given "after effect" tests (without feedback) at the beginning and end of each training session. The errors recorded were in the direction of the displacement when the prism was present and in the opposite direction on the "after effect" tests. To simplify presentation and make direct comparison between both phases of the experiment easier, both sets of errors are given "positive" values.

The main findings are depicted by figure 1 which shows that (all) subjects improved dramatically over the series of training sessions even though each session was separated by an interval of three days; by session 5 virtually no error is recorded. The plot of "first trial" errors per session shows, furthermore, that subjects learnt to predict the correct response and not merely to adapt faster following a mistake. Figure 1 also shows that retention of this adaptation over periods of two and four weeks respectively is excellent. The "after effect" errors, recorded with clear glass and no visual feedback remain constant and are of considerable magnitude. These results clearly show, therefore, that perceptual adaptation need not be a transient phenomenon. Like the monkey, the human appears capable of storing at least two separate visuo-motor correlations.

In our second condition, we tested for the possibility that additional correlations might also be learnable by humans. Group 2 (28 subjects) were given repeated training on each of three conditions of prism base left, prism base right and plain glass for 10 sessions.

During each session, 10 trials were given per condition (20 trials per condition were given for the first two sessions only). The order of presentation of each of the conditions was random for 12 subjects (Group 2a) and consistent for 16 subjects (Group 2b). In this latter condition, subjects were assigned to either the (fixed) training sequence of prism A ---→ prism B ---→ Glass, or prism A ---→ Glass ---→ prism B. Half the subjects were given the base right, half the base left prism as their first prism during the first training session.

Although each training session was also separated by three days, the results depicted in figure 2 show significant inter-problem improvement for both prism conditions. Because the errors induced by the two prisms are in opposite directions, the error values reflect absolute magnitudes only and thus permit direct comparisons of the relative accuracy achieved under all three conditions. As in the case of Group 1, error was small during the terminal sessions. An analysis of variance of the errors for all sessions shows that the differences found between errors committed on session 1 as compared to session 10 are significant for both prisms (1st prism: $p < .01$; 2nd prism: $p < .01$). Trend analysis on the data revealed significant linear ($p < .001$) and quadratic components ($p < .001$), which reflect the overall improvement in adaptation to both prisms recorded which is more dramatic in the earlier sessions. In short, the results from Group 2 show successful multistate adaptation which indicates that the human can store multiple, if conflicting, visuomotor correlations. There is little doubt, furthermore, that these multistate adaptations are learnt, as errors are progressively eliminated and the error pattern is fully consistent with those observed in several well known "learning to learn" paradigms not involving prisms but using a similar design(2, 5).

References

1. Flook, J.P. and McGonigle, B.O. Perception, 6, 15-29, (1977)

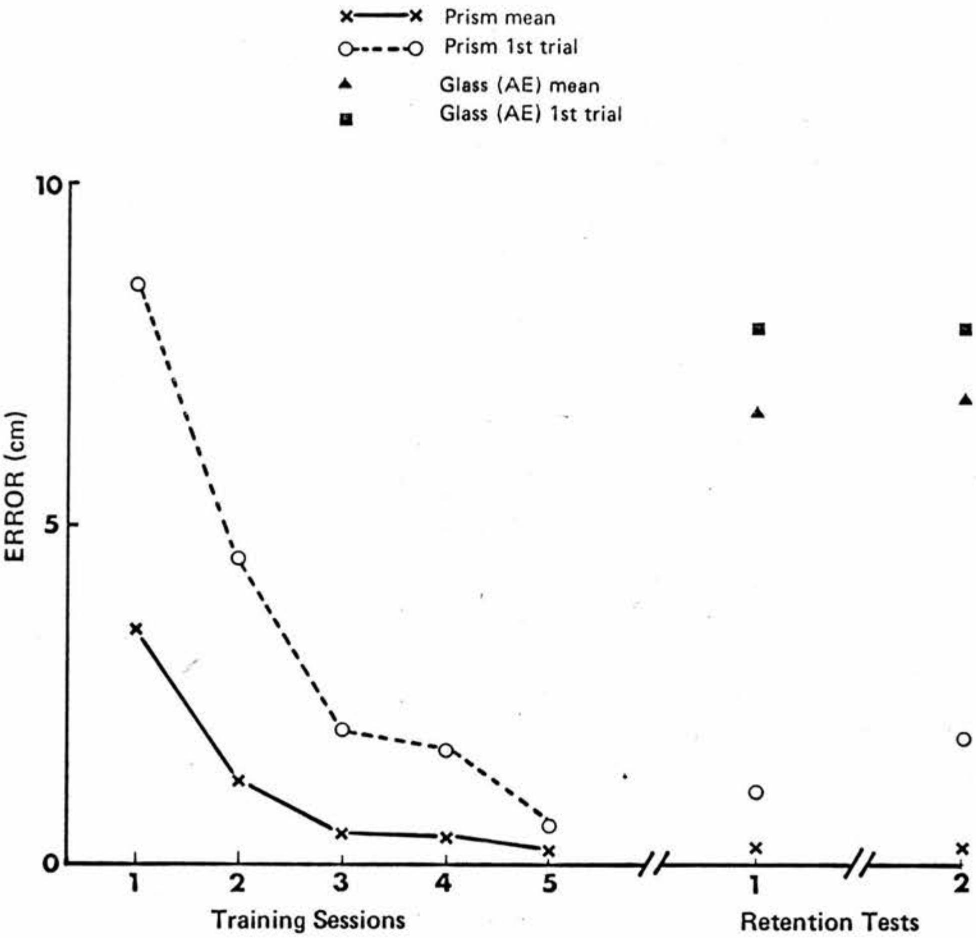
2. Harlow, H.F. Psychol. Rev., 56, 51-65, (1949)

3. Klapp, S.T., Nordell, S.A., Hoekenga, K.C. and Patton, C.B. Perception and Psychophysics, 15, 399-400, (1974)

4. Kornheiser, A.S. Psychol. Bull., 83, 783-816, (1976)

5. McGonigle, B.O. and Flook, J.P. Psychol. Research, 40, (in press)

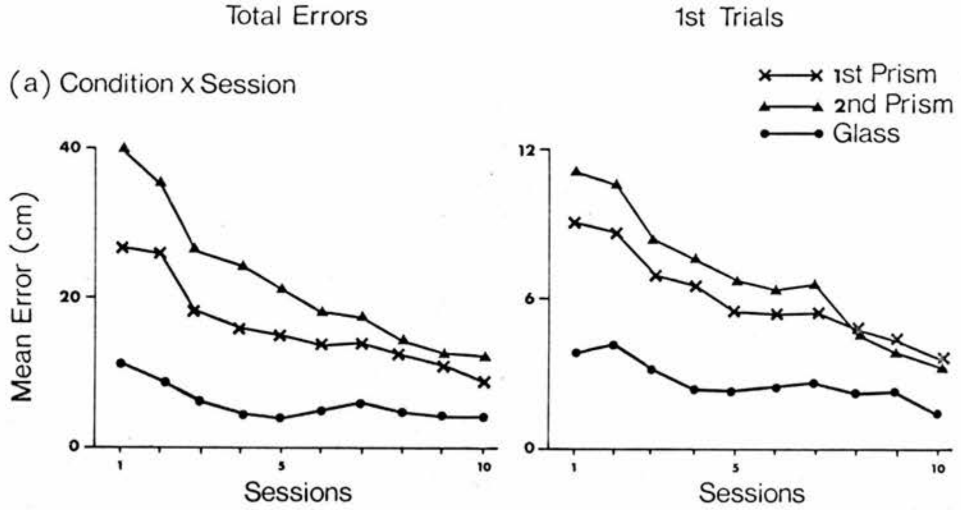
Figure 1



Mean (absolute) errors for the first ten trials of each session (corrected for normal reaching errors) and First Trial errors, for five training sessions and two retention tests(after two and four weeks) for Group 1 (six subjects). The mean and First Trial errors for the after effect (AE) tests are also shown for the two retention tests.

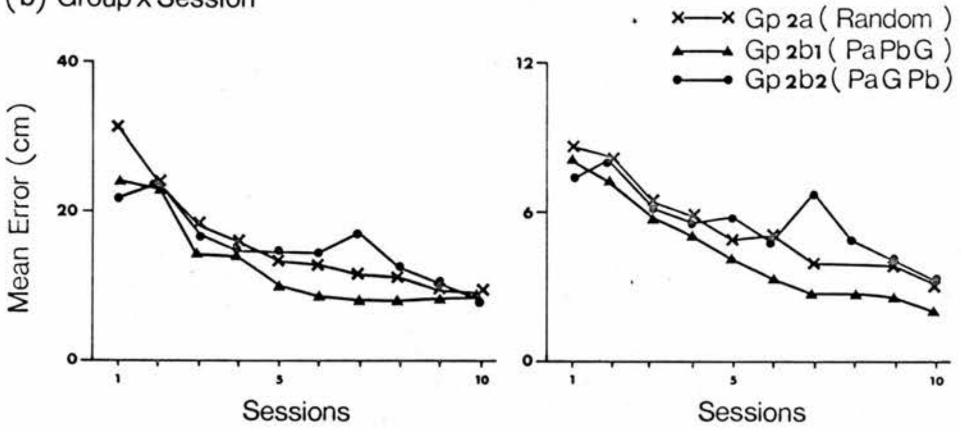
NB. The errors recorded with the prism present were in the opposite direction to the after effect errors.

Figure 2



(a) Condition x Session

(b) Group x Session



Mean Total (absolute) errors (corrected for normal reaching errors) and First Trial errors per session (a) for each condition - Condition x Session interaction, (b) for each group - Group x Session interaction. These values reflect the magnitudes only of the errors, the direction depending on the displacement induced by the present or preceding prism.

BIBLIOGRAPHY

ASHBY, W.R. (1952). Design for a brain. London: Chapman and Hall.

BMD (1971). Health Services Computing Facility. Los Angeles: University of California.

BMD (1976). Health Services Computing Facility. Los Angeles: University of California.

BAILY, J.S. (1972). Adaptation to prisms: do proprioceptive changes mediate adapted behaviour with ballistic arm movements? Q. Jl exp. Psychol. 24, 8-20.

BAUER, J.A. Jr. & HELD, R. (1975). Comparison of visually guided reaching in normal and deprived infant monkeys. J. exp. Psychol. 1, 298-308.

BERNSTEIN, N. (1967). The coordination and regulation of movements. Oxford: Pergamon Press.

BOWER, T.G.R. (1966). The visual world of infants. Scient. Am. 215, 80-92.

BOWER, T.G.R. (1974). Development in Infancy. San Francisco: Freeman.

BRESSON, F., MAURY, L., PIERAUT-LE BONNIEC, G. & de SCHONEN, S. (1977). Organisation and lateralisation of reaching in infants: an instance of asymmetric functions in hands collaboration. Neuropsychologia, 15, 311-320.

BROOKSHIRE, K.H. & WARREN, J.M. (1962). The generality and consistency of handedness in monkeys. Anim. Behav. 10, 222-227.

COHEN, M.M. (1973). Visual feedback, distribution of practice, and intermanual transfer of prism aftereffects. Percept. mot. Skills, 37, 599-609.

DALLETT, K. (1969). Problems of Psychology. London: Wiley.

DODWELL, P.C. (1970). Visual Pattern Recognition. New York: Holt, Rinehart & Winston Inc.

EDWARDS, A.L. (1960). Experimental design in psychological research. New York: Holt, Rinehart & Winston Inc.

EFSTATHIOU, A, BAUER, J. GREENE, M. & HELD, R. (1967). Altered reaching following adaptation to optical displacement of the hand. J. exp. Psychol. 73, 113-120.

ETTLINGER, G. & BLAKEMORE, C.B. (1967). Cross modal matching in the monkey. Neuropsychologia, 5, 147-154.

ETTLINGER, G. & MOFFETT, A. (1964). Lateral preferences in the monkey. Nature, Lond. 204, 606.

EWERT, H. (1930). A study of the effect of inverted retinal stimulation upon spatially coordinated behaviour. Genet. Psychol. Monogr. 7, 177-363.

FLOOK, J.P. & McGONIGLE, B.O. (1977). Serial adaptation to conflicting prismatic rearrangement effects in monkey and man. Perception, 6, 15-30.

FREEDMAN, S.J., HALL, S.B. & REKOSH, J.H. (1965). Effects on hand-eye coordination of two different arm motions during compensation for displaced vision. Percept. mot. Skills, 20, 1054-6.

FREEDMAN, S.J., WILSON, L. & REKOSH, J.H. (1967). Compensation for auditory rearrangement in hand-ear coordination. Percept. mot. Skills, 24, 1207-1210.

GELLERMANN, L.W. (1933). Chance orders of alternating stimuli in visual discrmination experiments. J. genet. Psychol. 42, 206-208.

GIBSON, J.J. (1933). Adaptation, after-effect and contrast in the perception of curved lines. J. exp. Psychol. 16, 1-31.

GIBSON, J.J. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. II Simultaneous contrast and the areal restriction of the after-effect. J. exp. Psychol. 20, 553-569.

GIBSON, J.J. (1959). Perception as a function of stimulation. In S. Koch (ed.), Psychology: A study of a Science. Vol. 1 London: McGraw Hill.

GIBSON, J.J. (1966). The senses considered as perceptual systems. London: Allen & Unwin.

GIBSON, J.J. (1968). What gives rise to the perception of motion. Psychol. Rev. 75, 335-346.

GIBSON, J.J. & RADNER, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I Quantitative studies. J. exp. Psychol. 20, 453-467.

GRAYBIEL, A.M. & HELD, R. (1970). Prismatic adaptation under scotopic and photopic conditions. J. exp. Psychol. 85, 16-22.

HAMILTON, C.R. (1964). Intermanual transfer of adaptation to prisms. Am. J. Psychol. 77, 457-462.

HARDT, M.E., HELD, R. & STEINBACH, M.J. (1971). Adaptation to displaced vision: a change in the central control of sensorimotor coordination. J. exp. Psychol. 89, 229-239.

HARLOW, H.F. (1949). The formation of learning sets. Psychol. Rev. 56, 51-65.

HARRIS, C.S. (1963). Adaptation to displaced vision: visual, motor or proprioceptive change? Science, N.Y. 140, 812-813.

HARRIS, C.S. (1965). Perceptual adaptation to inverted, reversed and displaced vision. Psychol. Rev. 72, 419-444.

HAY, J.C. & PICK, H.L. Jr. (1966). Visual and proprioceptive adaptation to optical displacement of the visual stimulus. J. exp. Psychol. 71, 150-158.

HEBB, D.O. (1949). The Organisation of Behaviour. New York: Wiley.

HELD, R. (1955). Shifts in binaural localisation after prolonged exposures to atypical combinations of stimuli. Am. J. Psychol. 68, 526-548.

HELD, R. (1961). Exposure-history as a factor in maintaining stability of perception and coordination. J. nerv. ment. Dis. 132, 26-32.

HELD, R. (1962). Adaptation to rearrangement and visual-spatial aftereffects. Psychol. Beiträge, 6, 439-450.

HELD, R. (1965). Plasticity in sensory-motor systems. Scient. Am. 213, 84-94.

HELD, R. & BAUER, J.A. Jr. (1967). Visually guided reaching in infant monkeys after restricted rearing. Science, N.Y. 155, 718-720.

HELD, R. & BAUER, J.A. Jr. (1974). Development of sensorially-guided reaching in infant monkeys. Brain Research, 71, 265-271.

HELD, R. & BOSSOM, J. (1961). Neonatal deprivation and adult rearrangement: complementary techniques for analysing plastic sensorimotor coordinations. J. comp. physiol. Psychol. 54, 33-37.

HELD, R., EFSTATHIOU, A. & GREENE, M. (1966). Adaptation to displaced and delayed visual feedback from the hand. J. exp. Psychol. 72, 887-891.

HELD, R. & FREEDMAN, S.J. (1963). Plasticity in human sensorimotor control. Science, N.Y. 142, 455-462.

HELD, R. & GOTTLIEB, N. (1958). Technique for studying adaptation to disarranged hand-eye coordination. Percept. mot. Skills, 8, 83-86.

HELD, R. & HEIN, A.V. (1958). Adaptation of disarranged hand-eye coordination contingent upon reafferent stimulation. Percept. mot. Skills, 8, 87-90.

HELD, R. & HEIN, A. (1963). Movement produced stimulation in the development of visually guided behaviour. J. comp. physiol. Psychol. 56, 872-876.

HELD, R. & MIKAELIAN, H.H. (1964). Motor-sensory feedback versus need in adaptation to rearrangement. Percept. mot. Skills, 18, 685-688.

HELD, R. & REKOSH, J. (1963). Motor-sensory feedback and the geometry of visual space. Science, N.Y. 141, 722-723.

HELD, R. & SCHLANK, M. (1959). Adaptation to disarranged eye-hand coordination in the distance dimension. Am. J. Psychol. 72, 603-605.

HELMHOLTZ, H. von (1866/1962). Treatise on physiological optics. Vol. 3. Translated and edited by J.P. Southall. New York: Dover. (First published 1866).

HELSON, H. (1964). Adaptation-level Theory. New York: Harper.

HOLST, E. von (1954). Relations between the central nervous system and the peripheral organs. Br. J. anim. Behav. 2, 89-94.

HOWARD, I.P. (1968). Displacing the optical array. In S.J. Freedman (ed.), The Neuropsychology of Spatially Oriented Behaviour. Homewood, Ill: Dorsey Press.

HOWARD, I.P., CRASKE, B. & TEMPLETON, W.B. (1965). Visuo-motor adaptation to discordant exafferent stimulation. J. exp. Psychol. 70, 189-191.

HOWARD, I.P. & TEMPLETON, W.B. (1966). Human Spatial Orientation. New York: Wiley.

HULL, C.L. (1934). The concept of the habit-family hierarchy and maze learning. Psychol. Rev. 41, 33-54; 134-152.

KALIL, R.E. & FREEDMAN, S.J. (1966). Intermanual transfer of compensation for displaced vision. Percept. mot. Skills, 22, 123-126.

KLAPP, S.T., NORDELL, S.A., HOEKENGA, K.C. & PATTON, C.B. (1974). Long-lasting aftereffect of brief prism exposure. Percept. Psychophys. 15, 399-400.

KOHLER, I. (1964). The formation and transformation of the perceptual world. Psychol. Issues Monogr. 12, vol. 3, No. 4.

KÖHLER, W. & WALLACH, H. (1944). Figural aftereffects: an investigation of visual processes. Proc. Am. phil. Soc. 88, 269-357.

KONORSKI, J. (1967). Integrative activity of the brain. Chicago: Univ. of Chicago Press.

KOUNIN, J.S. (1938). Laterality in monkeys. J. genet. Psychol. 52, 375-393.

KRAVITZ, J.H. (1972). Conditioned adaptation to prismatic displacement. Percept. Psychophys. 11, 38-42.

KUHN, T.S. (1970). The structure of scientific revolutions, 2nd ed. Chicago: Univ. of Chicago Press.

LASHLEY, K.S. (1933). Integrative functions of the cerebral cortex. In F.A. Beach, D.O. Hebb, C.T. Morgan & H.W. Nissen (eds.) (1949), The Neuropsychology of Lashley. New York: McGraw Hill.

LAZAR, G. & LAER, J. van (1968). Adaptation to displaced vision after experience with lesser displacements. Percept. mot. Skills, 26, 579-582.

LEE, D.N. & ARONSON, E. (1974). Visual proprioceptive control of standing in human infants. Percept. Psychophys. 15, 529-532.

LISHMAN, J.R. & LEE, D.N. (1973). The autonomy of visual kinaesthesis. Perception, 2, 287-294.

MACFARLANE, D.A. (1930). The role of kinesthesis in maze-learning. University of California Publications, 4, 277-305.

McGONIGLE, B.O. (1976). A visual analogue of the "diplophonic" effect. Paper presented at the 138th Annual Meeting of the British Association for the Advancement of Science, University of Lancaster, September, 1976.

McGONIGLE, B.O. & CHALMERS, M. (1977). Are monkeys logical? Nature, Lond. 267, 694-696.

McGONIGLE, B.O. & FLOOK, J.P. (1978a). The learning of hand preferences by squirrel monkeys. Psychol. Research, 40, in press.

McGONIGLE, B.O. & FLOOK, J.P. (1978b). Long term retention of single and multistate prismatic adaptation in humans. Nature, Lond. (in press)

McGONIGLE, B.O., FLOOK, J.P. & FAULKNER, A. (1974). Simultaneous multiple adaptation to sensory distortion in squirrel monkey A preliminary report. Unpublished manuscript.

McGONIGLE, B.O. & JONES, B.T. (1975). The perception of linear Gestalten by rat and monkey: sensory sensitivity or the perception of structure. Perception, 4, 419-429.

McGONIGLE, B.O., OSBORNE, R. & JONES, B.T. (1971). Inhibition and reversal learning: a theoretical and experimental analysis. In R. Boakes and S. Halliday (eds.), Proceedings of Brighton Symposium on Inhibition and Learning, University of Sussex.

MACKINTOSH, N.J. (1965). Selective attention in animal discrimination learning. Psychol. Bull. 64, 124-150.

MACKINTOSH, N.J., McGONIGLE, B., HOLGATE, V. & VANDERVER, V. (1968). Factors underlying improvement in serial reversal learning. Can. J. Psychol. 22, 85-95.

MIKAELIAN, H.H. (1971). Interpedal generalisation of rearranged eye-foot coordination. Psychon. Sci. 24, 257-258.

MIKAELIAN, H.H. (1974a). Restricted adaptation to prism rearrangement. Percept. Psychophys. 16, 547-550.

MIKAELIAN, H.H. (1974b). Generalised sensorimotor adaptation with diminished feedback. Psychol. Forsch. 36, 321-328.

MIKAELIAN, H. & HELD, R. (1964). Two types of adaptation to an optically-rotated visual field. Am. J. Psychol. 77, 257-263.

MIKAELIAN, H.H. & MALATESTA, V. (1974). Specialised adaptation to displaced vision. Perception, 3, 135-139.

NOTTERMAN, J.M. (1966). Force emission during bar pressing. In T. Verhave, Experimental Analysis of Behaviour. New York: Appleton-Century-Crofts.

NOTTERMAN, J.M. & MINTZ, D.E. (1966). Exteroceptive curing of responses force. In T. Verhave, The Experimental Analysis of Behaviour. New York: Appleton-Century-Crofts.

PAILLARD, J. (1960). Mechanisms of Self-Adjustment. In J. Field (ed.), Handbook of Physiology: Section I Neurophysiology, Vol. 3 American Physiological Society.

PAILLARD, J. & BROUCHON, M. (1968). Active and passive movements in the calibration of position sense. In S.J. Freedman (ed.), The Neuropsychology of Spatially Oriented Behaviour. Homewood, Ill: Dorsey Press.

PAPOUSEK, H. (1967). Experimental studies of appetitional behaviour in human newborns and infants. In H.W. Stevenson, E.H. Hess, and H.L. Reingold (eds.), Early behaviour: comparative and developmental approaches. New York: Wiley.

PAPOUSEK, H. (1969). Individual variability in learned responses in human infants. In R.J. Robinson (ed.), Brain and early behaviour. London: Academic Press.

PAVLOV, I.P. (1927). Conditioned Reflexes. An investigation of the physiological activity of the cerebral cortex. Translated by G.V. Anrep. New York: Dover.

PETERSON, G.M. (1951). Transfers in handedness in the rat from forced practice. J. comp. physiol. Psychol. 44, 184-190.

PETERSON, J. & PETERSON, J.K. (1938). Does practice with inverting lenses make vision normal? Psychol. Monogr. 50, 12-37.

PIAGET, J. (1953). *The origin of intelligence in the child.* London: Routledge & Kegan Paul.

PICK, H.L. Jr. & HAY, J.C. (1965). A passive test of the Held reafference hypothesis. *Percept. mot. Skills*, *20*, 1070-1072.

PRABLANC, C., TZAVARAS, A. & JEANNEROD, M. (1975). Adaptation of the two arms to opposite prism displacements. *Q. Jl exp. Psychol.* *27*, 667-671.

RIOPELLE, A.J. & COPELAN, E.L. (1954). Discrimination reversal to a sign. *J. exp. Psychol.* *48*, 143-145.

ROCK, I. (1965). Adaptation to a minified image. *Psychon. Sci*, *2*, 105-106.

ROCK, I. (1966). *The Nature of Perceptual Adaptation.* London: Basic Books Inc.

ROCK, I., GOLDBERG, J. & MACK, A. (1966). Immediate correction and adaptation based on viewing a prismatically displaced scene. *Percept. Psychophys.* *1*, 351-354.

ROCK, I. & HARRIS, C.S. (1967). Vision and touch. *Scient. Am.* *216*, 96-104.

ROCK, I. & VICTOR, J. (1964). Vision and touch: an experimentally created conflict between the two senses. *Science, N.Y.* *143*, 594-596.

RUCH, T.C. (1951). Motor Systems. In S.S. Stevens (ed.), *Handbook of Experimental Psychology.* London: Wiley.

RUSSELL, D.G. (1976). Spatial location cues and movement production. In G.E. Stelmach (ed.), *Motor Control: Issues and Trends.* London: Academic Press.

SIEGEL, S. (1956). *Nonparametric statistics for the behavioural sciences.* New York: McGraw Hill.

SIIPOLA, E.M. (1935). Studies in mirror drawing. *Psychol. Monogr.* *46* (*6*, Whole No. 210), 66-77.

SIQUELAND, E.R. & LIPSETT, L.P. (1966). Conditioned head-turning in human newborns. *J. exp. child Psychol.* *3*, 356-376.

SKINNER, B.F. (1938). *The Behaviour of Organisms.* New York: Appleton-Century-Crofts.

SMITH, K.U. & SMITH, W.M. (1962). Perception and Motion. Philadelphia: W.B. Saunders Co.

SNYDER, F.W. & PRONKO, N.H. (1952). Vision with spatial inversion. Kansas: Univ. of Wichita Press.

STARCH, D. (1910). A demonstration of the trial and error method of learning. Psychol. Bull. 7, 20-23.

STRATTON, G.M. (1896). Some preliminary experiments on vision without inversion of the retinal image. Psychol. Rev. 3, 611-617.

STRATTON, G.M. (1897a). Vision without inversion of the retinal image. Psychol. Rev. 4, 341-360.

STRATTON, G.M. (1897b). Vision without inversion of the retinal image. Psychol. Rev. 4, 463-481.

STRATTON, G.M. (1899). The spatial harmony of touch and sight. Mind, 8, 492-505.

TAUB, E. (1968). Prism compensation as a learning phenomenon. In. S.J. Freedman (ed.), The Neuropsychology of Spatially Oriented Behaviour. Homewood, Ill: Dorsey Press.

TAUB, E. & BERMAN, I.A. (1968). Movement and learning in the absence of sensory feedback. In S.J. Freedman (ed.), The Neuropsychology of Spatially Oriented Behaviour. Homewood, Ill: Dorsey Press.

TAUB, E. & GOLDBERG, I.A. (1974). Use of sensory recombination and somatosensory deafferentation techniques in the investigation of sensory-motor integration. Perception, 3, 393-408.

TAYLOR, J.G. (1962). The Behavioural Basis of Perception. New Haven: Yale Univ. Press.

TEMPLETON, W.B., HOWARD, I.P. & LOWMAN, A. (1966). Passively generated adaptation to prismatic distortion. Percept. mot. Skills, 22, 140-142.

TEUBER, H-L. (1961). Sensory deprivation, sensory suppression and agnosia: notes for a neurologic theory. J. nerv. ment. Dis. 132, 32-40.

THOMSON, J.A. (1977). Maps, programs and the visual control of locomotion. Unpublished Ph.D. thesis, University of Edinburgh.

TINBERGEN, N. (1951). The Study of Instinct. Oxford: O.U.P.

UHLARIK, J.J. & CANON, L.K. (1970). Effects of situational cues on prism-induced after effects. Percept. Psychophys. 7, 348-350.

WALK, R.D. & BOND, E.K. (1971). The development of visually guided reaching in monkeys reared without sight of the hands. Psychon. Sci. 23, 115-116.

WALLACH, H. (1968). Informational discrepancy as a basis of perceptual adaptation. In S.J. Freedman (ed.), The Neuropsychology of Spatially Oriented Behaviour. Homewood, Ill: Dorsey Press.

WALLACH, H., KRAVITZ, J.H. & LINDAUER, J. (1963). A passive condition for rapid adaptation to displaced visual direction. Am. J. Psychol. 76, 568-578.

WARREN, J.M., ABPLANALP, J.M. & WARREN, H.B. (1967). The development of handedness in cats and rhesus monkeys. In H.S. Stevenson, E.H. Hess and H.L. Rheingold (eds.), Early behaviour: comparative and developmental approaches. New York: Wiley.

WATSON, J.S. (1966). The development and generalisation of "contingency awareness" in early infancy: some hypotheses. Merrill-Palmer Quarterly, 12, 123-135.

WEINSTEIN, S., SERSEN, E., FISHER, L. & WEISINGER, M. (1964). Is reafference necessary for visual adaptation? Percept. mot. Skills, 18, 641-648.

WELCH, R.B. (1971). Discriminative conditioning of prism adaptation. Percept. Psychophys. 10, 90-92.

YACHZEL, B.R. & LACKNER, J.R. (1977). Adaptation to displaced vision: evidence for transfer of adaptation and long-lasting aftereffects. Percept. Psychophys. 22, 147-151.