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Craske, Brian

Craske, Brian (1963) *An analysis of human adaptation to prismatically displaced vision*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8816/

An Analysis of Human Adaptation to Prismatically Displaced Vision

by Brian Craske

A Thesis Presented for the Degree of
Doctor of Philosophy

Acknowledgements

I wish to acknowledge the many people who have been of assistance in the preparation of this thesis, particularly:

Professor F. V. Smith for the opportunity of working in his Department, and for the particularly generous laboratory space and facilities which were made available.

Dr. I. P. Howard, who interested me in these problems.

W. B. Templeton, with whom many ideas were discussed.

The many colleagues and friends amongst the staff and students of the University who have lent assistance, especially Miss S. J. Gregg, and B. P. Moulden, and all those who have acted as subjects.

Lastly my wife Janet, for the many ways in which she has contributed.

I am indebted to the Science Research Council for financial support during my post graduate studies.

Abstract

Experiments were undertaken on prism adaptation in humans. Two treatment conditions were used. The restricted, where only localising movements of the arm were allowed and the free situation, where the subject was free to walk about.

In the first situation:

a) Adaptation takes place in effect at the level of the position sensors of the used joint. This is a change in felt limb position.

b) Movement of the joint is a prerequisite condition.

c) The sensory channel feeding in the error information is a passive instrument.

d) Adaptation does not affect automatic movements: these take place without using information about joint position.

In the second situation:

a) Adaptation takes place in the positioning system of the eye; i.e., a change in the appreciated eye position.

b) This form of adaptation takes place when the limbs are inspected, with or without repeated voluntary positioning movements of the eye. Immobility of the limbs favours this type of adaptation, but it will occur when gross limb movements are taking place.

c) Ambulatory experience is unnecessary to the generation of eye position adaptation.

It is concluded that the dichotomy between restricted and free situation is not fundamental. The experiments are consistent with the idea that the fundamental factors are: how long the subject sees his limbs, and whether the limbs are moving or not. Joint sense is more labile than the eye control system and a change in the former is probably an emergency response of the system.

The restricted situation will normally lead to joint adaptation if the limb is moved. If limb movement is not undertaken, there will be adaptation of internally registered eye position. In the free situation, used limbs will adapt rapidly, followed by a gradual take-over of adaptation by the system controlling appreciated eye position.

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Part I. Introductory.

Section 1

The General Statement

The ideas presented in the General Statement on the process of adaption to prisms represent general conclusions drawn from the work published up to February 1967, and from the experiments carried out for this thesis.

In the course of the General Statement, no references to published work in the field will be given in order to assist clarity of presentation. Any major experiment which is part of this thesis is given in brackets at the end of the relevant paragraph.

The General Statement will be in two parts, each part corresponding to the distinction drawn about the adaptation situation in the introduction.

Part a: Adaptation in the restricted situation.

Part b: Adaptation in the free situation.

a) Events associated with adaptation in the restricted situation

In this situation, the subject remains immobile with the exception of the limb which is being used in the adaptation procedure. Typically his head is secured by a dental wax bite, and the prisms are mounted in a holder close to the face. The subject is asked to point at one or more visual targets, and only receives knowledge of results at the termination of the excursion of the limb.

The evidence strongly supports the idea that the end result of this sort of training is to change the positional relationship between the used segment and the one adjacent, that is, adaptation takes place in effect at the level of the used joints. For example, a subject who is holding his adapted arm at 90 degrees to the coronal plane, behaves as if it were at 80 degrees to this plane. (Experiment 2a)

The course of restricted situation adaptation is hypothesised to be as follows. The location of the target is perceived visually; since the starting position of the arm is known from the output of the receptors in the joint capsule, an appropriate time-force pattern of outflow to the muscles to start and stop limb excursion can be generated. This is produced on the basis of the visually known 'desired position' and the kinaesthetically known starting position. As soon as knowledge of results is obtained, the subject sees that this movement is not effective in reaching the 'desired position'. The suggestion is made that a change in transfer function of joint receptor output is made as if it were necessary to preserve the normal time-force pattern appropriate to moving the limb from the kinaesthetically known starting position to the visually perceived desired position. Such a change in the 'felt' arm position means that the system can operate as if the limb were really in an altered position and produce the motor outflow time-force pattern appropriate to this.

A change in felt arm position occurs with each trial, and in a direction which minimises the error of localisation until the imposed distortion is nullified, and the arm can be accurately moved to the visual target. This hypothesis might be taken to imply that at no time does the subject produce a motor outflow time-force pattern which is different from that normally required by a limb felt to be in one position, and required to achieve another position which is visually indicated. On the idea that adaptation is a response brought about in a matter of seconds, and that it is not a necessary result of longer term adaptation experiments in the free situation, it could be argued that this form of adaptation is quite a common emergency response of the system.

Finally it must be noted that a fundamental premise about the adaptation process is that it is concerned with the position senses; thus in the restricted condition the appropriate position sense is that of the limb, and it is assumed that this is based on <u>afference</u> from the used joint, not efference to the muscles.

b) <u>Events associated with adaptation in the free situation</u>

After putting on the prism spectacles, the subject is asked to walk about. The space perceived by the subject is asymmetical about his median sagittal plane, and since the goal for which he is making is often objectively straight ahead, e.g., a door at the end of a corridor, he has the choice, either of turning his eyes to one side, or of turning his head to one side in order that the object is fixated. Since this latter is noticed considerably less than the former, holding the head skew to the body will be the first occurrence. This can lead to a change in the subject's perceived orientation of his head on his shoulders. (A fuller explanation of why the head is held skew on the shoulders appears in subsidiary experiments 7a and 7b).

In terms of the final adapted state, the ambulatory experience is <u>not</u> considered important, the prime factor associated with the free situation is that the subject has many opportunities to see parts of his own body, more especially the extremities of his limbs, the position of which is known kinaesthetically. The position of his limbs as understood via the visual channel will be considerably different due to the imposed distortion. The end result of prolonged exposure to this discordant input is a recalibration of the positioning system of the eyes. It is argued that this change is on the efferent side and is such that, for example, symmetrical innervation of the medial and lateral rectus muscles is interpreted as the eye pointing to one side. (Experiments 6, 7 and 8).

Before full adaptation of the eye positioning system has taken place in the free situation, an intermediary stage will occur when the 'emergency response' of adaptation at the level of the joint has occurred within the most seen limb, (normally the preferred arm), as well as some adaptation of the eye positioning system. Thus, after a limited exposure time a greater prism after effect is expected when reaching with the most seen arm than with the contralateral arm.

Section 2a

Introduction

Adaptation to Prismatic displacement: Preliminary remarks.

Czermak, (1863) was the first to observe that if prisms are worn in front of the eyes, and a reaching movement is made to a nearby object, the result of this movement is in error and the hand grasps to one side of the object. It must be noted, however, that this is true only if the observer makes fast or ballistic movements of his limbs. If he took care to move more slowly and visually guide his limb it is clear that no error of reaching would be made. Helmholtz, (1962), further noted that the mis-reaching becomes less with practice, and very rapidly nearby objects are reached for correctly. However when the prisms are removed, mis-reaching occurs in the opposite direction to the original error.

This compensation for the lateral displacement imposed by the prism, such that correct reaching becomes as natural and automatic as in the normal world, will be called 'adaptation to prisms' or very often merely 'adaptation'. The concomitant fact of misreaching in the opposite direction subsequent to training trials and after removing the prisms, will be called the 'prism after effect'.

The terms 'restricted situation' and 'free situation' will indicate adapting procedures which seem to be related to the mechanism responsible for the observed adaptation. The first is typically one in which the observer is held immobile and is allowed to move only one limb to point at a target; and only when the reaching movement is complete does he get knowledge of results. The latter situation is one in which the observer wears the prisms like spectacles, and is allowed to move about freely. It must be made clear that there are other distortions of objects seen through the prisms which are not the prime consideration of the experiments to be reported here. However the fact that there is a change in angular magnification of the image in the base apex meridian with lateral angle, (Ogle, 1951), has necessitated that whenever possible visual targets have occupied a relatively small visual angle. The two other main distortions of the image due to plane surface ophthalmic prisms are respectively curvature of vertical lines, and colour fringes to objects. Both these effects are ignored for the purposes of the investigation for the following reasons. Concerning the first case each subject makes localisations in one horizontal plane, and ideally is using only a small sector on either side of the centre of the base-apex (right-left) meridian of the prism, and not using vertical eye movements at all. As for colour fringes, since the concern is that of localisation of visually perceived targets, we may dismiss their effect as negligible compared to errors of measurement, since at worst they would affect visual acuity, which is not a factor in gross localisation procedures.

In experiments where the observer who is wearing prismatic spectacles is allowed to move around freely, one other effect on the image is noted, namely that as he rotates his head about a vertical axis, rigid objects will undergo lateral contraction as they come into view from the base side of the prism, and expand as they move apexward. An analysis of these effects can be found in Taylor, (1966). There is no doubt that such shrinkage and expansion of the world is adapted out with prolonged exposure, and both Erisman and Kohler have reported considerable after effects of this sort, (Kohler, 1964). After taking off wedge prisms, Kohler observed that the walls seemed more curved than before removing them, but in the opposite direction. Likewise he reported that as soon as he moved his head, any object was apt to become smaller or larger. The world behaved in exactly the opposite fashion to that which he observed when he first started wearing the prism spectacles, and this includes the appearance of illusory colour fringes, (Kohler, 1964). Since this latter appears to give differential adaptation in proportion to relative target luminance, Hay, Pick and Rosser, (1963), have hypothesised that the colour fringe adaptive response is mediated by the sort of mechanism which subserves colour contrast.

The above is sufficient to illustrate that there are many distortions due to wearing prisms which can adapt out with exposure, and that it is likely that the explanations of these adaptive effects will involve many of the processes associated with the visual pathway. It must be made clear that these distortions and associated adaptations form no part of the investigation to be reported. To a great extent the same is true of adaptation to the inverted and reversed vision first reported by Stratton, (1897), and subsequently investigated by Ewert, (1930, 1936, 1937), Peterson and Peterson, (1938), Snyder and Pronko, 1952, and Kohler, (summary of all reports, 1964). The major reason for excluding this form of adaptation is that in these situations success at one skill does not transfer to other skills. For example, Taylor (1962), found that training on one visual-motor task was specific to that task, e.g., walking around an obstacle, and did not transfer to others, e.g., riding a bicycle. This is contrary to the situation observed subsequent to adaptation to laterally displacing prisms in the free situation, in which a fully adapted subject finds it just as easy to pour tea as to climb stairs or ride a bicycle. Thus the argument is that in many ways adaptation to inverting and reversing spectacles is qualitatively different to that of lateral displacement, and probably involves the efferent pathway a good deal more, (Sperry, 1947). What points there are in common with adaptation to lateral displacement are more likely to become clear as the mechanism for the latter is more fully understood. This is preferable to attempting a synthesis at an early stage which is likely to lead to confusion rather than clarification. It is possible to say at this stage, however, that the resemblance of restricted situation adaptation to adaptation to inverted and reversed vision seems no more than superficial, for the former is consistent with the idea of adaptation occuring on the afferent side of the control loop, (see the General Statement), while the latter would seem to be associated with the efferent side.

There are two other exceptions to the content of this thesis; one is that no attempt will be made to include all experiments involving infra-humans exposed to distortions as a matter of course. The criterion for inclusion will be that the experiment is germane to the issue in hand, and is productive of ideas. The second exception follows from the fact that some adaptive effects may be produced by visual asymmetry alone, and by the plane of artefacts objectively normal to the median plane being apparently rotated, (Bruell and Albee, 1955; Harris, Harris and Karsch, 1966). These effects do not have as prerequisite conditions either positional discordance or error reduction, and have not been investigated here since they appear to form a sub-category of effects reasonably distinct from those which are the subject of this thesis.

2b. The nature of the problem

The term adaptation when used in the context of prism experiments has blanket coverage, but it is clear that any analysis of human adaptation in these situations must be made in the terms of questions of the form, 'Are we looking for one adaptational mechanism or many? Do different procedures lead to adaptation of a different part of the system?' It would clearly be dangerous to assume that adaptation was a unitary phenomenon, and then seek for its nature. Thus the modus operandi of the pre-investigatory search has been to put conflicting experimental results into different categories, and then to see if appropriate linking explanatory hypotheses could be erected.

Closely related to the question of the mechanisms subserving adaptation, is that of the pre-requisite conditions for adaptation to take place. It will be necessary to enquire as to the sort of error input which the observer is using in order to adapt; the sort of movements he is using, whether active or passive, ballistic or visually and kinaesthetically monitored.

An ordering of the type of experimental conditions used by other investigators relates to type of error input and type of responses allowed; and it is hypothesised that these may bring into operation different adaptational mechanisms.

Briefly then the aim of the investigation is to be able to throw light on the question, '<u>what part of the system adapts, and under what circumstances?</u>'

In breaking down the prism wearing situation, it is immediately apparent that we are concerned with adjustment of localising ability. Now in order to locate a visually perceived distal object by pointing, the human system must have usable information as to the position of the eyes in the head; of the head on the shoulders; and of the arm on the trunk. In other words, it is necessary to make clear the mechanisms responsible for the position sense of the eyes and the limbs, and since voluntary movement is also concerned in these localising activities, we are in effect interested in muscles, joints, and motor outflow.

It follows that if these are the mechanisms of localisation, then changes in these may well be the changes which we call 'adaptation to prisms'.

Before considering human position sense, however, it would be useful to review some of the findings of the effects of wearing prisms on human behaviour.

2c. Commonly observed effects of wearing laterally displacing prisms

The necessity for knowledge of results must be noted. If an observer is placed such that he can see a visual target which is prismatically displaced by a certain number of degrees, and is asked to point at it without being allowed to see his limb, then he will continue to point in error by a constant amount and no adjustment will take place. If it is supposed that there is only one target mounted in the median sagittal plane of the observer, then it can be seen that no adaptation is taking place despite the fact that his eyes are turned from their primary position by an amount corresponding to the power of the prism. This has been the experience of the investigator, and doubtless of others, but probably because it accords well with common sense, no report of this effect has appeared in the literature. However, there is one report where adaptation to the extent of 40.5% took place when it is claimed there was <u>no</u> knowledge of results, (Wooster, 1923). She tries to explain the result as 'unconscious adaptation' due to kinaesthetic information from the eye muscles. Howard and Templeton, (1966), interpret this as meaning that the subject came to behave as if the eyes were pointing straight ahead. However there is no evidence that there is usable kinaesthetic feedback from the eyes; this will be discussed in Section 4c. Secondly, experiment 8b shows that there is no effect on the voluntary straight ahead of the eyes after prolonged periods of maximum asymmetrical convergence. It would seem that the explanation of Wooster's result (it not having been repeated) must be either that there was some kind of error input, (for example, the subjects could know what the room <u>really</u> looked like), or possibly it could be a subsidiary effect such as that due to visual field asymmetry as reported by Bruell and Albee, (1955). It is certainly true that the world as viewed through prisms is distinctly asymmetric; with base right prisms, the field of view to the right of the median sagittal plane is several times greater than that to the left.

A finding which is surprising when first encountered, is that in a restricted experimental situation where one arm is used to reach for a visually deviated target, the prism after effect does not transfer to the unused limb. This is now well substantiated for humans, (Cohen, 1963, Harris, 1963, Hay and Pick, 1966, McLaughlin and Bower, 1965a, McLaughlin and Rifkin, 1965, Mikaelian, 1963), and for monkeys, (Hamilton, 1964). It must be noted however that Lund, (1965), found significantly altered reaching with the untrained arm of immature rhesus monkeys. It can be plausibly argued, however, that this reflects the fact that free head movements were allowed, a factor which has been found to produce altered reaching in the unused arm (Hamilton, 1964b; Harris, 1963b). It is interesting to note that Helmholtz, (1962), who presumably did not trouble to immobilise his head, reported that while wearing prisms the unused hand could locate targets, 'with perfect certainty and precision'.

The explanation as to why 'intermanual transfer' should occur in situations where the head is not immobilised will be presented later. It is puzzling to Howard and

Templeton, (1966), that transfer from trained limb to untrained limb occurs in this situation, and yet not in one which is possibly similar, that of mirror drawing. They argue that 'there is no obvious reason why' this should occur. However, if one argued that mirror drawing was a skill based on strategies about tackling the problem and control of efferent commands, and that prism adaptation in the restricted situation was none of these things, the problem is nearly resolved. Both Hamilton, (1964a), and Harris, (1963a), have put forward evidence that restricted situation adaptation is explained by a change in felt position of the used limb. Such a mechanism constitutes a sufficiently good reason to account for the difference between mirror drawing and prism adaptation. The weight of evidence for a 'proprioceptive change' as Harris calls it is discussed in the introduction to experiment 2a, and throughout Section 3 of this thesis.

Very little stress has been placed on the need for the observer to <u>try</u> to reach the target in restricted situation prism training situations. In fact if he does not, then adaptation does not take place; or if it does, it is exceedingly slow. However, it is considered that it is not a true reflection of the situation to go on to maintain that a 'conscious effort' is necessary to adapt, which would suggest that we have conscious control over the feedback system responsible for adaptation - a patent falsehood insofar as we cannot adapt unless we are placed in a situation which calls for it. A more sensible way of looking at this fact, it is argued, is to assume that the observer can ignore error feedback. If he chooses to take notice of the error, he is then faced with correcting the resultant misreaching. Here it is being stressed that even though subjects have to try to be accurate, the process of adaptation is not under conscious control.

It might be argued that the whole business of adaptation is no more than modifying voluntary movement. That is, after the first mis-reach, the subject operates on the basis of some such rule as, 'In future I must aim my hand four inches to the right of the place I would normally send it'. However, such a rule would predict that as soon as the subject took off the prisms, he would be able to point correctly without difficulty, this has been repeatedly shown not to be the case, for example, by Hamilton, (1964b), Harris, (1963a), Held and Hein, (1958), Kohler, (1953).

When a subject's head is not immobilised, or he is allowed to move freely while wearing prisms, then he subsequently points incorrectly with both arms, (Bossom and Held, 1957). Harris, (1963a), indicates that even in the situation where head immobilisation is partial, (i.e., in situations where a chinrest was used rather than a dental-wax bite), there was some 40% transfer of adaptation between limbs. An explanation for this is suggested in the final conclusion. What must be made clear at this juncture, however, is that the two types of adaptation situation, (restricted and free), very likely produce adaptation in different parts of the system. For example, the fact of altered pointing with the unused arm need not implicate the arm at all. There is evidence that there is no activity in muscle units in the unused limb when the contralateral limb is moved, provided the load is not abnormal, (Gregg, Mastellone and Gersten, 1957). Hence it is difficult to believe that adaptation has occurred in the limb when there has been no activity in any part of the system controlling its movements, and therefore no change in joint angle which is in any way connected with the movement produced by the active arm. Thus on most views of adaptation, implication of the unused arm as such is unlikely.

Hamilton, (1964b), when considering the reason for the unused arm showing a change in reaching behaviour which was less than half that of the used arm, put forward the idea that this may be ascribed to 'the neck implication', i.e., the appreciated position of the head on the shoulders. This is certainly a possibility; if the head was thought to be pointing straight ahead with respect to the shoulders while in fact it was to one side, then the unused limb would reflect the amount of this error, while the used limb would reflect this plus the amount of adaptation which was limb specific. This proposal has also been made by Harris, (1963a), and Mittelstaedt, (1964).

Further weight is lent to this point on considering Kohler's, (1964), observation that subjects who wore prisms in a 'free' situation developed the habit of holding the head at some six or so degrees to the median sagittal plane without being aware of it.

A discussion of the probable reasons for unnoticed change in head orientation in the free situation appears in the introduction to subsidiary experiments 7a and 7b. Hein, (1965), has taken this one step further and shown that if subjects are asked to hold their heads to one side for ten minutes, (no prisms being worn), they subsequently pointed incorrectly at visual targets.

It seems quite likely that such a factor as misperceived head orientation could account to some extent for changes in egocentric orientation, (Held and Bossom, 1961), and for changes in pointing behaviour. That this is not the most important factor is made clear by experiments in Section 6 of part 2.

The last general finding to be considered is that of 'inter-ocular transfer'. Cohen, (1963), using a restricted situation showed that after effects on a pointing task were identical for each eye separately when only one eye was exposed to the distorting conditions during training; Pick, Hay and Pabst, (1963), report a similar observation. Hajos and Ritter, (1965), have also shown 'complete readjustment' of the unexposed eye; however their conclusion that, 'transfer of spatial displacement from prism eye to covered eye is approximately perfect' shows a failure to appreciate the limb specificity of adaptation in the restricted situation. Thus if 'hand-eye recalibration' is at all an appropriate way of describing the end result in such a situation, it is argued that it is not the 'eye' part of the system which is affected. Hamilton, (1964), reinforces this view with his work on monkey, in which he showed that both normal and midline section animals, (cerebral and midbrain commisures and other structures), showed normal adaptive ability with all eye hand combinations.

That lack of intermanual transfer can be conveniently thought of as due to something like a change in the felt position of the used limb has already been indicated, and it is clear that such a view would predict perfect 'interocular transfer' in that the eyes are fulfilling the function of a passive spatial data feed. Hence on this view and in these situations, the term 'interocular transfer' is a complete misnomer.

By the same token, in the free situation where intermanual transfer takes place, the explanation of interocular transfer, which also occurs, could well be quite different. In fact implication of the eye positioning system as generating both these findings seems a possible and likely hypotheses. The work of Lund, (1965), using monkeys which were allowed head and trunk movements, (which puts them into the 'free' not 'restricted' category), shows that under these conditions the degree of interocular transfer is altered by optic chiasma and midline cerebral commisure section, which indicates an involvement of the visual system.

Section 3

Detailed Discussion of Certain Contributions to the Area of Prism Adaptation

The following section is devoted to a consideration of the ideas and experiments which now form the core of the work in the area of adaptation to prisms.

3a. Harris

Harris has presented a number of ideas and experiments in this area primarily drawn from his doctoral thesis, (1963a, 1963b, 1964, 1966). He reviewed and interpreted the work in the field, (1965), contributed to the literature on right left reversal, (Harris & Harris, 1965), and has put forward ideas which help clarify the reasons for a number of apparently conflicting results, (Harris, Harris and Karsch, 1966). The following account is drawn from these sources.

His basic testing situation used subjects who were not wearing prisms and who sat with immobilised heads in front of a table with a transparent top. They were tested for accuracy of pointing at five visual targets on the table top without knowledge of the results, (the table was covered with a cloth). Alternatively they were asked to point at the source of a click with eyes shut, or were asked to put their arm straight ahead. His training situation involved pointing to visual targets while wearing prisms, with subsequent visual knowledge of errors of pointing.

The results of all these experiments were that the effects of adaptation transferred to the same extent to pointing to all targets, whether visual, auditory, or the judgment of the straight ahead. A further finding was that the effect did not transfer to the unused arm. It was also found that the apparent straight ahead of an auditory target was not affected. This evidence all strongly supported the thesis which Harris was putting forward, namely, that adaptation to prisms was due to a 'proprioceptive change'. More specifically Harris says that 'the subject comes to feel his arm is where he saw it through the prisms'. On the basis of these results, Harris claims that an alteration in visual perception cannot be an appropriate explanation of adaptation, and nor could a conscious correction of pointing. This would seem a reasonable conclusion.

Harris's subjects adapted on only one target, and yet showed an equally large adaptive effect when pointing to targets four and eight inches on either side of this. He claims that this response generalisation shows that the adaptive effect is not due to motor learning: i.e., is not due to substituting a new motor response in order to achieve the desired position. That motor learning is not the explanation has considerable support in experiments which show errors of pointing when the unadapted arm points at the adapted, (Efstathiou and Held, 1964, Goldstein, 1965, and Experiment 2a). However, contrary to Harris's result, Goldstein, (1965), and Sekuler and Bauer, (1966), indicate that varying the starting position of limb excursion can have a significant effect on amount of adaptive shift; but this does not mean that a motor learning factor has to be incorporated. A more satisfying explanation, (that it is a result of receptive angle of joint receptors), is put forward in the Discussion.

Another experiment reported by Harris uses the technique of magnitude estimation. The subject's adapted arm was passively moved, while the unadapted arm could be moved actively in order to make the distance between the finger tips correspond to some figure called out by E. This technique generated results which showed a change in the distance apart which the hands felt. The significance level of the mean results before and after adaptation was at the level of .01, which indicates that the change in the felt position of the arm is a powerful effect. The argument is put forward however that the technique of magnitude estimation is a weak one, (Brindley's type B), and that the experiment was badly designed in terms of the criterion that an experiment should test primary and not secondary events associated with the phenomenon under investigation. On consideration of the training technique used in this case, a change in felt position of the arm would be expected to be mediated primarily by receptors in the shoulder joint, and yet in the test for the after effect, passive movement which was predominantly about the elbow was used. Additionally, the subject was allowed independent movement of the fingers when making final adjustments to the judged distance. It is clear that these factors will tend to minimise differences, not show them up.

Held and Bossom, (1961), observed that subsequent to a treatment condition in the free situation, subjects displayed intermanual transfer of after effects and called objects straight ahead when they were off to one side. Harris explains this by the idea that the measured adaptation in the unadapted limb results wholly from adaptation of the felt position of the head on the body. But also presents the competing idea that the results might equally well be due to a change in the registered relationship between eyes and head. Now Harris puts neither explanation forward as being more likely, or more important, nor are the prerequisite conditions for the occurence of either discussed at any length. One suggestion which was made was that the change in the appreciated position of the head on the body was due to moving the head. However it is difficult to see in what way movement of the head can generate such an effect. The hypothesis put forward in the general statement of this thesis is that such a change in the norm for the appreciated head position is due entirely to holding the head to one side, and is of the same class of events as the postural effects noted by Jackson, (1954), and perhaps of kinaesthetic figural after effects. It is also suggested that this is a minor effect.

Concerning the idea of change in the appreciated eye position, Harris makes the point that such a misperception is of the same general kind as misperception of limb position. It is indeed the case that adaptation of this sort is not in any way like colour adaptation, or dark adaptation, i.e., change in appreciated eye position is not a retinal phenomenon, (experiment 8a).

What Harris misses is the important role of change in appreciated eye position as the primary mode of prism adaptation in the free situation. This is brought out very clearly by a view often expressed in his published work. For example, 'where vision and position sense provide conflicting information about where the subject's hand is, the (limb) position sense yields immediately and rather completely'. However experiment 8c shows that in the free situation, adaptation of the appreciated position of the eye accounts for the sort of pointing errors observed, which illustrates that Harris' contention is too general.

The extent to which Harris sees 'proprioceptive adaptation' as fundamental is further indicated by his analysis of the results which Stratton, (1897), obtained after wearing a device which inverted and reversed the optical array. He argues that the adaptation is proprioceptive and not visual, for since the subject felt his legs to be where he saw them, he was acting as if his head and shoulders were inverted. Again, commenting on experiments where the visual field is inverted, Harris maintains that the subject adapts by coming to feel that legs and body are on the other side of his eyes; and in the reversed visual field situation, the subject comes to feel that the right hand and the right side of the body are nearer to the left eye than the right eye.

The general criticism to this analysis is in the form of a question. What can such changes in feeling mean? They cannot be the same kind of change which constitutes the basis of restricted situation adaptation to prism displacement, which can sensibly be thought of as a change in sensed angle, (see General Statement). No such meaning can be given to a feeling that the right hand is under the left eye. Although these observations by Harris may furnish some ideas about mechanisms subserving these adaptations, these mechanisms are unlikely to be couched in the relatively simple terms of a change in the transfer function of joint receptor output.

It is possible that Harris may well have been confused by his use of the verb 'to feel', this may be instanced by an example from a recent publication, (Harris and Harris, 1965). The subject was asked to doodle while viewing his hand through reversing prisms, Harris reports that the subject eventually <u>feels</u> his arm to be moving in the direction it looks to be moving. It is here argued that this feeling of appropriateness when moving the arm is not served by the same mechanisms as the feeling that the arm is in a given place. The former could, for example, be a reversal of the right-left 'value' given by the system to the motor volley which is moving the arm; and the latter by joint receptors. It seems reasonable to argue that it is an overextension of the hypothesis to explain newly appropriate movement-feelings as an proprioceptive change. The conclusion of this argument then, is that although it is agreed that 'proprioceptive change' may well underlie restricted situation adaptation, it is a wrong approach to assume it is primary to all or most of prism adaptation. Experiments will be reported which indicate that in the free situation adaptation of the appreciated position of the eyes is the result. It is therefore necessary to qualify the statement, 'after seeing your hand through prisms, you feel that your hand is displaced relative to your body', (Harris, 1966). The necessary qualifications are to add, 'in the restricted situation' and to substitute arm for hand, (see experiments 2a and 2b).

3b. Hamilton

In his thesis, (Hamilton, 1964a), experiments are described on both split brain monkeys and normal humans. In general, his results and conclusions cohere very well with the mechanisms of adaptation put forward in the General Statement.

It was found that normal monkeys could adapt as readily as humans; and this was equally true for monkeys with surgically separated hemispheres, irrespective of whether the practised eye and arm were represented in the same or opposite hemispheres. It was also shown that if the animal was adapted using one eye, there was no decrement of adaptation exhibited when the visual information was derived through the other eye, (see also Bossom and Hamilton, 1963). In the case where only one arm was used in the training situation, adaptation was restricted to that limb. However in some cases generalisation of adaptation to the unpractised limb occured, Hamilton suggested that in this situation the critical factor was the kind or amount of movement allowed the animal. This was considered further in a later publication, (Hamilton, 1964b). Two groups of human subjects were used, one group of which wore prism goggles which allowed unrestricted head movements, and another which looked through a fixed prism. Both groups adapted using the Held and Gottleib, (1958), technique. The results showed no intermanual transfer in the restricted situation, and considerable transfer in the non-restricted situation. The arm used for adaptation, however, showed a greater prism after effect than the unused arm. From the General Statement it can be seen that this would be explained by a combination of change in the felt position of the limb used for adaptation, plus change in the appreciated position of the eyes.

Hamilton, however, thought that a prerequisite condition for this 'transfer' was due to the increased stimulation from movement and kinaesthetic feedback. This adaptive technique, he thought, may generate a change in the sense of position of the unadapted arm, plus further adaptation resulting from changes in the neck implication. It has been argued in the General Statement that the former does occur and that this latter factor exists, but plays a minor role in the observed change in pointing, the possible exception to this is when the subject shows intermanual transfer after looking through fixed prisms.

Hamilton's major confusion lies in his failure to see the restricted and non-restricted situation as being served by a different adaptation mechanism. Thus he continues by arguing that because there was no intermanual transfer in the <u>restricted</u> condition, adaptation does not alter the judged position of the eyes under either condition. Since it can be shown by a direct method that change in judgement of eye position is the result of various adaptation procedures, (experiments 6, 8a, 8c), it is clear that the remainder of Hamilton's argument, (that this lack of adaptation of the eye system correlates well with the evidence for the lack of proprioceptive position-sense for the eyes), must be fallacious. Since the evidence for the above lack of position sense is good, (see section 4c), this makes it all the more evident that position sense of the eye is mediated on the outflow side, and the adaptation shown in the free situation is in the control mechanism responsible for eye position. Thus it is not possible to agree with the contention that, 'adaptive changes affected only those members of the body whose position-sense is determined by information from joint receptors', since this is only one of the adaptive mechanisms.

One of Hamilton's interesting findings is that inter-limb transfer occurs subsequent to prism exposure in the <u>restricted situation</u>, the limbs involved being the legs. The subject lay prone and kick-pointing took place to visually displaced targets. A variety of tests took place after adaptation; pointing without knowledge of results using all four limbs, and a task whereby the erect subject looked at a dot on the floor nine feet away, closed his eyes, and walked to it, (these tests with no prisms). <u>All these estimates of target position were equally displaced</u>, and yet when Hamilton discusses whether there has been a change in the visual localisation of the target, he concludes there has not. His grounds were that when a prism is worn in front of the eyes, errors of localisation on the above tasks are <u>not</u> equal. Now he argues that since a prism induces a constant change in visual information, these unequal errors should also be expected in the former situation if there _had_ been a change in the mechanism of visual localisation.

This is an odd argument, the expected result of changing the signal relevant to eye position by a constant is to affect all localisation estimates based on that signal by a constant, and this was the observed result; strong evidence surely, for a change in appreciated eye position.

The last of Hamilton's contributions to be considered here is that of decay of adaptation. After adapting his subjects they were exposed to one of two conditions, under the first the subjects were allowed to look at one of their hands, (without prisms), which was moved back and forth. Under the second, they merely sat in the dark. In both cases there was a reduction in adaptation as shown by after effect, and the active condition did not show significantly more effect than the passive condition, (Hamilton, 1964a; Hamilton and Bossom, 1964), although in terms of mean effect, the active condition showed a decay of 80%, and the passive of 52%. Cohen, (reported in Hamilton, 1964a), found 'slight loss of adaptation when subjects sat motionless in the dark, moderate loss when either movement or vision were permitted, and most when movement and visual feedback were allowed'.

That decay of adaptation can take place without overt movements taking place seems quite clear. But the reports that decay of adaptation is accelerated by 'movement' alone, and the possibility that viewing the limb does not rapidly generate loss of adaptation are worthy of further examination.

3c. Howard and Templeton

This account of their views on prism adaptation is drawn primarily from chapter 15 of Howard and Templeton, (1966).

The basic idea adopted is to assume that learning to adapt to distorted vision involves a high-level habit substitution mechanism. In terms of their own distinction, this states in effect that the major implication in adaptation is the efferent side of the control system. Thus in criticising the work of Harris who used a stereotyped movement of the arm in the adaptation procedure, the following phrase is noted, 'Small wonder therefore that the recalibration affected the arm and not the eye'. This line of reasoning is carried further by quoting an experiment by Howard, Craske and Templeton, (not reported in the literature) whereby subjects who were wearing prisms had to turn their eyes to their finger in the dark, were then allowed visual knowledge of results, and so on until they could do this task correctly. The after effect showed intermanual transfer. Although it was not explicitly stated, it might have been realised that this was the first experiment which strongly supported change in the felt position of the eyes as a factor in adaptation to prisms. However the emphasis was put elsewhere, namely to support the contention that adaptation was on the efferent side of the system. This was put as follows, 'recalibration occurs only in that part of the system which the training procedure demands'. The hidden assumption here is that voluntary movement is in some way the activator of change, the crucial experiment to test this has still to be done, (see discussion). However, the amount of adaptation produced by this method is no more than that produced by the technique of experiment 7 where no voluntary movement of the eyes takes place at all.

Howard's and Templeton's analysis of the nature of adaptation was hampered by adherence to the tenet that, 'transfer experiments do not provide an adequate criterion for deciding what is meant by the locus of recalibration'. However, it is argued that Mittlestaedt, (1964), is right when he claims that the human localisation system consists of a number of identifiable subsystems. It is further argued that many of these subsystems are within limits functionally autonomous, and thus there is no reason why changes in the behaviour of these subsystems should not be studied, and give answers as to the locus of change.

As an example; intermanual transfer could imply change in appreciated position of the eyes, this could be followed by a direct test of eye positioning. Howard and Templeton on the other hand claim that it is possible to identify affected linkages, and <u>not</u> affected loci.

The view of the process of adaptation which is adopted by Howard and Templeton is as follows. When a subject first starts to adapt his reaching behaviour, he inhibits the normal reaching responses, and substitutes new ones. This eventually becomes automatic, thus all experiments on adaptation should use situations where response substitution must occur.

Now this is merely a variant of the 'change in motor outflow' view of adaptation. That is, it involves the subject in changing the motor outflow to the limb, and thereby making a movement which is more appropriate to the displaced visual input. This is perhaps made more clear in the statement concerning Harris's experiments, he 'failed to consider the change in motor outflow which is probably involved in visual-motor adaptation'. Now what meaning can be given to this proposed change in

motor outflow? Suppose that in an experimental situation the subject at first undershoots, and subsequently learns to 'move his arm further' to be correct. It might seem then, that from a given felt starting position a larger motor volley is being used in order to move the limb to the target in the prism situation. Now if the kinaesthetically known starting position of the limb does not alter throughout the experiment, and no change is suggested in this view of adaptation, the world has expanded as far as the subject is concerned. Thus a larger motor volley is required to move through a given appreciated distance. This would predict that the subject's estimation of angle of limb excursion be affected by adaptation. Subsidiary experiment 6 shows that this is <u>not</u> the case. <u>This is the only manner in which change is motor outflow could explain adaptation</u>, because the alternative is to assume that the kinaesthetically known starting position changes during the course of adaptation, (see the General Statement). If this is so, then the motor outflow <u>cannot</u> change, it must remain the outflow necessary to move the limb from its felt starting position to the target.
If it were greater than this the limb would overshoot, (the adaptive shift of the felt position of the arm, and the increase in motor outflow being summative). This

point was not recognised by Howard and Templeton, because when discussing the possibility of believing the arm was pointing straight ahead when it was in fact off to one side, they comment that, 'it is reasonable to suppose that both kinaesthesis and motor innervation would have been relabelled'. As has been indicated, <u>one can change, but not both</u>, and the evidence suggests that it is kinaesthesis which does so.

Howard, (1965), seems latterly to have moderated his view somewhat in that he argues that response substitution occurs only in the first few corrective hits when the subject consciously moves his arm differently. However he continues to argue that the end products of adaptation are new habits, which does not fit in with the idea that the subject moves his arm from a felt location to a seen one; and that with adaptation the felt location changes through time. For it is clear that the subject already <u>knows</u> what size motor volley should get his arm to the target from that final felt position, (it is the same knowledge that he had before adaptation procedures were begun), and doing something in the same way as he is accustomed hardly constitutes a new habit.

It is interesting to note that Howard has applied a variant of the animal learning technique of discrimination without error to the adaptation procedure; he asks the subject to point at visual targets with knowledge of results, and while the subject is doing this, the power of the prisms is gradually increased. As a result, 'it is possible to train a subject without his knowing that his vision has been displaced'. Presumably as a result of this sort of demonstration, Howard concludes that he does not think that the (hypothesised) response substitution phase is important because it is conscious.

An interesting experiment was carried out by Templeton, Howard and Lowman, (1966), in connection with their ideas on response substitution, but it was an experiment which had wider implications. This involved a situation in which a subject's arm was moved passively until he was satisfied that his forefinger was under a visual target, he was given knowledge of results, and the procedure repeated. Sixteen trials showed adaptation of about 1/3 the prism displacement. It is unfortunate that the post-adaptation test used only the adapted arm. It is possible that this generated adaptation in terms of felt limb position, and to show lack of intermanual transfer would have made the case more watertight. If this was the case, then this experiment constitutes a reasonably strong argument against the position adopted by Held and his co-workers, (for example see Held, 1961), that voluntary movement is necessary for adaptation to take place. It clearly is not a perfect argument against Held's view insofar as there is no measure of the degree to which the subject's arm really was passive. An E.M.G. record showing that muscular activity in the prime movers for horizontal abduction and adduction, (namely the anterior and posterior portion of the deltoid, the corecobracialis, the infraspinatus, and the teres minor), did not rise above resting level, would have made their case much stronger.

Another attack on the need for active movement was an experiment carried out by Howard, Craske and Templeton, (1965). A rod was mounted in the median sagittal plane, but was seen with a two inch lateral displacement. Thus as it was moved forward it appeared as if it was going to hit the subject just under the eye, in fact it hit him in the mouth. Thus the training situation involved no movement by the subject; constant fixation was also used. The result of this training technique was to change the error in pointing at visual targets by about 1/3 the displacement. This experiment is difficult to interpret, it would seem that the only likely adaptation is of appreciated eye position. If this is so, then it means that there are at least two types of information by reason of which adaptation of this sort will occur; the discordant exafferent variety as above, and the discordant positional information from two positional indicators, for example vision and kinaesthesis, (see the General Statement).

3d. Held and his co-workers

These workers have contributed considerably to the area of adaptation and sensorimotor co-ordination in recent years, and with this work has been articulated ideas concerning spatial co-ordination in the neonate, which is claimed to have a common underlying explanation, (Held, 1966). The basic rationale of many of the experiments performed has as its keystone the following views on the role of a specific sort of motor sensory feedback. For the sake of clarity, the background to Held's thesis will be presented fully without comment.

Held's model

Held's model of the process of adaptation assumes that efferent signals to the appropriate limb muscles are monitored in a central memory storage, this storage also receives reafferent feedback from the distance receptors. Since a reafferent signal is an afferent signal which is due to self produced movement, it can be seen that the storage mechanism has access to information about the command signals for movement, and the resultant afference which is directly related to this movement.

Thus the view is adopted that normally any particular signal to the muscles should be accompanied by a unique reafference. The efference and the reafference are assumed to be correlated in the memory storage, and it is an alteration in the correlation of these which is responsible for adaptation to prisms. These notions are an extension of the Von Holst reafference principle, (Von Holst, 1954), and are described in detail in Held, (1961), and Hein and Held, (1962).

It will be seen that natural movement plays a very important role in Held's ideas on adaptation, this can be appreciated more easily from the following sort of analysis. When moving the hand there is a given relationship between the position of the hand and its image on the retina, provided a suitable modification is made to take account of eye and head position. Thus there is a relation between normal movement and visual feedback. Through time a correlation will build up between efferent copy to the limb muscles, and the consequent visual feedback. The process of adaptation is that wearing the prisms alters the visual feedback which is consequent upon a given movement, and new correlations of output signals to feedback will take place. Eventually, the 'newly correlated information becomes available to the nervous system. This invariant order is...... responsible for adaptation to the prism transform', (Held and Freedman, 1963). Thus with full adaptation, the input-output relation of this sensorimotor system becomes identical with that which existed before adaptation. Put another way, the efferent and reafferent information are related to each other in the same way after adaptation as before.

Points about the theory

At this juncture the following two points on the theory must be made. Reafferent feedback from the distance receptors consequent on self produced movement is central to the model. Thus a criticism of Held's model is the fact of passive adaptation which has been shown, (Howard, Craske and Templeton, 1965; Templeton, Howard and Lowman, 1966; Wallach, Kravitz and Lindauer, 1963; Weinstein, Sersen, Fisher and Weisinger, 1964), but this criticism lacks strength, for it will be argued that some at least of these adaptation situations did not produce adaptation at the level of the joint, which is the occurrence under discussion. The major criticism is that adaptation can occur without reafference from the distance receptors. (See subsidiary experiments 3 and 4). The first of these shows that adaptation and after effect occur when the subject never gets visual knowledge of results subsequent to attempting to point to a visual target, but merely has his arm moved to the correct position by E. The second situation has the subject try to point to the visual target, and after this localisation has been made, visual knowledge of results is given following a 30 second time delay. In both cases a large measure of adaptation takes place within a few trials. Kinaesthetic reafference is available in both cases, and is probably fundamental to the adaptation process, but the point being made is that there is no reafference from the distance receptors, and furthermore the level of efficiency of the adaptation process is at least as high as in those situations where such reafference is available.

The second point to be made about the theory is to question whether the use of expressions like, 'commands to the musculature', (Held, 1966), may disguise the facts about the way the limbs are moved. A limb is not moved by a series of motor volleys which cause the muscle to contract and the limb to be dragged along. Rather, for all speeds in excess of about one third the maximum for the segment, the limb is started by one volley, and stopped by another after an appropriate time delay, (Hubbard, 1960). The point being made here is that the efference being fed into the hypothesised 'storage' is to both agonist, (to initiate the movement), and antagonist, (to stop it). Thus there is no simple way to knowing the position of the limb from efference, the storage mechanism will have to interpret a motor outflow time-force pattern, (M.O.T.F.P.) Furthermore, it is quite clear that there are a considerable number of these patterns which will move the limb from one position to another, as many as there are discriminably different rates for limb excursion. The importance of this will be developed in what follows.

Held's experiments in the restricted situation

It is clear that a major prediction from the theory is that active movement is essential for adaptation, and this was the first hypothesis to be tested. This was tackled by asking subjects to mark the position of visual targets without receiving knowledge of results, both before and after an adaptation procedure, (a mirror device was used to achieve this, see Held and Gottleib, 1958). Now in that the same mechanism was hypothesised to underlie both eye-hand co-ordination in the infant, and adaptation to prisms, and because infants acquire co-ordination without error recognition, an adaptation procedure was employed which did not involve recognition of errors in reaching, (Held, 1965). Thus the adaptation situation involved the subject in inspecting his hand through a prism while moving it back and forth through a small arc, the pivot point being the elbow, (Held and Hein, 1958). The findings were that there was a significant prism after effect subsequent to movement of this sort when it was self produced, and none when the same movement had been produced passively, or the motionless hand was inspected. In similar fashion, the necessity for active movement to adapt to apparently changed distance (increased light path), has been shown, (Held and Schlank, 1959).

On the basis of experiments using the active and passive movements as indicated above, (see also Mikaelian and Held, 1964), Held has repeatedly reaffirmed his contention that, 'full and exact adaptation to sensory rearrangement in adult human subjects requires movement-produced sensory feedback', (Held and Hein, 1963), or again, 'We have repeatedly emphasised the production of movement as the prime causal factor', (Held, 1963). Even more specifically, from one of his co-workers, 'Held and his associates have asserted that the information available to the nervous system in the form of its internally monitored efferent output to the musculature together with the concurrent sensory feedback, (reafferent stimulation) is critical for the observed adaptation', (Efstathiou, 1963).

It is now necessary to examine the extent to which these claims may be accepted, and also to look a little more closely at the method of adaptation used. The latter point will be discussed first, and will briefly introduce some of the writer's views on the rationale behind prism experiments.

Discussion of Held's experiments in the restricted situation

It would seem that the 'arm wagging' method of prism adaptation was first used by Held in order to make the situation similar to that which he supposed was used by infants, i.e., no target-to-hand error feedback. Presumably this method has been used ever since in order that this hypothesised link with the development of the neonate be preserved. However observation of a subject adjusting to prism displacement using an alternative system whereby the arm is raised under a board, the finger put under the target, and then visual knowledge of results given, will convince anyone that the method employed by Held is decidedly sub-optimal in both speed of adaptation and magnitude of after effect. For example subsidiary experiment 2 shows 66% of full after effect in 30 seconds, while Held and Hein showed only 33% in three minutes.

In attempting to understand the low efficiency of arm wagging, a point made by Howard and Templeton, (1966), is relevant; they have pointed out a distinction made by Kohler between two types of movement. One is like kicking a football, and another is visual guidance of a limb; this latter is not much disturbed even by Kohler's inverted and reversed visual input situations. Now viewing a hand which is being moved back and forth, which is the essence of the arm wagging technique, is not very different from visual guidance, so relative inefficiency of adaptation might be expected. Further evidence in support of this observation about types of movement comes from subsidiary experiment 1. This shows that when the subject moves his arm from a seen starting position A, to a visual target B, both of which are prismatically deviated, and the experimental set-up is such that his arm disappears from view one third of the way through the excursion, then the distance moved by the arm is very nearly equal to the objective distance A-B. This is quite unlike the result found when the limb is moved from a position not visually indicated, (a 'felt' position), to a visual target. Here the error is of the order of the prism deviation.

Now the former situation has similarities with that used by Held, while the latter is an integral part of the perceived error technique, and it seems quite likely that the former will not yield as much information to the system about the deviation due to the prism as will the latter. Also in support of this contention, Hamilton and Hillyard, (1965), have shown that back and forth movements are less effective than pointing movements in producing an after effect. Freedman, Hall and Rekosh, (1965), have shown the same.

It is a common experimental observation that any moderately competent subject can adapt his pointing behaviour to a single target while wearing 20 dioptre prisms within a dozen or so attempts. It is argued that if adaptation per se is being investigated, then techniques which are most efficient should be used, since by definition such techniques serve to provide the sort of information which the nervous system processes most readily. The 'perceived error' technique outlined above is much more effective than the arm wagging technique, (sample data are presented in subsidiary experiment 2). Thus a criticism of Held's basic experiments in the restricted situation is that for reasons of theory he has used an experimental technique which is not the most powerful in producing the changes being studied. The question now arises as to how this is so.

The hypothesis is put forward that a fundamental difference between the two techniques is that when the finger is seen in the 'perceived error' technique, it is not moving. It may be argued further that in terms of knowing the position of a limb, we are most accurate when it is stationary.

The writer is not aware of any direct evidence that we do not know limb position, or do not know it well, while the limb is moving. However, it is argued that humans certainly have no need to know position while movement is under way, and it is likely that they do not. For example, changes of direction of limb can take place by precisely timed motor volleys, rather than a volley when the limb signals that it is in the right place to change direction, i.e., instantaneous knowledge of limb position is unnecessary. What is more, as Chernikoff and Taylor, (1952), have pointed out, feedback of kinaesthetic information has too great a time lag to be of use in anything approaching ballistic movements of the limb. That motor volleys can be precisely timed is supported by an argument of Lashley, (1951), who has cogently argued that since movements can be made faster than one kinaesthetic reaction time, (while playing the piano, for example), it must be concluded that an effector mechanism can be pre-set or primed to discharge at a given intensity and for a given duration.

It is here being argued that eye and arm position information are important factors, and that it is reasonable to suggest that kinaesthetic information as to limb position is not easily appreciated during movement. Thus the relative inefficiency of the 'arm wagging' technique would be predicted, in fact it might be argued that prism adaptation occurs in Held's situation in spite of his technique rather than because of it.

In his analysis of adaptation, Held neglected the kinaesthetic sense entirely, but is it not more likely that adaptation is intimately concerned with just this; namely the readjustment of relative appreciated positions. Thus adaptation is concerned with the matching up of the visually perceived position of the limb and the kinaesthetically perceived position of the same limb, rather than reafferent visual stimulation due to limb movement correlating with the efferent signal to the muscles of that limb, as in Held's model. This latter is a considerably more roundabout method of arriving at essentially the same information, namely, a visual and a non-visual record of limb position.

The question as to the end point of adaptation in the restricted situation is argued to be a change in appreciated limb position. This may be redescribed in terms of a possible mechanism by referring to the hypothetical construct of change in transfer function of joint receptor output, (Craske, 1966a).

That change in appreciated position takes place in effect at the level of the used joint is capable of direct experimental demonstration, (experiment 2a). But it is quite plain that such a change is not envisaged by Held, and nor is the possibility of such a change predicted by his model. Further, in Efstathiou and Held, (1965), a claim is made that change of appreciated arm position does not occur. However the experimental evidence on which their claim was based was inaccurate, as is shown in experiment 4. A direct result of the experiments which show that adaptation in the restricted situation is due to change in appreciated arm position, is to make implausible an efference-reafference model in this situation. This claim is supported by the illustration that reafference from the distance receptors is not necessary for fast, efficient adaptation in the restricted situation.

However there can be no doubt that Held and his associates have shown that when the arm is wagged passively while being inspected through prisms, no adaptation takes place, (Held and Hein, 1958). This lack of adaptation is not predictable on the strict view that the only important factors are the position senses.

So thus far, the experimental findings are contrary to both the efference reafference view, (because of the fact of change in appreciated limb position), and to the view which stresses position senses alone, (due to the adaptation in the passive movement situation). It is desirable, however, to extend the 'position sense' view further than has been indicated so far. This extension is made in terms of its relation with the motor command in the restricted situation.

Derivation of an hypothesis on the place of motor commands in change of limb position sense

It is certainly the case that when a limb is moved rapidly to a visual target, it is moved from a kinaesthetically known position to the visually known position by means of two motor volleys. That is, one volley to initiate the movement, a time gap during the momentum phase, and one volley to bring the limb to rest, (Hubbard, 1960). This is an efferent pattern, with kinaesthesis not being involved, except to provide information about starting position.

Lashley, (1951), noting the speed with which certain complex movements could be carried out argues that 'there is a control of motor discharge which is independent of duration of excitation'. Within the present context this could be rephrased thus: a motor outflow with a specific time-force pattern (M.O.T.F.P.) is produced. Further, the M.O.T.F.P. can be calibrated in terms of the desired limb excursion. To apply this idea to the prism situation, let us assume that base left prisms are worn, and the subject is bringing his arm in from the right and using only his shoulder joint, the movement being horizontal adduction.

The limb is moved to the visual target from its felt starting position using an M.O.T.F.P. appropriate to that intersensorily perceived distance in the normal world. Since the prisms have, in effect, expanded the world, an error of localisation occurs. Now the system can nullify the error either by producing an M.O.T.F.P. which is larger than that normally used in the situation as it is perceived, as in response substitution, (Howard and

Templeton, 1966), or change the felt starting position. That is either the M.O.T.F.P. gives way and the felt limb position stays intact, or vice versa. It has already been argued that the former change would leave the fully adapted man feeling his arm too far to the right, while seeing it as on-target. Also in the light of the difficulty experienced in developing any new M.O.T.F.P., (i.e., learning a new skill), the former possibility is seen to be both unlikely and unsatisfactory. Likewise it has already been argued that a change in the appreciated position of the used arm does occur.

Thus it would seem that in this prism situation, a plausible argument could be erected to the effect that the system alters as if a <u>change in appreciated limb position occurs in order to preserve the M.O.T.F.P</u>. Clearly with a change in appreciated limb position, the subject can act as if his arm were where it was felt to be, and <u>therefore produce the M.O.T.F.P. which is appropriate to that position and the visually perceived desired position</u>.

This removes the stumbling block of adaptation in the passive situation, for the above view of restricted situation adaptation <u>would predict that none would occur when movement of the limb takes place passively</u>. The requirement is that adaptation at the level of the joint takes place in order to produce a result appropriate to the situation, yet sparing the learnt M.O.T.F.P; thus in the absence of motor outflow, no adaptation at the level of the joint will occur.

It can now be more clearly appreciated why the perceived error technique is more efficient at producing adaptation than is arm wagging, not only is there the argument that knowledge of position is likely to be less good when the limb is moving, but there is the fact that the perceived error situation is <u>considerably less ambiguous</u> to the adapting subject. The components of the situation taken through time are: appreciated starting position of the limb; M.O.T.F.P. to reach desired position as indicated via the visual channel; and a measure of error which indicates directly the direction and amount of error to be nullified. The subject can then 'reset' his system on an informed trial and error basis.

Held's basic experiment in the free situation

The method of egocentric orientation was used, whereby the subject turns himself until a visual target is straight ahead. Errors on such a task were taken both before and after exposure to a prism wearing situation, where the subject walked about in the everyday environment. One hour of such exposure produced an adaptive effect of 10% of maximum, but no adaptation was recorded when the subject was wheeled along the same course in a wheelchair, (Held and Bossom, 1961). The conclusion was drawn that adaptation only takes place when there is self produced movement and consequent reafference. There is no mention of the possibility that this situation utilises a different mechanism of adaptation. For this and the following reasons, their conclusion can be subjected to the severest criticism. First consider self produced movement and reafference.

It has been shown by Templeton, Howard and Lowman, (1966), that a passive movement situation based on a perceived error training technique can lead to an amount of adaptation equal to one third of the optical displacement in a maximum of 16 trials, (this figure is according to Howard and Templeton, 1966).

Experiments 7 and 8a, in which there was no movement of the limbs at all, voluntary or otherwise, and only involuntary eye movements, provide evidence of considerable change in the appreciated eye position, which experiment 8c shows to be the form of adaptation appropriate to the free situation.

The results of Howard, Craske and Templeton, (1965), though in a different situation, showed significant adaptation with no voluntary movement or reafferent input, and those of Weinstein, Serson, Fisher and Weisinger, (1964), using four different conditions with wheelchair borne, normal subjects, (passive; move only; direct only; and move and direct), showed significant adaptation in all four conditions, with no significant difference between the adaptation produced in each condition.
This latter experiment is most parsimoniously explained by supposing that under all four conditions there was one significant factor in common. It could well be that this factor was that the subject could see his own lower limbs, which Wallach, Kravitz and Lindauer, (1963), showed produced adaptation, and which experiment 6 shows produces the sort of adaptation which would give a change in egocentric orientation.

A second experiment carried out by Weinstein et al, (1964), was a variant of the perceived error technique in the egocentric orientation situation. The chain in which the subject sat throughout the experiment was rotated through the number of degrees error he made after each localisation in the training situation. Training of this sort produced about 14% mean adaptation in half-an-hour, which was more than Held and Bossom's, (1961), active group showed in one hour.

It is argued that all these procedures produced adaptation within the eye positioning system, although this cannot be proven in the case of Templeton, et al, (1966), or for Howard, et al, (1965). The fact to note is that these experiments constitute a strong case against Held and Bossom's assertion for the necessity for self produced movement and consequent reafference in order for adaptation to occur in the free situation. The additional fact that experiments 6, 7 and 8 produce considerably more adaptation of the appropriate type than does the 'walk about' situation, and that walking about wearing prisms but not seeing the limbs, (Hay and Pick, 1966), shows no adaptation, lends support to the contention that the necessary and sufficient condition for free situation adaptation is seeing the limbs. The findings of Craske and Templeton on the conditions for the resetting of eye positioning system imply that it is the extremities of the limbs which are most important. The ambulatory experience itself would seem to have no effect on adaptation to lateral displacements at all.

This latter point is a strong argument contrary to the claim of Held and Freedman, (1963), that to achieve complete adaptation requires gross movement of the head and eyes. The explanation which they offered as to why such movements are necessary, revolves around the notion of Gibson, (1958), concerning flow patterns of the image on the retina, the direction, rate and type of which will depend upon the sort of movement involved. Thus, for example, if the subject walks towards a wall on which there is a spot which he is fixating, then the flow pattern of the texture of the wall will radiate in all directions from the fixation point. Held now argues that wearing a prism shifts the centre of flow on the retina by an amount equivalent to the prism power. Presumably, then, the argument is that the translation of the eye relative to an array is necessary in order that this shifted flow pattern is recorrelated with output signals in the CNS storage device, with the proviso that information regarding eye, head, and trunk position is available to the mechanism.

It is clear that doubt is cast on the liklihood of this idea being related to the facts of free situation adaptation insofar as the appropriate adaptation occurs without the ambulatory experience. But the argument could be put forward that it is possible that flow patterns play some part when gross movement <u>does</u> take place; however consider the following. The subject is wearing prisms and is required to walk towards a wall which has a fixation spot upon it. The subject will orient himself such that he is fixating the spot, either by turning the eyes, turning the head, or something of each. This means that the image of the spot is on the fovea, (<u>not</u> displaced). The information as to the position of the spot will be in error by an amount equal to the prism power, thus he will set off towards the spot with this much error. However very soon the fact of his incorrect course will make it necessary for him to turn his head or his eyes further to one side in order to maintain fixation, or, (and this will occur quite soon), fixation will be maintained by altering course. The effect of such adjustments is to keep the image of the spot on the fovea, and for the subject to reach the spot via a curved course. There will be very little difference in the flow pattern with or without prism spectacles.

The results of experiments 6 and 7, and of Templeton, Howard and Lowman, (1966), mentioned above, raise queries about the experimental technique used by Held and Hein, (1958). They reported no adaptation after inspecting the immobile limb, and none for the passively moved limb.

Some possible factors involved in Held's and Hein's results may be:

a) The subject seeing his own limbs after the adaptation procedure, such exposure is known to reset the eye positioning system subsequent to its adaptation, (Craske and Templeton).

b) The time taken to unstrap the subject from the arm swivel in the adaptation apparatus. The personal equation of some subjects could be such that considerable decay of effect took place before being tested for post-exposure localising ability.

c) In the passive training situation with no task to perform, the subject may have 'switched off' and not attended to the error input at all.

Whether or not these are the reasons for the failure of Held and Hein to show adaptation after inspecting the immobile limb and the passively moved limb, it is clear that reasons will have to be sought, for their results conflict with subsequent findings.

By now it is apparent that the model put forward by Held is inadequate in not differentiating between adaptation at the level of the joint, and within the eye positioning system; and also because of the important place given to reafference from the distance receptors. The stress on active movement is also misplaced in that it only seems to be required in the situations which produce a change in appreciated limb position, but not for adaptation which involves the eye positioning system. Nonetheless it is necessary to discuss and consider the results of experiments performed on the basis of the remaining implications of the model.

One such implication is that if the normal relation between efference and reafference is disturbed by a device which introduces what he terms as 'one many' relationship instead of the normal 'one to one' relation, then adaptation is unlikely to occur. Such a device was used by Held and Freedman, (1963), when the subject was placed in an adaptation situation which utilised a constantly varying prism power. Not surprisingly, the subsequent finding was an increase in the variability in indicating a visible target. However, this result can also be predicted on the view of adaptation based on change in position sense. A more interesting variant of this 'decorrelation' idea is to put the subject in to an adaptation situation whereby his arm is strapped on to a swivel pivoted about the elbow, and he watches his arm as it is moved back and forth through an arc of 30 degrees by a powerful motor. During the whole of the adaptation procedure the subject tries, and fails, to move the arm in the opposite direction, (Efstathiou, 1963). The result of such a procedure was to reduce adaptation almost to zero, (inspection of the results suggests a very small adaptive effect). Certainly adaptation produced by arm wagging without decorrelation was significantly different from the above results at the 1% level of t. Efstathiou suggests that this result is what is expected on the reafference model because, 'to the extent that the sensory feedback contingent upon motion is decorrelated, adaptation will not take place'. The interpretation of these results within the framework of the present thesis is as follows. In this situation the M.O.T.F.P. is completely destroyed, in fact there cannot be an M.O.T.F.P., there is merely an approximation to excentric action on the part of the appropriate agonists. If adaptation in the restricted situation is based on the preservation of a normal M.O.T.F.P., no adaptation is predicted.

A similar situation to that used by Efstathiou would be for the subject to inspect his finger while gripping a peg set into the bench top and rhythmically straining to move the peg to the right and left. On the basis of the results of experiment 8a it is predicted that there would be a change in appreciated eye position, i.e., this sort of efference is irrelevant to adaptation. Since Efstathiou's experimental situation is essentially similar it might be argued that with sufficiently long exposure, her subjects would have shown adaptation of the same type. However, the subject's arm was moving, and from the argument that position information is not easily available to the system when the arm is moving, it would be predicted that only a small amount of eye adaptation would occur with long exposure. The experiment of Abplanalp and Held, (1965), was a development of that of Efstathiou. Subjects had to move the arm they were inspecting under one of four conditions, namely, no torque; highly variable torque; constant torque, and a situation where the subject exerted an unavailing force in the opposite direction to that of the motor. The actual results are not available to the writer, but from the discussion it would appear that the final condition gave no adaptation, (like Efstathiou's result), the first situation gave most adaptation, and the middle two conditions gave an intermediate amount of adaptation.

Given the low efficiency arm wagging adaptation situation, these results would be predicted on the 'preservation of the M.O.T.F.P.' argument, i.e., insofar as there is any correlation between the normal M.O.T.F.P. and the outcome of the situation, there will be a change in appreciated arm position.

The last paper to be considered in this section is that of Held, Efstathiou and Greene, (1966), in which is reported the following experiment. The subject moved his hand back and forth 21 times per minute, but instead of observing his hand through prisms, as in Held and Hein, (1958) he saw a line which moved with, and was in the same plane as his hand. The line was prismatically displaced, and his hand was invisible. This line was subject to a time delay of between zero and three seconds.

Before and after the above treatment condition, which lasted half-an-hour, the subjects were tested on a localisation task which involved marking the position of the virtual images of targets seen in a plane mirror which obscured the hand.

The findings were that adaptation took place in the zero delay condition, but with delay introduced, no adaptation took place. Their conclusions were that, 'the correlating mechanism cannot handle a feedback signal delayed by as little as 0.3 seconds'.

The first thing to note is that the results in the no delay condition showed only 25% of full adaptation after thirty minutes exposure, whereas Held and Hein, (1958), showed 33% in three minutes in a comparable setup where the subject saw his hand move, and not just a line. It has already been argued that even this latter is a sub-optimal training technique, (see subsidiary experiment 2), and it seems quite clear that the former is considerably more so. Apart from the arguments already put forward against the arm wagging technique, there is the additional question as to why the subject believes that the moving line has anything to do with him at all. It would seem that he is not very convinced that it is anything to do with him, considered in the light of the small adaptation shown in 30 minutes. A further query is raised as to the reason for the rejection of 18 of the original 24 subjects.

It is necessary to formulate some notion as to how it is that the moving line produces any adaptation at all. It could be argued that the subject identifies the line with his hand. Presumably this can be done because the line is doing the same thing as his hand in the no-delay situation, i.e., it is moving back and forth in the same manner in which the subject knows his hand is moving. (That the subject knows the manner in which he is moving his limb is a matter of common experience, and for this analysis it is not necessary to ask how this is known). If adaptation takes place because the subject is prepared to accept the line as representing his hand, (to a greater or lesser extent), on the criterion of identity of phase of movement, it would seem quite likely that adaptation would not occur when the phase relation is different. In this latter case it seems probable that the movement of the line is identified as belonging to a class of events <u>not</u> related to the arm movement.

This hypothesis seems quite plausible, and more likely than the 'correlation mechanism' not being able to handle 0.3 sec delay. This assertion can also be based on the fact that an experiment using the perceived error technique and delaying visual feedback of position error of the hand by as much as 30 seconds, and delaying the subsequent localising movement by a further 30 sec has shown that efficient adaptation takes place, (subsidiary experiment 4).

It is argued that this experiment by Held et al is theoretically very weak in that reliance must inevitably be placed on a process like 'identification' of the hand with the line, and there is no evidence to enable predictions to be made how strongly this will occur, and under what circumstances. This uncertainty must make it extremely doubtful whether very much can be said about the underlying mechanisms of prism adaptation from this experiment.

It is reiterated that the cause of the failure of Held et al to show adaptation in the delayed feedback situation is more likely to be due to inability on the part of the subject to accept the delayed trace as being related to his hand movement, and therefore adaptation would no more take place in this situation than it would when an observer looked at an oscillating line in any circumstances.

Section 4

A consideration of the position senses in man

Since the explanation of prism adaptation is held to be rooted in the position senses, an outline of their operation is presented.

4a. General considerations

A limb can produce information which enables the owner of that limb to know its position in relation to other parts of his body. This 'interior information' about both position and movement (position over time), is generally known as kinaesthesis, and operates irrespective of whether the movement was produced, or the position was taken up, actively or passively. Primarily it seems that we are interested in information from muscles, joints and stretch receptors.

The structure of the system

The long bones are adapted for weight bearing and swift excursion. The ends of such bones have protrusions which serve as attachments for tendons and ligaments. The articular surface has a cap of cartilage to absorb shock and permit smooth movement.

The junction of two bones is called a joint, and here we are interested in the diarthrodial, or freely movable kind. A ligamentous sleeve or capsule encloses the joint completely, and there will typically be other ligaments which join the two bones and are separate from the capsule. The joints are articulated by muscles.

A muscle fibre is an elongated polynucleated cell, and 100 to 150 of these are bound together to form a fasciculus, these are formed into larger bundles which are in turn enclosed in a covering to form a whole muscle. The various sheathes merge to form the tendon which attaches the muscle to the bony surface at the origin or insertion of the bone.

Innervation

Nerves containing both motor and sensory fibres enter each muscle from the central nervous system. At the fasciculus the nerve divides into a number of fibres each of which has its end plate embedded in a single muscle fibre. The group of muscle fibres innervated by a single nerve fibre is called a muscle unit. That contractions of whole muscles do not occur on an all-or-none basis is common observation; gradation of contraction can occur due to timing of motor volleys which gives rise to more or less summation, (which directly affects shortening). The major mechanism for gradation is recruitment in which the volleys are sent to a greater or lesser number of motor units.

The muscle spindle is located among and in parallel with the extrafusal fibres, the equatorial region contains two kinds of sensory ending, primary, annulo-spiral endings, and secondary flowerspray endings, (Barker, 1962), and these receptors respond to changes in length and tension of the spindle only. When a muscle contracts, the tension on the spindle is released, and the sensory end organs cease firing until the intrafusal muscle of the spindle re-adjusts its length, thus taking up the slack. These intrafusal muscles are situated in the polar regions of the spindle, (Barker and Gidumal, 1960), and are innervated and controlled by the gamma efferent fibres, (Kuffler, Hunt and Quilliam, 1951; Hunt and Kuffler, 1951a and 1951b). Gamma discharge produces contraction of intrafusal fibres, this stimulates the sensory endings, which in turn affect the contraction of the extrafusal muscles, (Whitterage, 1959). Thus it can be seen that the spindles act like a strain gauge which sends information to the centres from which the length and rate of movement of our muscle fibres is constantly monitored. The gamma system is a further refinement which can be used to preset the tension within the spindle, and thereby the length of the extrafusal muscle, (Katz, 1966).

From this brief resume it would seem reasonable to argue that the spindles are misalignment detectors which signal the difference between the length of the muscle and the length of the spindle, and the rate of change of muscle length. Also, because stretching the spindle activates the muscle's own motoneuron, the spindle can act as a length servo and as a device which compensates for fatigue, (Hammond, Merton and Sutton, 1956). The gamma system serves to maintain tension on the spindle at a constant level with respect to the extrafusal muscles; also, by means of what Howard and Templeton, (1966), have called 'gamma leading', initiation and facilitation of careful movements can be brought about.

This consideration of the function of the gamma-spindle system seems to indicate that it is not related to position sense in any way. This is supported by the observations of Granit, (1955), and Lloyd and McIntyre, (1950), which indicate that afferent information from the spindle projects into the cerebellum, but does not reach the cortex; i.e., it is not likely that we would be conscious of such information, whereas we are patently aware of limb position. Further, lesions in the cerebellum do not produce defects in kinaesthesis, Holmes, (1917).

The Golgi tendon organs are in series with the extrafusal muscles, and respond to the tension developed by the contracting muscle, or the tension due to stretch. Afferents from the tendon organs feed into the dorsal roots, and serve to inhibit the alpha motoneurone of the extensor muscle and the gamma efferent system when tension on the organ gets too high. This seems to be the prime function of the tendon organs, and there is no evidence to suggest, nor reason to suppose, that they play any part in the determination of limb position. By elimination this leaves joint receptors to provide the main basis of position sense, the evidence on this proposal will now be reviewed.

4b. The position sense in limbs

That the ligaments of joints are provided with sensory endings is no longer in doubt, (Andrew and Dodt, 1953; Skoglund, 1956), and that these endings are related to the position of the joint has been shown by Andrew, (1954). The joint receptors themselves fall into two classes, those which adapt slowly to produce a steady state discharge, and those which respond only during movement, (Andrew and Dodt, 1953; Boyd and Roberts, 1953; Skoglund, 1956). Those which show steady state output have joint angle as independent variable, thus they function as joint angle detectors. A given receptor will function over a range of 15 to 20 degrees, and a population of receptors will encompass a succession of overlapping excitatory angles.

Psychological experiments on the position sense in limbs seem to confirm its locus as being in or near to the joint. Goldscheider, (1899), found that anaesthetising the joint capsule of the index finger reduced sensitivity to passive movement, and Angier, (1905), showed that sensitivity to movement was not affected by the position of the limb, i.e., is independant of muscle length. More recently, Browne, Lee and Ring, (1954), showed that appreciation of downward movement of the metatarso-phalangeal joint of the great toe was impaired by anaesthesis of the dorsal area of the capsule; this suggests that joint receptors are stretch receptors. Complete anaesthesia of the capsule resulted in loss of position sense and Lee and Ring, (1954), showed that skin anaesthesia alone did not significantly alter it. They also showed that active movement sense was unimpaired in this former situation. To conclude that muscles and tendons are involved in active movement sense is premature however, for the 'command' to the limb or segment would be sufficient; i.e., sense of active movement need not be fedback from the periphery, a fedback command could provide the same information. Provins, (1958), gives data which support the contention that the active position sense is different from the passive, but which throw no light on the active movement sense. Lashley, (1917), however, did a series of experiments on a subject having complete anaesthesia of the knee as a result of a gunshot wound of the spinal cord. These showed that the extent of active movement could be controlled with normal accuracy, i.e., active position sense was not impaired. The subject knew when he had made a movement, and could make the same movement consistently. However, he could not report on the extent or duration of <u>passive movements</u> of the limb. These results are consistent with the idea that active position sense is feedback from the command to the musculature. This is true also of Merton's observation, (1964), that with ischaemia due to a pneumatic tourniquet around the wrist, the top joint of the thumb becomes insensitive to passive movement. Accuracy of active movement is not affected however unless the thumb is restrained, in which case the subject is not aware of the restraint. A model based on that proposed by von Holst, (1954), concerning feedback of efference would seem to be appropriate to the active position sense; i.e., the knowledge that voluntary movement has been attempted.

There is still more evidence that the passive and immobile limb position sense is associated with the joints, Sarnoff and Arrowhead, (1947), applied procaine to the lumbar spinal region of humans; this abolished the stretch reflex, but did not affect position sense. Stopford, (1921), has similarly observed that nerve injuries with no muscle involvement can result in loss of appreciation of position sense.

Howard and Templeton, (1966), in discussing the conditions required for kinaesthetic judgments, predict that the spindle-gamma system and tendon organs are essential components of the total position sense system, and that it was not possible to conclude that they are unnecessary for position sense in skeletal muscle, (emphasis mine). This misses the point and confuses the issue by inferring that muscle is involved in position sense in jointed parts of the body, yet there is no evidence at all that muscles produce any usable positional information. They argue that length tension feedback is essential, and without this, desired amplitude of movement will not be achieved because limbs operate under multi-load conditions. No one will argue with this as a statement about the production and control of *movement* but it has nothing to do with the *position sense*, which is what they appear to be arguing.

The most relevant work on the position sense for the present purpose is that of Mountcastle and Powell, (1959), who have presented evidence gathered from monkey by means of implanted electrodes recording from single neurons in the post-central gyrus, (P.C.G.) The thesis derived from Mountcastle, (1957), was that joint position sense was given via organs in the joint capsule and pericapsular tissue which project into the dorsal column of the spinal cord, the medial lemniscal system, the ventral posterior nuclear complex of the thalamus and thence to the somatic sensory cortex.

When cells in the P.C.G. which were related to a particular joint were observed, the findings were:

1. Neither muscles nor tendons affected these neurons.
2. Representation on the P.C.G. is of the contralateral limb.
3. When the toe, for example, was in the anatomical position, the neuron for flexion was quiet.

4. Cortical cells began discharge at a certain absolute value of joint angle, but the speed at which the joint was moved into the excitatory angle determined the frequency of the onset transient discharge.

5. The final adapted rate of discharge depended upon joint angle, and was on a plateau lower than the observed maximum; 81% of the population examined showed this steady state discharge, but some neurons showed rapid adaptation to very low discharge rates. Some of these quickly adapting neurons showed a burst of activity as the joint entered the excitatory angle which that neuron subserved, and another as the joint was moved back out of that angle. This type which fires with movement in both directions is rare, more usually, neurons have only one excitatory direction.

6. Some 80% of the neurons activated by joint displacement were sensitive over a wide range of motion, for joints with only one axis of rotation, the beginning of the excitatory angle corresponds with the beginning of flexion, and the steady state discharge gradually increases with increase in flexion, with maximum frequency of discharge occurring at maximum flexion. A smaller number, some 14%, had narrow excitatory angles. A result which is particularly interesting in terms of the experiments

carried out for this thesis is as follows:
'Cortical cells related to polyaxial joints such as the shoulder subtend solid cones rather than two dimensional angles. Position of the shoulder anywhere within this cone produces an acceleration of discharge over the background rate. Usually, however, movement in only one direction within the solid angle will produce the maximal rate of discharge'.

The experiments of Boyd and Roberts, (1953), and Skoglund, (1956), showed that joint receptors produced the same output for identical movements and positions; likewise,

7. The cortical neurons associated with the joint receptors show the same fidelity of response.

8. There seems to be evidence for reciprocal activity of pairs of cortical neurons. As the joint moves into the excitatory angle for one neuron, the evidence is consistent with the notion that the activity of the neuron subserving the same angle, but from the opposite direction, is both actively suppressed by an inhibitory mechanism as well as having a low response level due to receptor unloading.

9. The excitatory angle of the P.C.G. neurons is between 60 and 90 degrees. Thus one cortical neuron would seem to be driven by a series of joint receptors with over-

lapping excitatory angles.

Lastly, Mountcastle, Poggio and Werner, (1963), indicate that cells with wide static response range of joint angle are related to joint angle by a power law which is claimed to be the transfer function between the stimulus and the response of this part of the sensory pathway.

Summary of position sense in limbs

The spindle receptors of muscle are excited by muscle stretch, and cease discharge with shortening of extrafusal muscle. Thus they may be silent when output from the Golgi tendon organ is maximal. The output of this latter is related only to tension, and therefore will fluctuate with load on the limb. The spindle can be conditioned by the gamma efferent system, and therefore spindle activity may be at any of a wide range of values for any given muscle length, and hence of joint angle. Neither of these receptors have the properties to allow them to subserve the function of detecting joint angle, thus it would seem that they play no part in such detection. This is supported by the observation that stretch afferents from the muscle terminate in the cerebellum.

The joint receptors seem best suited to indicate joint angle, and a given receptor will have a functional range of some 15 to 20 degrees. These receptors drive cortical neurons located in the postcentral gyrus, and these neurons have stable output properties. The fact that the cortical neurons serve joint angles of between 60 and 90 degrees indicates an integration of joint receptor output. The spatial and temporal patterning of this sensory activity is put forward as the neural substrate serving position sense.

4c. The position sense in eyes

It is quite clear that humans have information as to the position which the eyes take up with respect to the head in that we can use visually determined positional information to behave appropriately towards external objects. This is the way in which 'position sense of the eyes' is being used, and the question is in what way is this information made available to the system?

It is a fact that on the receptor surface of the retina each point is associated with a specific visual direction; this can be easily demonstrated by turning an eye in towards the nose and touching its back surface, a spot in a given direction from that eye will be seen. Whether this visual direction is innate as Walls, (1951), has argued, or not, need not concern us here. The problem is to determine how it is that when the eye is moved from one position to another, an image falling on a given point on the receptor surface is known to be in a certain position with respect to the head and body, is how the position of the eyes in the head is known.

The two alternatives are that the position is determined by sensory feedback from the eyes, or via the motor outflow to the eye muscles.

a) Position information from sensory feedback.

Sherrington, (1918), argues that the muscular sense which he attributes to the extrinsic ocular muscles is a source of certain space attributes, and contributes to the perception of the direction of visually perceived objects. That is, muscular sense is a factor in absolute localisation. This conclusion is based on a consideration of the after-image experiments used by Helmholtz, (1962), which lead Sherrington to state that in order to make visual judgments of the vertical, the orientation of the eyeballs must be known. This is quite true, but to conclude that this is known through a muscle sense is a non sequiteur; notwithstanding the more recent discovery of muscle spindles in extraocular muscle of various animals including man, (Cooper and Daniel, 1949; Cooper, Daniel and Whitterage, 1955; Cooper and Fillentz, 1955).

Fender and Nye, (1961), in a servo analysis of eye movement control have pointed out that a control system for the eye can make use of first derivative position feedback to control speed of response, and that this function can be ascribed to proprioceptive signals. However, the use of these signals has not been definitely established, and they are only weakly associated with position sense as the term is used here. Similarly for Begbie's work, (1962), on the vestibulo-ocular reflex. Ludvigh, (1952), has proposed that the output of the spindles serves to alter some centre for 'parametric adjustment'. However such a mechanism is hypothesised to be a means by which innervation sent to the muscles is modified so that a desired effect is achieved, and is not directly concerned with providing the sort of position information with which we are concerned.

A summary of this very meagre evidence would seem to take the form that there _is_ no worthwhile evidence that knowledge of eye position is based on sensory feedback. This conclusion is reinforced by one of the conclusions of the previous section, namely that the afference from muscles did not provide position information. The evidence against sensory feedback as a factor is reviewed in the section which follows.

b) Position information from motor outflow.

In section 29 of his Physiological Optics, Helmholtz, (1962), put forward a number of observations germane to the topic of visual direction, and some of what follows is drawn from his elegant exposition.

That a given eye posture does not directly determine visual direction can be directly adduced by varying the position of the eye by means other than voluntary movement. For example, pulling on the outer canthus of the eye produces apparent movement of perceived objects; that is the direction of the visual axis is shifted. However, our judgment of positions of objects takes place as if the axis had not been altered. On the other hand, when moving the eye voluntarily, after-images do seem to move, while external objects do not. It is possible to conclude from these observations that judgments of visual direction are not formed on the basis of position of the eyeball, or the state of contraction of the muscles.

That tension changes do not affect judgment of direction may be inferred from Kornmuller, (1930). His data show that attempts to make voluntary movements of an eye with one or more paralysed muscles lead to apparent movement of objects in the field of view. In this case tension is not altering yet perceived objects share the intended eye movement. Apparent movement also occurs when the otherwise normal eye is prevented from moving, (Brindley and Merton, 1960; Irvine and Ludvigh, 1936; Mach, 1959).

One way of expressing the conclusion from these observations is to say that the observer has knowledge of voluntarily produced efference to the eye muscles, and this view is consistent with the reafference principle of von Holst, (1954), as is the following additional evidence.

Brindley and Merton, (1960), showed that a subject with an anaesthetised conjunctiva and occluded cornea was not aware of passive deviations of up to 40 degrees of one or both eyes. It is a common observation that during involuntary movements of the eyes, for example, post-rotatory nystagmus, it is not the eyes, but the world which is reported as being in movement. Under these circumstances there is little doubt that the feedback from the stretch receptors is identical to that produced when voluntary movement is undertaken, yet it is clearly not sufficient to indicate change in position of the eye.

Knowledge of efference, or 'sense of effort' is supported by quite direct evidence. Merton, (1964), argues that this is the information which enables us to position our eyes in the dark , and likewise that it is the sense of effort which accounts for the fact that an anaesthetic thumb, (produced by a pneumatic torniquet around thewrist) can be moved accurately with no knowledge of results. Thus it is argued that the muscles have their own private feedback mechanism. This is consonant with the findings of Lashley, (1917), who observed that his subject, a man who had no afference from below the level of his knee joint, was always correct when he stated that he had over or undershot the intended end-point of his limb movement.

Summary of position sense in eyes

The balance of the evidence strongly favours the view that appreciated position of the eye is based on a knowledge of efference to the eye musculature, and since the eye is a one-load system, it is perfectly sensible to judge eye position on the basis of the size of the motor volleys leaving the brain, rather than rely on the more conventional sensory afference.

Part 2. The Experiments.

Introduction

The experiments were carried out during a time which saw a sudden surge of activity in the field of prism adaptation, and a consequent expansion of ideas. This led inevitably to experiments being performed by the writer in response to the situation, and as time progressed, there was a change in emphasis of the work undertaken for the thesis. At its inception, experiments were undertaken which were designed to test the 'felt position' hypothesis, which was then a subject of controversy. As evidence accumulated in support of this hypothesis, the experiments undertaken for the thesis changed in direction in order to examine those situations which gave results which were not compatible with it. This led to a series of experiments which were concluded by a direct test of the involvement of the eye positioning system in the free situation.

The experiments relevant to change in appreciated position of the limbs will be presented first, followed by those relevant to change in the appreciated eye position, and lastly a number of subsidiary experiments.

The prism spectacles were a standard B.A.O. trial frame adjustable for pupilliary distance, rake and length of ear piece, and height of frame on the face. These were modified by the addition of lightweight, black rubber-covered linen which was attached in such a way as to make it impossible for any subject wearing the spectacles to gain undistorted visual information.

The prisms were specially made by B.A.O., and were ophthalmic plane prisms of standard size to fit trial frames. The experiments carried out used prisms of powers 20, 25 and 30 prism dioptres. (A prism of power one dioptre produces a deviation of 1 cm. at a distance of one metre).

In that the experimental set-up varied from one experiment to another, a detailed description will be given of this in the method section to each experiment. The introduction to each experiment will review the appropriate experimental literature to an extent which is based upon whether a detailed discussion of the literature has already appeared in section 3 of part one.

General Assumptions:

1. Prism adaptation is a genuine adaptive phenomenon, i.e., the adapted state differs from the unadapted in a qualitative fashion.
2. Adaptation is displayed in the error reduction which occurs when subjects learn to point at visual targets while

wearing, or looking through, the prism spectacles.

3. The after effect is a meaningful index of adaptation. (By after effect is meant the difference in pointing, or similar localising behaviour, between the unadapted state and that state which is consequent upon the previous training received while wearing or looking through the prism spectacles). This after effect is not conceived as necessarily being equal and opposite to the previous state of adaptation, but within the limits of the variability which a given subject displays, it is assumed that it will show a consistent relationship with the adapted state for that subject.

4. With appropriate experimental procedures, adaptation can be shown to be associated with a given part or parts of the total system involved in the behaviour studied.

The main experiments will be considered in Sections 6 and 7. The experiments to be considered in these sections are designed according to a distinction between training situations which the writer had previously made in his thinking. Prominence is given to this in the General Statement at the beginning of this thesis. The distinction takes the form of the statement that there are two broad kinds of training situation:

a) The restricted situation, which conforms to the criteria elucidated below, these being derived from categorising previous experimental work.

b) The free situation, which in its original sense was that of a freely moving subject wearing prism spectacles. This will be further discussed in the introduction to section 7 of the main experiments.

As has already been discussed in part 1, section 2, training in the restricted situation typically produces adaptation which does not show intermanual transfer, while in the free situation intermanual transfer does occur; working back from the two kinds of experimental result, the two training situations are quite distinct. The nature of the difference of effect became clear on pursuing the two lines of enquiry independently, but at this stage, the fact of a difference in effects was good enough reason to separate the training procedures.

During the course of pilot experimentation, the criteria for the restricted situation seemed to be:

a) Little or no head movement.

b) Sight of body parts through the prisms to be brief and to occur only while the subject is obtaining knowledge of results. Alternatively, no sight of body, but direct knowledge of results obtained by some other method, e.g., the shadow method of experiment 1. The brief nature of the sight of body parts is stressed in that experiments show that the significant factor of the free situation is reasonably prolonged exposure to the sight of body parts, (see section 7, also Hay and Pick, 1966). This finding increases the importance of which adaptation technique is used. The one advocated on the grounds of efficiency is the perceived error technique, (see subsidiary experiment 2), in which the duration of the sight of body parts can be very small. This is in contradistinction to the arm wagging technique used by Held and his associates.

Added to the criteria is the preferred, but not essential, condition that the training movements involve only one joint and be simple in nature. This is preferable on the grounds of parsimony; if, as it will be argued, change in position sense of the used limb is involved in adaptation to prisms, and if this is mediated by receptors in or near joints, restriction of movement to only one joint will facilitate the prediction of the outcome of experimental procedures.

Section 6

The Restricted Situation

Experiment 1

The decay of prism after effects

Many experiments in the area of adaptation to prismatic deviation must by their very nature make an assumption about the time in which the after effect will not differ significantly from the maximum which is obtained immediately after the training procedure. Even though this assumption must be made quite frequently, there is still surprisingly little evidence as to the decay of these after effects.

Hamilton and Bossom, (1964), used subjects who were trained by viewing the active movements of their arm for fifteen minutes through twenty dioptre prisms. A subsequent condition where subjects sat passively in the dark for fifteen minutes produced a decrement of after effect not significantly different from that obtained when active movement had been used to negate it. Hamilton, (1964), observed the same rapid decrement in one arm while the other was being adapted.

It is argued here that it is a necessary preliminary to further work on this kind of adaptation to know the time within which it can reasonably be assumed that there is no significant decrement of after effect. It is only within such a temporal interval that it is justifiable to consider the results obtained as being drawn from the same population. It was for this reason that a number of observations were taken to ascertain the 'no significant decrement' period prior to testing specific hypotheses about the adaptation process.

Apparatus

The apparatus used for this experiment was also used for others, so it will be described at some length.

A triple topped table was constructed, the two uppermost surfaces being made of quarter inch plate glass. The lower of these was 4' 6" from the ground, and the other 5' 0". The lowest surface was of wood, and was 4' 0" from the ground. The lower plate glass sheet had its upper surface sprayed with P.T.F.E., which due to its very low coefficient of friction, served to reduce drag when the subject moved his arm over it. The lower surface of the lower glass sheet was marked out in degrees, the point of origin being some 5" beyond the front edge of the glass, and 9" to the right of centre.

On the lowest, (wooden), surface was a small holder which could slide smoothly over the surface, on this was mounted a miniature 100 watt point source of light.

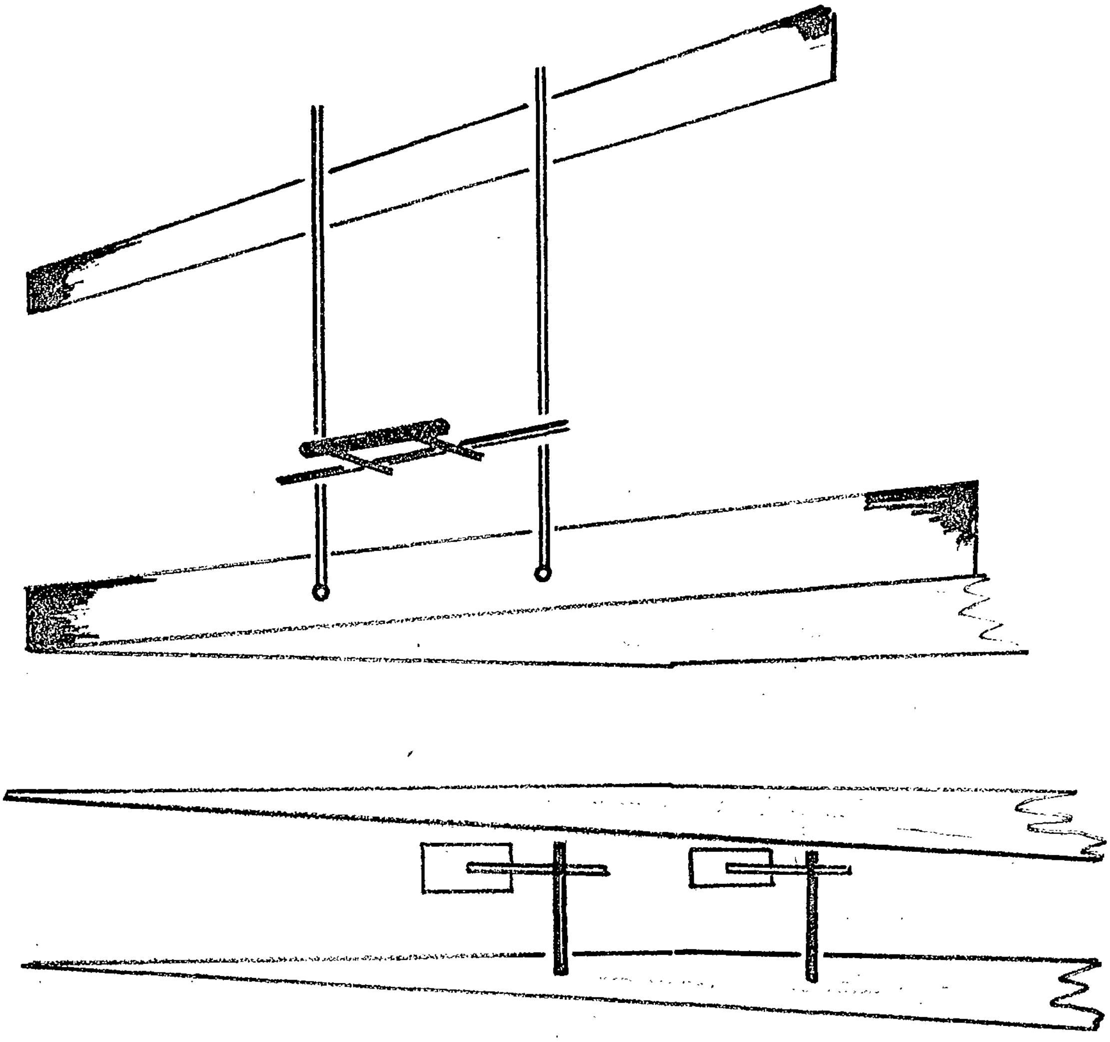

Plate 1. Showing arrangement of bite bar, two plate glass sheets and table top.

The upper glass sheet could be covered with plain paper if appropriate. This upper sheet was mounted on Dexion which was bolted to the wall; parallel to this and 1' 0" above it was a similar length of Dexion also bolted to the wall. A pair of vertical ⅜" brass rods were mounted side by side between these two Dexion lengths, and the device holding the dental wax bite could be adjusted in height on them, (see plates 1 & 2).

Method

Subjects: Ten subjects were used, all undergraduates at the University. No subject showed manifest deviation of the eyes.

Procedure: The subject was seated, then raised until his right forearm could lie horizontally on the lower glass sheet. This meant that for most subjects the shoulder was an inch or two higher than elbow. The right shoulder was palpated by E in order to locate the acromio-clavicular joint, (see appendix), it being assumed that a perpendicular dropped through this point would be a good approximation to the axis of rotation of the arm when it was moved in horizontal abduction and adduction. (It must be noted that there is no true axis of rotation, because whatever action is required of the arm, the scapula moves to align the glenoid cavity so that it will be in the best position to receive the head of the humerus).

The subject was now positioned such that this axis of rotation coincided with the point of origin of the scale on the lower glass sheet. In order to keep the subject in this position during subsequent arm movements, a nylon webbing harness was developed which could be adjusted on each subject such that when leaning forward he was restrained the appropriate 5" from the edge of the glass sheet. Sideways movement was controlled by a post which projected horizontally from the table top, and which could be adjusted sideways until it was pressing firmly against the subject's left side. These measures could not prevent movement on the part of the subject, (indeed that would have been undesirable), but if the subject co-operated and leaned into the harness and against the post to his left, then he could move into and out of his dental impression and regain the same place each time.

In front of the subject, and symmetrical about his prism deviated visual median plane were five fine line targets, drawn vertically on white blocks 1" high and ½" wide. These blocks were spaced 7 degrees apart, and were on the arc defined by the tip of the finger as the arm was adducted. The centre target was objectively 11 degrees 19 minutes to the right in order that it lay along the line of the deviated visual median plane. The subject's right arm and hand were held semi-pronated, and rested on the lower glass sheet; the fingers of this hand were flexed with the exception of the index finger which was maintained in the extended position. The left arm was held loosely in the lap.

Pre-training measures: The subject placed himself in the bite and his arm on the lower glass sheet, no prisms were worn. The E called out the letter associated with each target five times in random order, and on each of 25 occasions the subject ballistically* adducted his arm from some position on the far right, (about 70 or 80 degrees to the right of the sagittal plane passing through the point of rotation of the arm, there being no need to specify the starting position with precision). He brought his limb to rest such that he thought his index finger was underneath the specified target. This took place without the subject gaining knowledge of results since the top glass sheet was covered with white paper. When the arm had come to rest, the subject turned his index finger down, and E read off the error from the scale.

Training: The subject's interpupilliary distance was measured, and the trial frames adjusted for this, and for

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* See appendix for definition.

length of rake of ear piece. The E put the two 20 dioptre prisms in place with their bases right, and the subject was asked to put on the trial frames with his eyes shut, and move himself into the dental impression. Subsequent to this, exactly the same procedure was adopted as in the pre-training, except that the subject was given knowledge of results. This was achieved by E moving the point source of light until it was beneath the subject's index finger; when it was so positioned and turned on, the subject could see a sharp shadow of his finger and its relation to the target at which he was trying to point. After 25 readings had been taken, and irrespective of how completely the subject had adapted, the training was stopped, the subject shut his eyes and the spectacles were removed from him. As soon as this had been done the subject opened his eyes and the post-training readings were taken.

Post-training measures: As in the pre-training, E called out target letters, and the subject made a ballistic movement to place his index finger under the appropriate target. Knowledge of results was withheld. Since as many readings as possible were required within the time interval used, and since decay of effect through time was the subject being investigated, readings were taken at 7 second intervals. For convenience, each target position was called twice in every ten readings. Fifty readings were taken, E noting the error made each time to the nearest 1/10 degree. It must be noted that all movement takes place at the right shoulder joint only.

Results

Table 1.

Prism After Effects Through Five Time Intervals
Mean Errors in Degrees
All Errors in Same Direction

Subject	Time in Seconds				
	t1	t2	t3	t4	t5
	0-70	71-140	141-210	211-280	281-350
1	5.0	4.9	4.3	3.8	1.4
2	6.8	6.0	6.6	6.2	5.7
3	5.4	7.2	4.0	2.4	2.5
4	12.5	9.8	11.4	10.3	11.0
5	7.6	8.1	9.3	10.1	10.6
6	1.8	2.1	0.9	0	0
7	5.0	4.3	2.9	2.0	1.5
8	6.3	6.0	4.7	3.6	2.0
9	11.0	8.6	7.2	6.1	5.0
10	8.0	8.1	8.7	8.6	8.8
Mean	7.4	6.8	5.9	5.2	4.5

The above results have been corrected to 'subject zero' by subtracting the mean of the errors made in the pre-test from each of the readings.

If the mean of the readings taken during time t1 is taken as 100, then the respective values of t2 through t5 are 92%; 80%; 70%; and 61%, showing a remarkably consistent drop through each time period, see Fig. 1. These results suggest that any experiments which are modelled on a pre-test, training, post-training paradigm should have the post-training readings taken as quickly as possible if maximal after effect is required. In terms of minutes, a post training time of not more than two is suggested by the data. Certainly, the readings taken during time t1 are significantly different from those taken during t2. Students $t = 2.47$ with $df = 9$, thus $0.01 < p < 0.025$.

The above results bring out a side issue which has not been followed up, namely that some of the subjects show strongly atypical results. For example, subject 5 shows gradually increasing errors while subjects 2 and 10 remain reasonably constant over the whole of the 350 sec period. It is intriguing to speculate whether these subjects are merely slow to begin the normal decay process, or whether they are maintaining the probability of the particular response by emitting it. That is, do they have a very slowly descending decay curve, or is the population bi-modal when subjects are asked to perform in the manner described.

These speculations do not affect the main point at issue, namely that when using an unselected group of subjects, and in order that it may be assumed that significant decay has not taken place, it is sensible to take the post-training readings promptly, e.g., within two minutes subsequent to short term training with 20 dioptre prisms.

Experiment 2a

Evidence to implicate the joint in restricted situation adaptation

When these experiments were performed, there was a certain amount of evidence that there was a change in the 'felt position' of the arm after exposure to visual displacement in a prism wearing situation, (Harris, 1963, Hamilton, 1964, Pick et al, 1963). The evidence seemed convincing, though in the main presumtive, Harris had shown that there was little or no intermanual transfer of adaptation to the unused limb, but intermodal transfer occurred when the adapted limb was used to point to a sound, or to the straight ahead position. The latter two findings had been supported by Pick, Hay and Pabst, (1963). Hamilton, (1964a), used normal and split-brain monkeys for a series of prism experiments, and had observed that monkeys with midline section showed no deficit of adaptive reaching with the used limb when tested for inter-ocular transfer, and concluded that under some conditions adaptation seemed to be restricted to the level of the used joint.

Harris, (1963a), performed an experiment using the techniques of magnitude estimation of distances between forefingers before and after adaptation, i.e., an experiment requiring estimates of distances in figures relating to a remembered separation of the fingertips which had been given an arbitary reference number. This experiment showed that the estimates moved in the predicted direction after adaptation. However, such an experiment would fall under Brindley's, (1960), category of class B observations, and thus conclusions in terms of the way in which the system functions must be regarded with caution.

When the following experiments were done, this was the evidence for change in felt position, or kinaesthetic change, subsequent to exposure to prismatic displacement. At the same time, Efstathiou and Held, (1964), had disagreed with the 'felt position' formulation on the basis of a theory formulated by Held, and the possibly relevant observation that accurate reaching can take place without the hand being visible. They suggested that both the object to be localised and the intended position of the hand are mapped on an internal representation of space. Thus they argue that adaptation involves a change in the mapping of the intended position. The experiments reported in their paper, (which are the subject of experiment 4 in this thesis) lead them to accept this mapping hypothesis, and to conclude that ".... adaptation to displaced vision cannot be interpreted as a change in the felt position of the arm in relation to the body". It was because these two conflicting views had been put forward that further experiments seemed desirable.

The problem was to devise a situation which could unequivocally test between the view that the felt position of the arm was implicated in adaptation, and the alternative that it was not. It has already been argued that limb position is mediated by joint receptors at the periphery, thus to facilitate understanding the results of the experiment it was decided that only one joint, the shoulder, was to be used in the prism training session.

The experiment used the ability of the subject to point to one limb with the other without visual information. It involved measuring the accuracy with which a subject could point to specific locations along one arm before and after that arm was used in an adaptation procedure. The null hypothesis was that there should be no significant alteration in the lateral accuracy with which this task could be carried out. The position taken up by Efstathiou and Held would be consistant with accepting the null hypothesis, while that of the proponents of the felt position hypothesis would predict its rejection.

Apparatus

The apparatus was mounted on a bench top. Standing subjects could be raised so that when their left arm was horizontal it was three inches above the bench surface. Above the bench surface was mounted a triangular perspex sheet, with lines scribed in degrees, origin A, (see plate 3). At A, a ⅛" hole was drilled to facilitate positioning the centre of rotation of the arm beneath it. In the region of A was superimposed another scale, consisting of a line grating, the lines spaced 1/10" apart and lying in the sagittal plane. Two small groups of holes were drilled along the line scribed from A which coincided with the sagittal plane passing through the point of rotation of the left arm. These two groups were arranged such that one of the holes would be appropriate for the wrist region and another for the elbow region of any subject's arm.

The perspex sheet was supported by adjustable ball-jointed clamps, thus it could be bent to the contours of the left arm when it was in place. 1, 2, 3, 4, were nylon ended rods which could be adjusted so that the shoulder and arm could be held against them. 5 was a similar rod which could be adjusted such that the fingertip just touched

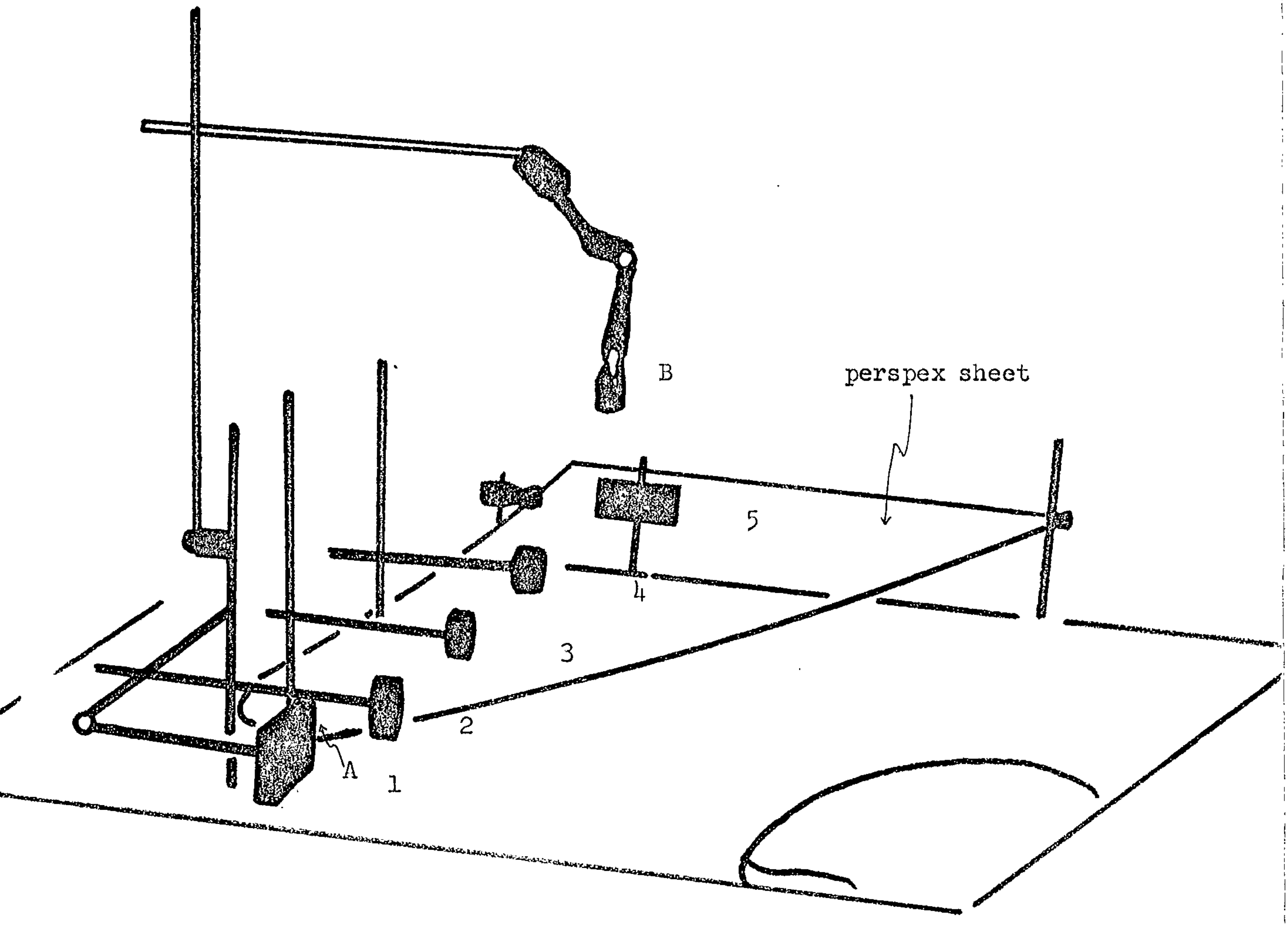

Plate 3. Diagrammatic representation of apparatus used for direct estimates of adapted limb position.

it. B was another ball-jointed clamp which held an opaque screen in which 20 dioptre base right prisms were mounted and which could be adjusted to a height appropriate to the subject's eyes.

Method

Subjects: The subjects were twelve undergraduates taking courses at the University of Durham; they were all right handed, and none showed manifest deviation of either eye.

Procedure: The subject was raised by means of blocks until his left shoulder was at the height of pad number 1 in the plate, and his shoulder was palpated to find the point of rotation of the arm, (see appendix). While that spot was retained, (either by marking the shoulder with indelible pencil, or by E keeping his finger tip at the appropriate place), the subject was asked to press his shoulder firmly against pad No. 1 and hold his arm horizontal. With the clamps holding the plastic scale only semi-tightened, the scale was then moved such that A, the point of origin, was over the point of rotation of the arm.

With the subject still holding his arm in the horizontal position, and oriented semi-prone, E moved forward rod No. 5 until the subject reported that he could feel distinct pressure on his extended index finger. E now moved forward rods 2, 3 and 4, which until now had been right back against their stops. These were tightened in position when they were bearing firmly against the subject's arm. The subject was now asked to come out of position and then regain it as swiftly as possible, the accuracy with which his shoulder was in the appropriate position was checked, and adjustments made to bring this about if necessary.

Pre-training measures: The subject positioned himself as described, his left arm held horizontally against the stops. In his right hand he held a black fibreglass nib pen, and his right forearm rested on a foam plastic pad, (on the bottom right of plate 3). The subject's task was to make a small mark on the top of the perspex sheet using the pen in his right hand, this mark was to be at the point which seemed to co-incide with the pin-prick which E was producing with a long handled steel pricker made for the purpose. E inserted the pricker through the hole in the shoulder, elbow and wrist region of the perspex in random order, and kept the point in contact with the subject's skin until he had made the mark. This mark was made without the aid of vision, the subject's eyes being closed throughout the whole session. Only twice was the subject sufficiently accurate to hit the pricker with the marking pen. Thirty readings were taken in two batches of fifteen; giving ten readings at each position. A two minute rest with the subject out of the apparatus was allowed between the two batches of fifteen. The subject was allowed to rest his right forearm on the pad in between each reading. Readings were taken about once every five seconds.

Once these readings had been taken, the subject was allowed to rest while E prepared for the training session.

Training: The E swung the prisms in front of the subject's eyes, and also swung into view three targets consisting of fine vertical lines lettered A, B and C respectively. These targets were mounted above the widest part of the perspex sheet, and were spaced five degrees apart, the central one being in the objective median plane of the subject's body. The perspex sheet was covered by a card such that the subject could not see his left arm when it was fully extended on the table top, but if the arm were raised, the index finger came into view.

The subject was then asked to move his left arm from left to right across the table top until he considered his index finger to be below the target which had been called out by E. The subject then lifted his arm, his index finger came into view, and immediate knowledge of results was obtained. The arm was then returned to the left and the procedure repeated for another target. The training was continued until the subject could perform the pointing task to a criterion of 5 consecutive responses at an accuracy of plus or minus ½ degree. As soon as this had been achieved, the subject was asked to close his eyes and put his left arm back into the initial position against the stops. The targets and the prisms were swung aside and the subject given a fibre-nib pen of a different colour to the first.

Post-training measures: These were identical to those of the pre-training situation. With his eyes closed, the subject marked on the perspex with his 'untrained' arm the apparent location of his trained arm as defined by the prick spots produced by E at shoulder, elbow and wrist.

There was one difference in procedure, and this was during the two minute interval between the first and second session of fifteen readings, instead of relaxing out of the experimental situation, the subject opened his eyes, looked through the prisms which were still in place, and was retrained by E to the same criterion as in the training session. If this did not take two minutes, the second session was begun before the end of this interval. It is clear that the two minute rest between the pre-training sessions was not strictly necessary in its own right, but was inserted for symmetry of design.

The Readings: The two sets of markings were read off by E at the close of the experiment, and were recorded as lateral errors from the true position correct to one tenth of a degree for the wrist and elbow readings. The errors for the shoulder were recorded on a different scale, and will be dealt with later. Although there was some danger of confusion with this procedure, the pre-training measures were not read off by E immediately after they were taken in order that the total time taken for the experiment was as little as possible. This policy was adopted on a precautionary basis. The writer has observed informally that even with no treatment condition intervening, means of errors in pointing to visual targets with no knowledge of results are often appreciably different on two different occasions. This could well reflect that the range of error as defined by a long series of readings is made up of a series of sub-ranges each of which was quasi-stable in the short term. Craske and Templeton have observed that this sort of spontaneous change is a characteristic of the response of the eye positioning control system when a series of readings of the eye resting position are taken. Since the eye is a part of the total mechanism which is involved in pointing to visual targets, it is not implausible that small spontaneous shifts of response could occur when readings are taken from a different part of the total pointing mechanism. Thus the time between pre-test and post-test was kept low in order that possible spontaneous fluctuations in the response of the system were kept to a minimum.

The error readings for the shoulder region were not read off in degrees since it is quite clear that there are several factors which make such a procedure quite impractical. These are: (a) that the subject may mark behind the origin of the scale, or (b) may mark exactly to the right or left along the coronal plane passing through the point of origin of the scale. (c) Near to the origin, the distance between the lines on the scale is small compared to the size of the mark made by the subject, and (d) following from this last factor, errors due to the inherent variability and inaccuracy in the pointing limb will be disproportionately magnified.

Factors of type (a) produce errors which are meaningless on the scale used for elbow and wrist error measures, unless some arbitary meaning is given to them. Those of type (b) are completely meaningless in that they will give a reading of 90 degrees even if the linear error tends to zero. Those of type (c) lead to readings with an accuracy of no better than to the nearest 5 or even 10 degrees; the difficulty and inaccuracy becoming greater the more truly accurate the subject is in performing the task. Those of type (d) will add a very considerable variability to the readings, and clearly this variability is spurious in that it is associated with the magnified errors of the measuring tool, (the pointing arm), and not the experimental object, (the treated arm).

As a result of these objections, an alternative scale was superimposed on the shoulder region; this consisted of a grating of lines spaced 1/10" apart, running parallel to the sagittal plane, and centred about the hole which was at the axis of rotation of the shoulder joint.

It is regrettable that the same measure cannot be used along the length of the arm, but the situation is such that this is not possible, the change in error units need not be too worrying, however, for it is quite clear that the hypothesis being tested predicts zero change at the point of rotation of the limb, provided that the plausible assumption is made that the position sense of limbs is mediated by receptors associated with the joints. It is less clear to see what prediction would be made by

Efstathiou and Held, but it would seem that a change in the mapping of the intended position of the limb extremity would not involve the shoulder. The analysis will therefore be to test for errors of lateral extent at the shoulder before proceding to extract further data.

Results:

Table 2.

Pointing to the shoulder of the adapted
arm with the unadapted
Mean errors before and after treatment
in tenths of an inch

Subject		Before Treatment	After Treatment
1		- 1	- 2
2		5	1
3		1	3
4		- 4	- 3
5		7	- 7
6		- 8	- 6
7		- 5	- 8
8		- 3	- 3
9		6	2
10		3	1
11		- 8	-10
12		1	3
	Sum =	- 6	-29
	Mean =	- 0.5	- 2.4
	SD =	5.2	4.52

It is now possible to test the hypothesis that the means of the two samples are equal. The assumption is made that the samples are drawn from a population which is normally distributed. An appropriate statistic is the dependant case for 't', where $t = \dfrac{\bar{D}}{\sqrt{S_{\bar{D}}/(N - 1)}}$

Table 3.

To test for significance of difference of means for the data of table 2

Deriving the difference scores D and D^2 from table 2

Subject	D	D^2
1	+ 1	1
2	+ 4	16
3	- 2	4
4	- 1	1
5	+ 14	196
6	- 2	4
7	+ 3	9
8	0	0
9	+ 5	25
10	+ 1	1
11	+ 2	4
12	- 2	4
	Sum of D = + 23	Sum of D^2 = 265

On the full data, $t = 1.48$, $df = 11$; for two tailed test $0.20 > p > 0.10$ which would not be considered significant on the normal criterion. However this level may be considered spuriously high due to the influence of the outlier, (S 5).

If this is rejected, then $t = 0.24$, $df = 10$ for which $p \gg 0.3$. This is clearly significant.

From the foregoing analysis it can be seen that the evidence is insufficient to warrant the rejection of the null hypothesis.

In terms of the purpose of the major part of the experiment which has yet to be considered, these are very satisfactory results, and show that no change of the appreciated position of the shoulder of the 'adapted' arm takes place as a result of the adaptation procedure. This leaves the way clear for the main hypothesis concerning the appreciated position of the arm used during the training procedure.

Table 4.

Mean errors in degrees in marking positions along one arm
(- indicates that the error was to the subject's right)

Subject	Before Treatment		After Treatment	
	Wrist	Elbow	Wrist	Elbow
1	-2.54	-0.90	-9.54	-8.42
2	1.80	0.80	-6.38	-6.80
3	0	-3.64	-5.16	-6.56
4	-3.28	-5.06	-6.56	-6.22
5	0.84	0.46	-7.60	-5.18
6	-2.10	-4.04	-9.78	-9.10
7	-1.06	0.72	-6.20	-4.38
8	-0.32	-1.28	-3.00	-2.44
9	-4.14	-2.74	-8.64	-7.96
10	-0.44	3.36	-8.58	-4.58
11	-3.46	1.04	-5.50	-2.76
12	-3.38	-0.88	-4.98	-2.88

If from table 4 the before treatment errors are subtracted from the after treatment errors for both wrist and elbow, an initial measure of the angular change observed for the two positions can be derived. Consulting the first two columns of table 5, it can be seen on inspection that a large undirectional change in appreciated position has occured for both wrist and elbow.

Table 5.

Angular change in degrees for wrist and elbow

Subject	Wrist	Elbow	Difference (D)	D^2
1	-7.0	-7.5	+0.5	0.25
2	-5.1	-5.2	+0.1	0.01
3	-8.2	-8.1	-0.1	0.01
4	-3.3	-1.2	-2.1	4.41
5	-7.1	-7.6	+0.5	0.25
6	-7.2	-5.1	-2.1	4.41
7	-5.1	-5.1	0	0
8	-2.6	-3.3	+0.7	0.49
9	-4.3	-5.2	+0.9	0.81
10	-8.1	-6.6	-1.5	2.25
11	-2.0	-3.8	+1.8	3.24
12	-1.6	-2.0	+0.4	0.16
		Sum of D =	3.0	D^2 = 16.29
		Mean of D =	0.25	

From the above results it is clearly of interest to determine the mean of the differences between wrist and elbow, and the confidence interval within which the population mean lies.

Standard error = 0.4

95% confidence limits = $\bar{X} \pm 1.96 \times 0.4$ degrees
= 0.25 ± 0.78 degrees

Thus the 95% confidence interval includes zero. This is a result consistent with the hypothesis that adaptation produces a change in the felt position of the used arm, which would predict that the difference between the angular errors when pointing with one limb to another before and after adaptation should be identical for any positions along the used limb. Thus subtracting one from another should produce a result of zero, which is within the confidence limit.

It is sensible to enquire at what level we may assume that the angular errors for pointing to wrist and elbow are alike.

Using the data of table 5,

$t = 0.73$ with df. = 11

This does not reach significance on a two tailed test at the 20% level of t. Thus the angular deviation displayed when pointing to various targets along an adapted limb with an unadapted one is consistent regardless of position of target.

This being so, the readings for wrist and elbow can be pooled in order to test the null hypothesis that there is no significant difference between the before and after errors on the pointing task.

Table 6.

Means of pooled errors before and after adaptation

Subject	Mean error			
	Before	After	Difference (D)	D^2
1	- 8.6	-44.9	-36.3	131.8
2	- 9.2	-35.0	-25.8	665.6
3	+ 6.8	-33.0	-39.8	1584.0
4	-20.9	-32.0	-11.1	123.2
5	- 1.0	-32.0	-31.0	961.0
6	-15.4	-45.9	-30.5	930.3
7	- 0.9	-26.3	-25.4	645.2
8	+ 2.4	-13.6	-16.0	256.0
9	-17.2	-41.5	-24.3	590.5
10	+ 7.3	-32.9	-40.2	1616.0
11	- 6.1	-20.7	-14.6	213.2
12	-10.1	-19.7	- 9.0	81.0

Sum of D = 309.0 D^2 = 7797.8

Mean of D = 25.8

$t = 3.4$ df. = 11

$p < 0.005$, two-tailed test.

The evidence is therefore sufficient to warrant rejection of the null hypothesis.

This result provides strong support for change in appreciated arm position as a factor in adaptation under the experimental conditions used.

Accepting change in appreciated arm position involves predicting that there should be a relationship between the size of the errors made in pointing to the adapted arm with the unadapted, and the size of the errors made when pointing with the adapted arm at a visual target without knowledge of results. Accordingly the following experiment was carried out.

Experiment 2b

Showing a relationship between the angular errors recorded in experiment 2a, and size of subsequent after effect

Apparatus: This was as for experiment 2a, except that the adjusters (numbers 1-5 in plate 3) were removed, thus enabling the subject to abduct and adduct his arm through a large arc in the horizontal plane. A bite bar was used in order to help maintain the subject's shoulder in the position appropriate to reading off errors in degrees. This placed reliance on the subject not moving the shoulder out of the coronal plane during arm movement, clearly this assumption cannot be made very confidently.

Method

Subjects: The subjects were the same as in experiment 2a.

Procedure: The experiment was in three parts.

a) Pre-treatment measures: The subject, who was not wearing prisms, was asked to point with his left arm at each of three targets used in the preceding experiment. The order of presentation was determined by E such that each target was called five times. Knowledge of results was withheld from the subject by covering the perspex sheet to a suitable distance, E however could see the extended fingertip, and read the error to the nearest 0.5 degree.

b) Treatment: The prisms were swung into place, and with no further adjustments necessary, the subject was trained with knowledge of results as in the previous experiment, using adduction of the left arm and continuing the training until the criterion of 5 consecutive responses with an accuracy of ± 0.5 degree was achieved.

c) Post-treatment measures: At the completion of the treatment condition the subject was told to close his eyes while E swung away the prisms, the situation was now as for the pre-treatment measures. The subject was then asked to open his eyes and point with his left arm without knowledge of results to each target as it was called out by E. Fifteen readings correct to the nearest 0.5 degree were taken.

Results: Although every attempt was made to keep the subject's shoulder in the appropriate position, this was an unreliable part of the situation, though the unreliability was unavoidable if experiment 2b was to conducted in essentially the same situation as experiment 2a. This being the case the results were considered unsuitable for any treatment more rigorous than ranking.

Thus the ranks of the size of error produced in this situation are compared with those produced by the same subject when pointing to the adapted limb in experiment 2a, these latter data are drawn from table 6. An appropriate statistic for testing association between these two sets of ranks is Kendall's Tau.

$$T = \frac{S}{\sqrt{\left(\tfrac{1}{2}N\,(N-1) - Tx\right)\left(\tfrac{1}{2}N\,(N-1) - Ty\right)}}$$

where Tx and Ty $= \tfrac{1}{2}\,t\,(t-1)$ where t is the number of ties on the X and Y rankings respectively.

Table 7.

Ranks of errors, least to greatest, on two tasks

Subject	Rank on pointing to used arm	Rank on pointing to visual target	$i < j$	$i > j$
1	9	8	3	0
2	7	7	5	0
3	12	11	12	11
4	4.5	3	7	0
5	2	5	7	3
6	10.5	12	0	1
7	8	9	3	1
8	6	6	6	0
9	4.5	4	7	1
10	10.5	10	2	0
11	3	2	9	0
12	1	1	11	0
			k = 60	1 = 6

T = 0.83

The significance of tau is found by dividing the calculated tau by its standard deviation. In this case:-

$$\text{S.D.} = \sqrt{\frac{2(29)}{108(11)}}$$
$$= 0.22$$

Testing tau for significance of difference from zero we divide by 0.22 to get the critical ratio.

$$\frac{0.83}{0.22}$$
$$= 3.77$$

Since there is a good priori reason to predict a positive association between the two sets of ranks, a one tailed test is the most appropriate. The above result is significantly different from zero at $p < 0.0001$. This is a strong positive association between the results of the two experiments.

Discussion:

The results for experiment 1 must not be generalised to experimental situations in which very different training procedures, exposure times or training criteria are used. For example, it seems that prolonged exposure in the free situation leads to prolonged after effects, as illustrated by the observations of Held and Bossom, 1961; Kohler, 1964; McLaughlin and Bower, 1965; and Pick and Hay, 1964. The responses of the individual subjects hold some interest in that some maintain the adapted state for a time within which other subjects have shown a decrement in error rate to zero error. The conditions governing these differences would be interesting to investigate, for example, from Hamilton and Bossom's paper, (1964), one would predict that there would be an inter-response time which would allow spontaneous decay to take place in those subjects who, in experiment 1, maintained their adapted state. The inference is that an important factor in producing the maintained adaptation is the rate of responding in the post-training measurement situation.

The actual form of the training technique is of interest insofar as it is a variant of the perceived error technique, (see subsidiary experiment 2), in which the subject never actually sees his hand or finger, but only the shadow of it, and this only when the limb is at rest. That this successfully produces adaptation is quite clear, and is in itself evidence contrary to the reafference view of adaptation. This is so unless some sort of memory unit is installed in the reafference model to enable a copy of 'what instructions have gone out' to be retained until the result of the instructions is received all-at-one-time at the end of the movement. This method of training certainly shows that continuous input of the results of commands to the limb is unnecessary.

The direct conclusion from experiment 1 is that if this training technique is used with a training criterion of 5 successive responses accurate to within plus or minus 0.5 degree, then an appropriate strategy is to take post-training measures within two minutes of the cessation of the training.

Experiment 2a used this finding in that the number of readings taken subsequent to adaptation was restricted to 15. A significant feature of the design was the number and type of movements used in the training situation, and the fact that only one joint was involved. This is equally true of experiment 1, and will generally be the case for experiments in the context of the 'restricted situation'. These particular constraints were put upon the situation since interest was centered around a hypothetical change in the position sense, and it has been argued that this is mediated at the periphery by joint receptors. The possibility that adaptation might stem from some recalibration of the motor outflow, especially in a restricted situation, is dealt with severally by the argument in section 4c of part 1, the results of experiments 2a and 2b, and lastly by subsidiary experiment 6 which tests the motor outflow involvement hypothesis directly, and finds no evidence to support it.

Experiment 2a may be criticised for not keeping the subject's head immobile, but this was difficult to do properly given the constraints of the situation. The expedient of using mounted prisms instead of letting the subject wear them was adopted. Thus inadvertent head movement was countered by compensatory eye rolling, and hence the eyes continued to look through the central part of the prisms. The lack of control over shoulder position in experiment 2b could also be criticised, but it is argued that to use any sort of device to do this would restrict the movement of the arm, and lead to less control over the situation rather than more. Not to restrict the shoulder, and using the less stringent ranking techniques in the analysis seemed a reasonable compromise.

The results obtained for pointing to the shoulder of the arm used in the treatment condition are quite clear and unambiguous; with the technique used there is no change in the mean position indicated by the subject, and equally as important, no change in standard deviation. This is fully in line with the prediction from the hypothesis that there is change in felt position of the arm mediated by receptors in the shoulder. There is a certain lack of clarity as to the prediction from the mapping hypothesis, and perhaps the safest course is to say that it makes no specific prediction for the shoulder region.

That there were no changes in the errors made in pointing to the shoulder aids the understanding of the following results considerably, for the errors for the wrist and elbow were in degrees with the axis of the shoulder as origin. The null-hypothesis was that there would be no difference between before and after errors in this situation; and this is the prediction made from Efstathiou and Held. Clearly the felt position hypothesis predicts significant difference at both wrist and elbow. Furthermore, the magnitude of the angular errors at the two points would be predicted as being identical. Inspection of table 5 and the following tests confirms this latter prediction by showing that the 95% confidence limit includes zero angular difference between wrist and elbow. It was also shown that the angular difference between the before and after measures was considerable, and led to the rejection of the null-hypothesis at $p < 0.005$.

This represents fairly sound evidence for a change in felt position of the limb after adaptation, and leads to a corollary, namely that errors in pointing to visual targets when the adapted arm is used should be strongly associated with the errors just noted. This is especially to be expected following the idea of the preservation of the M.O.T.F.P. put forward in section 4d of part 1, and from the assumption that in many circumstances humans move a limb from a kinaesthetically appreciated position to a position defined by the visual target. Table 7 and the tau test which follows it make it quite clear that the predicted positive association does exist, with a difference significant at $p < 0.005$.

The direct conclusion is to reject the criticism of Efstathiou and Held, and the mapping hypothesis associated with it, and to affirm that some change has taken place in the position sense of the used limb. Craske, (1966a), has suggested that a convenient way to think of this is as a change in the transfer function of the joint receptor output. This is argued on the basis that adaptation is unlikely to alter the output of the joint receptors themselves, but the system is acting as if this had occurred.

A change in the transfer function at some level between the joint receptor output, and the final perception of joint angle is consistant with the observed change in position sense. A significant question is at what level can the system be considered plastic? This is a problem which is open to the physiological technique technique of single unit analysis, which could be fruitfully employed using monkeys. Such a technique could be used for on-line recording of change during prism adaptation, provided a joint unit had been isolated before attempting prism adaptation, and its characteristic response rate for a given joint angle determined.

The findings of Hamilton and Bossom, (1964), and those of experiment 1 indicate that the change induced by prisms in the restricted situation is of transient nature. Specifying the nature of, or producing a model for this transient response will constitute a major theoretical problem for the future.

One last issue to be discussed at this juncture is that of size of after effect. The hypothesis that adaptation is due to change in appreciated limb position makes no specific prediction about the size of the after effect, though it might be expected on an everyday level that if the subject has learnt to hit the target every time for a succession of times, then he would miss the target by the amount of the prism deviation subsequent to the removal of the prisms. The fact is that this rarely proves to be the case; an example can be provided by table 5, inspection of the results shows that only about one third of the subjects show after effects of more than 7 degrees, which represents some 2/3 of full after effect. This sort of finding does not embarrass the hypothesis, but it does pose two problems which have not yet been investigated, the first is the relationship between the amount of correct response training, and size of after effect; and whether or not the asymptote of the after effect curve lies on the value of the imposed deviation. An extension to this problem is whether subjects have individual maxima; certainly this is one way of interpreting the fact that with identical training the subjects in experiment 2a between them showed a whole spectrum of after effects. Alternatively it could be assumed that different subjects require different amounts of training to produce similar after effects.

The second problem is that of the size of after effect as a function of a given amount of training across the range of prism powers, put another way, will training to a given criterion produce a constant percentage after effect for a single subject, for 1, 2. 3, n prism dioptres?

Notwithstanding these problems, the major conclusion from these experiments is considerable support for the hypothesis that adaptation in the restricted situation is associated with a change in the appreciated position of the used limb, most conveniently thought of as a change in the transfer function of the joint receptor output.

Experiment 3

An auditory analogue of prism adaptation

It had been shown by Harris, (1963), McLaughlin and Bower, (1965), and Pick and Hay, (1964), that restricted situation adaptation resulted in errors in pointing at auditory targets. This mislocation seemed readily explicable by the notion that adaptation produced a change in the appreciated position of the arm, and was of a size and direction identical to that which would have been predicted for the subject pointing to a visual target subsequent to adaptation.

This kind of intermodal transfer of effect, apart from supporting the 'felt position' by hypothesis, raises the following question. "If the effect transfers, why should it not be produced using non-visual input, and transfer back to the visual modality?" It is not known to what degree the human localisation system is plastic when displaced position information is presented non-visually, and for that reason alone, this question is interesting. Further, if the system shows 'adaptation' when such non-visual position information is used, it seems reasonable to hypothesise that the plasticity will take the same form as in the prism situation, and transfer to the visual modality would be predicted. Thus incorrect localisation of visual targets should occur subsequent to training which involved non-viridical position information derived from the sound localisation system.

On the basis of this sort of analysis, the following experiment was performed in an attempt to produce adaptation similar to that found subsequent to the prism wearing treatment condition. The experiment used position information mediated by the auditory system, and a displacement of 12 degrees was induced between where the subject felt his arm to be, and where he heard it to be. The degree to which any of the 'prism type' adaptation took place was measured by an intermodal transfer situation, namely taking measures of accuracy in pointing to visual targets before and after training on the auditory task.

The null hypothesis was that there would be no difference between the errors measured in the two situations.

Apparatus:

The apparatus consisted of a 4' x 3' bench top some 4' high, on this was a radial scale marking off degree intervals, with origin the long axis of the upper half of the subject's body when he was seated and zero his median sagittal plane, see figure 2. Above the scale was a sheet of plate glass which covered the table top.

During the pre and post-treatment conditions, a removable table top was placed above the first at such a height that when the subject horizontally abducted and

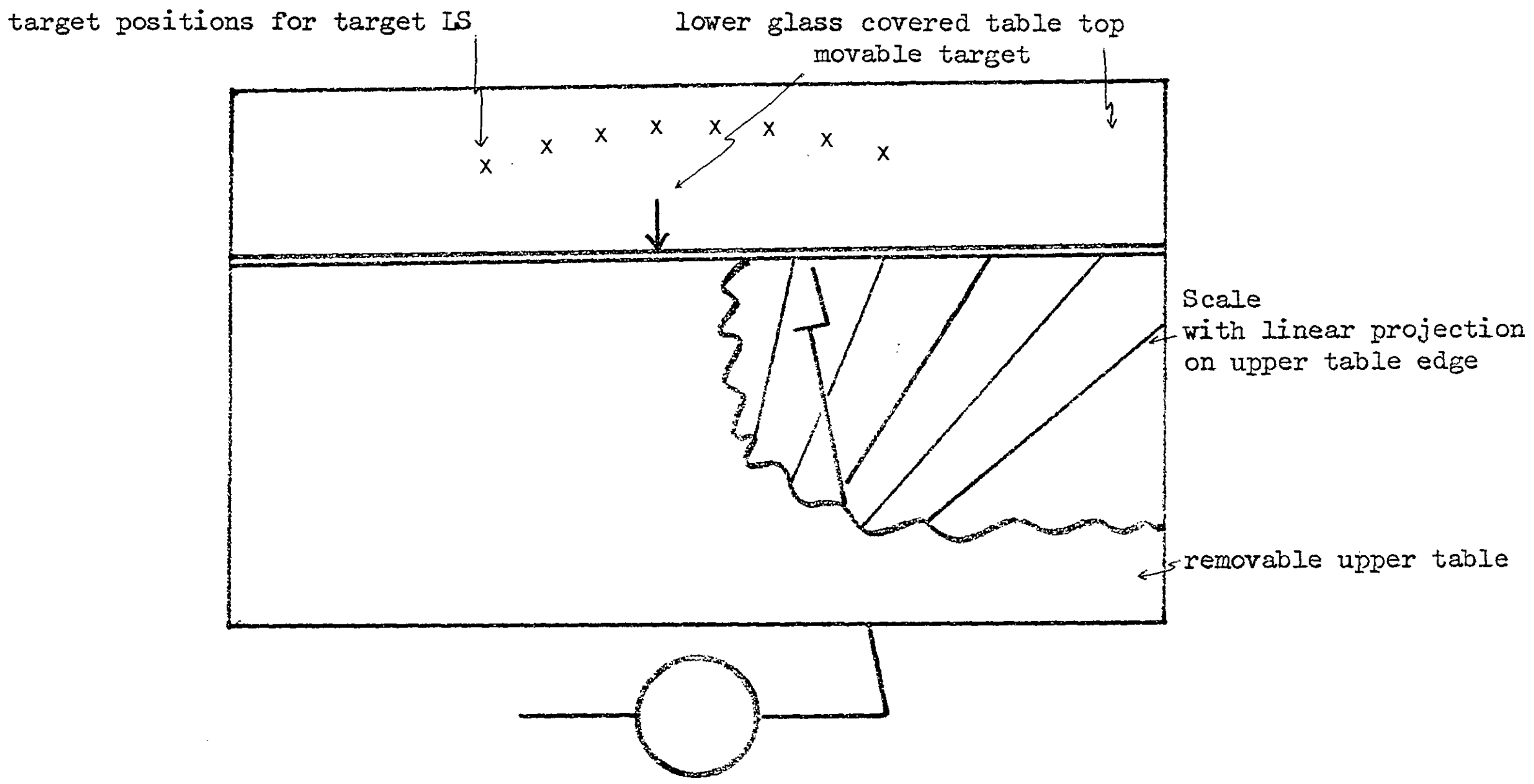

Fig. 2. Diagrammatic representation of set-up for auditory analogue experiment. Subject shown in the testing situation - pointing to line target with no K.R. The upper table top was removed during training and S localised the LS attached to his right arm to the E's LS which was on one of the target positions above. (Neither LS shown).

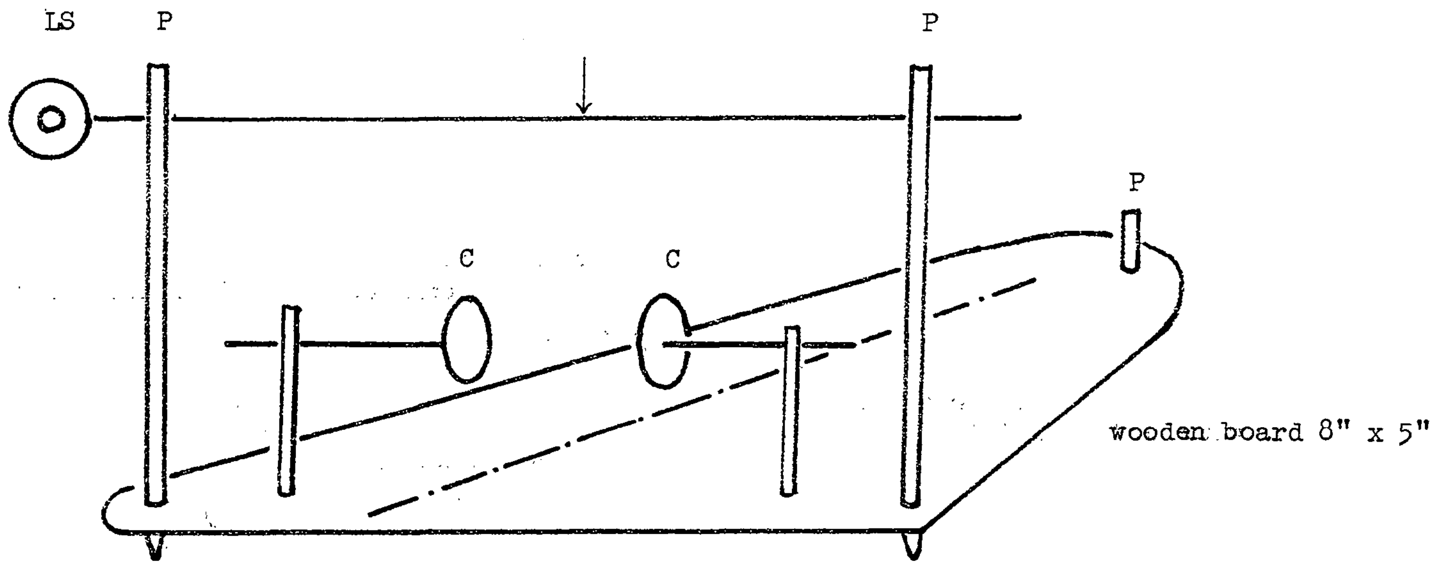

Fig. 3. The carriage, showing LS in position.

The S's hand was fastened between the flat-faced clamps (C); thus his hand lay along the path of the broken line shown. The pencils (P) protruded through the board so their tips could make contact with the glass table top. The LS was believed to be above the hand (arrow) but was offset as shown.

adducted his arm, it could move between the two surfaces without touching either. The edge of this table which was furthest away from the subject was marked with the linear projection of the lower scale, the zero points of the two coinciding. A visual target line could be moved along this back edge of the upper table top, and its position could be read off along the linearly projected scale. This upper table top served to screen the subject's arm when he was pointing to the line target. His error of localisation could also be read off directly from the top scale.

During the training the subject's right arm was kept horizontal, semi-pronated, and the fingers kept extended. The hand was clamped to a small, light carriage using foam padded, round ended clamps, see fig. 3. On top of the carriage was a framework of light rods, the top horizontal of the framework being above the hand and extending seven inches to each side of it; thus a small loudspeaker could be mounted anywhere along this rod. The carriage was mounted on three pencils, one at each vertex, the sharpened ends of the pencils protruding through the floor of the carriage, and thus allowing free sliding movement of the carriage over the glass surface. The carriage had a pointer attached such that the position of the loudspeaker could be read off by E from the radial scale beneath. This small 1½" loudspeaker (LS) was mounted on the top horizontal rod, and was oriented facing the subject.

The E had a similar LS which was mounted on a small stand, and could be moved at will over the surface of the glass. This LS was driven by a pulser which could be made to produce a regular click output at one second intervals. The subject's LS was attached to a Nife cell, and could be clicked by the subject when required by pressing a button suitably mounted by his left hand. These two clicks were both of wide bandwidth, but were easily discriminable. Pilot studies in which the subject was asked to localise the LS by using audition alone and then point to it, showed that in the room used, clicks could be localised the most accurately.

Subjects: The subjects were 18 undergraduates from the University population.

Procedure:

Pre-training measures: The subject was seated on an armless jacking chair and raised until his right arm rested horizontally on the lower table top. A stout wooden bar was moved over until it pressed firmly against the left side of his trunk, and another, attached at 90 degrees to the former was brought in until it was against his back as he was sitting upright. If the subject 'leaned' into the corner formed by these two bars, his body position was controlled fairly well. The head could not be clamped, as free head movements were required during the training session.

The second table top was placed on the first, and the subject was asked to close his eyes while the line target was moved to a position chosen at random by E. Nine target positions were used, namely 10, 15, 20 and 25 degrees to the left and right of the median sagittal plane, and the median plane itself. The subject's task was to open his eyes and then put the index finger of his right hand immediately beneath the target line by means of an adductive movement of the whole arm. This movement started from a point 30 degrees to the right of the median plane. Whole arm movement was ensured by using a splint at the elbow. Two readings were taken at each position.

Training: The second table top was removed, and the carriage was clamped to the subject's right hand. The E's LS and the one mounted <u>immediately above the subject's hand</u> were pointed out to him, and it was explained that he had to learn how to put his own LS in line with the target LS, and that this latter would be put into different positions at each trial. The regular click of the target LS was demonstrated, as was the way of operating the subject's LS which emitted a single click each time the button was pressed. The modus operandi for lining up the two speakers was explained to be as follows. The subject was to localise the target LS by moving his head, and was then to move his arm until he thought it was pointing at the target LS, he would then check by clicking the speaker attached to his hand. When the subject was satisfied that the two speakers were in line, he was to indicate this to E verbally. E advised that the best way to localise the sound was to turn the head from side to side until satisfied that he was pointing his nose at it. The subject was told to delay pointing until this procedure was complete.

At this point the subject was blindfolded, and without his knowledge the LS attached to his arm was moved twelve degrees to his left; the length of his arm having previously been measured in order to compute the appropriate offset distance. One dry run trial was given in order to ensure that the subject understood the procedure. The training proper was then undertaken, the subject attempting to locate the movable LS which was moved on each trial to one of 15 points symmetrical about the median sagittal plane, and spaced four degrees apart, each point appearing in random order without replacement. Each time the subject indicated that he was on target, E measured the error induced between the fingertip and the position of the target. This was done by reading off the error in degrees of the subject's LS from the target LS, and calling this negative when it was further left than target LS. Twelve degrees were then added to this reading, (the amount of the displacement). Thus induced errors in the appropriate direction were positive with a theoretical maximum of plus 12 degrees. Thirty training trials were given, with the subject moving his splinted arm across the table top from the 30 degree right position for each trial. At the end of the training the carriage was removed, and the subject kept his arm at the 30 degree right position, the second table top was put over the first, and the mask taken from the subject's eyes. The post-test was then carried out.

Post-training measures: The technique used to obtain these was identical to that used for the pre-training, consisting of 18 readings of accuracy of pointing with the index finger of the right hand to the visual targets. As before, knowledge of results was prevented by the second table top, and the arm was moved rapidly to the target by means of horizontal adduction. The splint remained on in order to ensure that movement took place via the shoulder joint only.

Results:

Table 8.

Mean errors in degrees in pointing to visual target before and after training with a displaced auditory target

Subject	Before training			After training		
	X	$X-\bar{X}$	$(X-\bar{X})^2$	X	$X-\bar{X}$	$(X-\bar{X})^2$
1	1.1	1.0	1.0	2.3	0.3	0.09
2	2.0	1.9	3.61	6.7	4.1	16.81
3	- 3.1	3.2	10.34	- 1.0	2.7	7.29
4	1.7	1.6	2.56	3.0	0.4	0.16
5	1.8	1.7	2.89	3.4	0.8	0.64
6	- 1.2	1.3	1.69	1.1	1.5	2.25
7	- 0.5	0.6	0.36	1.5	1.1	1.21
8	- 2.7	2.8	7.84	1.4	1.2	1.44
9	0.3	0.2	0.04	1.9	1.1	1.21
10	0.1	0.0	0.00	2.1	0.5	0.25
11	0.7	0.6	0.36	1.8	0.8	0.64
12	- 1.7	1.8	3.24	0.8	0.8	0.64
13	- 1.6	1.7	2.89	2.3	0.3	0.09
14	1.7	1.6	2.56	2.8	0.2	0.04
15	2.0	1.9	3.61	5.4	2.8	7.84
16	0.3	0.2	0.04	2.8	0.2	0.04
17	1.0	0.9	0.81	5.8	3.2	10.24
18	- 0.1	0.2	0.04	3.0	0.4	0.16
Sum	+ 1.8		43.78	+ 46.7		51.04
Mean	+ 0.1			+ 2.6		

Positive is to the subject's right, and in the direction of the induced deviation.

It is first necessary to determine the variances of each of the two samples in order to determine whether they are significantly different from each other.

Variance before = 2.56
Variance after = 2.89

The statistic F is the appropriate test of significance

$$F = 1.13$$

This value for F is not significant at the 5% level. In the light of the equality of variances, an appropriate test for significance of difference of means is t for correlated means. The difference method will be used.

Table 9.

Subtracting errors made before treatment
from those made after
Data extracted from table 8

Subject	Difference, (D)	$(D)^2$
1	1.2	1.44
2	4.7	22.09
3	2.1	4.41
4	1.3	1.69
5	1.6	2.56
6	2.3	5.29
7	2.0	4.00
8	4.1	16.81
9	1.2	1.44
10	2.0	4.00
11	1.1	1.21
12	2.5	6.25
13	3.9	15.21
14	1.1	1.21
15	3.4	11.56
16	2.5	6.25
17	4.8	23.04
18	2.9	8.41
	44.5	136.87

Mean = 2.47

It is first necessary to calculate the variance of the distribution of differences.

$$\text{Variance} = 1.5$$

$$\text{Hence } t = 8.29 \qquad \text{d.f.} = 17$$

For a one tailed test, $p < 0.0005$. The null-hypothesis that errors of pointing to a visual target before and after treatment are not significantly different is thus rejected.

An additional piece of information can be deduced from the average deviation of the subject's arm from the true target position during training if a coefficient of rank correlation between it and the size of the effect on subsequent pointing is calculated. The former is a measure of the extent to which the objective displacement was effective in producing erroneous pointing in training. It is approximate because the reasons for the deviation of the subjects' errors from the expected 12 degrees during the training may well be different from one subject to the next. For example, a high tolerance for positional ambiguity will produce a large variability which in a given small sample of readings could produce results with a low error rate. Alternatively, a given subject might place greater confidence in the positional information from his limb than in that from the LS attached to his hand. An elegant investigation of the relationship between deviation during training and after effect would require at least a measure of mean accuracy, and also the variance of positioning the arm when the subject's LS is not deviated in order that some attack could be made of the problems mentioned above. However the rank correlation as a bonus to the previous experiment may well prove to be informative. In the following analysis, Spearman's rho will not be used owing to the number of ties. Kendall's tau is appropriate.

Table 10.

Average deviation of hand from target during training, and after effect on subsequent pointing
Readings in degrees

Subject	Mean deviation of hand from target during training	Rank X	After Effect	Rank Y
1	6.8	1	1.2	3.5
2	11.2	17	4.7	17
3	7.7	6	2.1	9
4	7.3	5	1.3	5
5	9.6	8	1.6	6
6	7.0	2.5	2.3	10
7	10.0	10	2.0	7.5
8	9.7	9	3.1	14
9	10.1	11	1.2	3.5
10	10.2	12	2.0	7.5
11	9.2	7	1.1	15
12	10.5	14.5	2.5	11.5
13	10.3	13	3.9	16
14	7.2	4	1.1	1.5
15	12.6	18	3.4	15
16	10.8	16	2.5	11.5
17	10.5	14.5	4.8	18
18	7.0	2.5	2.9	13

Recasting the data

X	Y	$i < j$	$i > j$
1	3.5	14	2
2.5	10	8	8
2.5	13	5	10
4	1.5	13	0
5	5	11	2
6	9	7	5
7	1.5	11	0
8	6	9	1
9	14	4	5
10	7.5	6	1
11	3.5	7	0
12	7.5	6	0
13	16	2	3
14.5	11.5	3	0
14.5	18	0	3
16	11.5	2	0
17	17	0	1
18	15	0	0
		k = 108	l = 41

$$S = K - L = 67$$

$$T = 0.45$$

$$\text{Significance of } T = \sqrt{\frac{82}{2754}}$$

$$= 0.17$$

$$\text{Critical Ratio} = \frac{0.45}{0.17}$$

$$= 2.63$$

This value of tau is significantly different from zero at $p < 0.005$. Thus there is a highly significant relation between errors induced in the training and subsequent mislocations when pointing to visual targets.

Discussion

About the same time as the experiments described above were reported, (Craske, 1966b), and quite independantly, Freedman, Gardos and Rekosh, (1966), performed certain experiments among which was one on 'hand-ear co-ordination'. In this experiment they used a training period lasting 4 minutes in which the subject sat in a dark room and listened to an auditory stimulus moved back and forth by one hand. This was perceived via a pair of false pinnae offset by 20 degrees. This kind of training led to a shift of 1½ degrees in subsequent pointing to the median plane after training with the right ear leading. Freedman et al do not attempt to account for their results in the restricted situation experiments apart from commenting that, "spatial orientation is a function of the CNS which is nourished in several ways", and that if one source is altered, the orientation function is disrupted. This tells us very little.

Here it is argued that these auditory experiments which are analogues of prism wearing in the restricted situation, and which produce some form of adaptation which carries over to the localisation judgments for visual objects in the absence of knowledge of results, are consistent with the interpretation that the same form of adaptation has taken place as occurs in the restricted prism situation.

Considering this point, it is clear that the evidence from the auditory analogue experiment is not sufficiently strong to warrant a firm assertion of the 'felt position' explanation. Experiments showing that the unused arm was not affected by the treatment is the biggest piece of missing evidence. The writer, however, is confident that this result would be shown if an experiment which embodied a suitable control for possible adaptation of appreciated head position were undertaken. This is argued on the basis of experiments with prisms which indicate that knowledge of results can be of kinaesthetic origin, (see subsidiary experiment 3). This is meaningful in the present context if it is interpreted as showing that limb adaptation is a response to positional error input when no error was intended. That is, it is being argued that the same short term adaptive response may well accompany any situation which could be devised where a limb movement was involved in localising a target, unusual errors were made, and knowledge of these errors was made available to the subject. It is clear that the auditory analogue situation falls in the above category.

To restate, the suggestion is being made that the adaptation which accompanies the restricted situation prism exposure is the same as that produced by incorrect auditory position information in an analogous situation, and furthermore this form of adaptation may well underlie all situations where accurate limb excursion is intended but not achieved. An example of a test of this hypothesis would be to attempt accurate limb pointing using horizontal abduction and the perceived error technique, with the limb moving against a large constant load. Informal observations by by the writer suggest that training of this sort does produce errors in the predicted direction, although no controls were run for any effect which might be due to the Konstamm phenomenon.

To turn to the highly significant correlation between errors of pointing induced in the training situation and those exhibited in the subsequent localising of visual targets. This accords well with common sense expectation, and can be interpreted as indicating that when a distance is determined from a felt starting position and a heard desired position, and when the M.O.T.F.P. used to move the limb does not initially produce the desired result, a change in the felt limb position occurs; thus preserving the M.O.T.F.P. Furthermore this change produces an after effect proportional to the degree of change required to correct the error of localisation during training. It can be readily seen that if the word 'seen' is substituded in the above in place of 'heard', a prediction is made about the prism situation, and the argument is identical to that which has appeared in section 4d.

This identity of the two arguments, one appropriate to displaced auditory stimuli, and one for prism displaced visual stimuli, supports the contention that one form of adaptation underlies both situations, and leads to the possibility that it also underlies adaptation in all situations where accurate limb excursion is intended but not achieved.

Experiment 4

Identical prism after effects shown for pointing to visual targets and contra-lateral limb

When this experiment was undertaken, there was available to the writer considerable evidence supporting the hypothesis that there was a change in the felt position of the used limb subsequent to restricted situation training procedures. The thinking of Held and his collaborators however was still firmly against such an interpretation. Held and Efstathiou, (1964), claimed that they wished to show that, "these claims are based upon a dubious interpretation of the Helmholtz experiment, and that they reflect assumptions in need of revision". This paper went on to report two experiments. These experiments are also the subject of another preprint, (Efstathiou and Held, 1965), and of a paper, Efstathiou, Bauer and Held, (1967), and the claim is made in the former that the hypothesis relating to a change in the felt position of the used limb is "contradicted by new experimental evidence". One piece of this evidence is the subject of this experiment.

Efstathiou et al, (1967), make the statement that shifts in reaching to visible targets generalise to such non-visible targets as sound sources and the 'straight ahead'. Thus, they argue, if the 'felt position' hypothesis is true, such a change ought to effect the accuracy with which pointing can be effected both to visual targets and to targets such as the unexposed limb, the position of which is not visually derived. They went on to show that the accuracy with which the unexposed limb and a visual target were localised subsequent to adaptation, was significantly different at the 0.001 level for t.

The force of the argument cannot be denied, and their result constitutes a severe criticism of any mechanism put forward to explain restricted situation prism adaptation which is based on change in felt position of the limb. In that there was strong evidence supporting such an idea, (Hamilton, 1964, Harris, 1963, experiments 2a and 2b reported here), it was decided to repeat the experiment with the addition of certain controls and utilisation of the perceived error technique during training. The null hypothesis is that there will be no difference in the localisation of visual targets and the contra-lateral limb subsequent to prism training in the restricted situation. This also is the prediction based on the 'felt position' hypothesis.

Apparatus

The apparatus was identical to that used in experiment 1.

Method

Subjects: The subjects were ten undergraduates from the University.

Procedure: The subjects were seated so that their prone right arm could lie fully supported in a horizontal position on the lower glass sheet, and maintained so that the right shoulder joint was at the origin of the circular scale marked on the glass, which was used to measure errors of localisation in degrees. When required, the left arm was supported under the lower glass sheet, in the semi-prone position and in the sagittal plane which passed through the point of rotation of the left arm. The support was a pad of polyether foam plastic, and the position of the arm was controlled by means of nylon ended rods (similar to those used in experiment 2, see plate 3). Another glass sheet was mounted 5" above the first, and could be covered as necessary. It also served to support the five hairline targets which were always symmetrical about the visual straight ahead, i.e., when the subject was wearing prisms, the centre target was displaced by an amount appropriate to the power of the prisms, in this case, 11 degrees 19 minutes. The head was kept immobile throughout the experiment by using a dental wax bite.

The experiment was in five parts:-

1. Pre-training measures: a

The subject made 25 pointings, adducting the prone right arm from any position on the far right to one of five visual targets which were called in random order by E. These were placed at intervals of ten degrees, symmetrical about the mid-sagittal plane. The error in degrees of limb excursion was recorded by E for each localisation; the subject was not allowed knowledge of results.

2. Pre-training measures:

The subject made 25 localising responses, adducting the prone right arm as before. The target was the index finger of the contra-lateral arm. This arm was extended along the sagittal plane passing through its point of rotation, and was held semi-pronated, with the tip of the index finger in contact with the under surface of the lower glass sheet. This series of localisations were taken in batches of five, and as rapidly as possible. This was to balance conditions before and after the training procedure. Once again E recorded the errors made by the subject in degrees of limb excursion.

3. Training:

The subject wore twenty dioptre base right prisms as previously described. He was then seated appropriately with his right arm extended in the semi-prone position on the lower glass sheet. He was asked to point at the visual targets which E called out in random order. These targets were now arranged about an axis displaced by 11 degrees 19 minutes to the subject's left. The subject obtained knowledge of results by raising his extended index finger once the limb excursion was complete. These arm movements were ballistic in nature, the subject attempting to get on target with one smooth movement.

This training was continued until five consecutive localisations correct to within plus or minus 0.5 degree had been made.

4. Post-training measures: a

With the subject using his right hand five readings of the subject's accuracy in pointing to visual targets were taken, the subject not wearing prisms, exactly as in pre-training measures (a). This consisted of E calling out the five targets in random order. The training procedure as above was then repeated to criterion, and five more readings taken, and so on for a total of 25 readings. Knowledge of results was not allowed.

5. Post-training measures: b

Five readings of the subject's ability to point with his right hand to the index finger of his contra-lateral hand were taken. This was followed by the training procedure to criterion level, subsequent to which five more readings were taken, and so on for a total of 25 readings. Once again, no knowledge of results was allowed.

Results

A summary of the results is shown in table 11.

Table 11.

Mean errors in degrees in pointing to visual targets and the index finger of the contra-lateral limb (Measurements were to nearest 0.5 degree, means have been correspondingly rounded)

Subject	Mean error visual targets	Mean error for contra-lateral limb
1	5.5	6.0
2	3.5	3.5
3	3.0	3.0
4	1.5	1.5
5	4.0	4.0
6	3.5	4.0
7	5.0	4.5
8	5.0	5.0
9	4.0	4.0
10	4.5	4.5
Mean	3.95	4.0

Inspection of the above results is sufficient to lead to the adoption of the assumption that the variances of the two distributions are not significantly different. In order to quantify the level of confidence with which it is possible to assert that the means are not significantly different, t for dependent samples is an appropriate statistic.

The sum of the differences of the two columns of means is 0.5, and the sum of the squares of differences is 0.75. These figures are obvious from inspection.

$$t = 0.76 \quad df = 9$$

for two tailed test $p > 0.30$. The 95% confidence limits can be seen to be 0.05 ± 0.129 degrees. The evidence is clearly insufficient to warrant the rejection of the null hypothesis, and therefore these results are fully in accord with the hypothesis that adaptation to prisms in the restricted situation can be explained by a change in transfer function associated with position receptors in the shoulder joint.

Discussion

Firstly a note on procedure. It might be argued that one visual target would balance the single target in the other condition, namely the index finger of the contralateral hand. But the danger was that one visual target in the median plane might be pointed at without using vision as the only input source, i.e., the subject might use some kind of position preference, and point with little reference to his visual input. Thus five targets were used.

The above results are directly in conflict with those reported by Efstathiou et al., as would be predicted on the 'felt position' hypothesis, and provided that an explanation for their contrary results can be found, the ground is cleared of what seemed a serious objection. Latterly Hamilton and Hillyard, (1965), have also presented evidence consistent with the felt position hypothesis from a similar experiment to that reported above.

It would seem sensible to examine the way in which Efstathiou et al account for their result of $p < .001$ for t. They suggest that reaching for a visible target consists in "orienting the arm so that the direction of a line drawn from hand to eye matches the actual or potential direction indicated by the head when it is oriented to the target". Thus adaptation consists of the "establishment of a new set of matched orientations between the exposed arm and the head".

Now considering the sense of the above; one has only to ask <u>how</u> the arm can be oriented in a given position in the absence of vision. The only sensible argument in the light of what is known about position sense in limbs, is that the arm is moved <u>from a felt position.</u> Knowledge of the desired position is to a certain extent given by the position information indicated by the head; but more sensible it is argued would be to achieve the desired position by taking into account the position indicated by the eye, <u>and</u> the orientation of the head. The writer cannot give a meaning to a 'potential direction' indicated by the head.

It must be concluded that the 'matched orientations' referred to in fact mean matching the felt position of the arm to the position information from the head/eye complex. It is not clear how this differs from the felt position hypothesis. It seems then that the alternative theory offered by Efstathiou et al is no alternative, and the meaning of their results must be sought elsewhere.

Craske and Gregg, (1966), have argued that the original results of Efstathiou et al may be explained by change in the position sense of the eyes due to some part of their procedure. For instance they do not use the perceived error adaptation technique, and it is possible that their treatment condition provided enough discordant kinaesthetic/ eye position information to give rise to some change in the eye system. It is clear that if the eye position system was implicated, then the apparent position of their visual targets would be affected more than the position of the targets which were located without the mediation of vision.

At this juncture it must be remarked that there is another experiment reported in the paper by Efstathiou et al which claims the invalidity of the 'felt position' hypothesis. This is the subject of the next experiment.

Experiment 5

Effect of adaptation to prism displacement on reaching to remembered positions

The background to these experiments is experiment 2 reported by Efstathiou et al., (1967), first reported by Efstathiou and Held, (1964). In this it was shown that subjects who were exposed to prismatic displacement subsequently showed no increase in errors in reaching to targets the location of which had previously been learned without the aid of vision.

Now in the writer's view, the weight of evidence so far favours the felt position hypothesis as an explanation of restricted situation adaptation, thus this result, which runs counter to this notion justifies a closer look. Also there is the fact that prism adaptation affects pointing to the 'straight ahead', (Goldstein, 1965, Harris, 1963, Pick, Hay and Pabst, 1963); and it can be plausibly argued that the following two situations are similar. 'Point to a position coincident with your median sagittal plane', and 'point to a position at x degrees to your median sagittal plane'. It is readily appreciated that this latter situation can be thought of as identical to reaching for a remembered location provided distance from the body is specified. If this view is accepted, then it would be predicted that reaching to remembered targets would be affected by adaptation procedures.

Two separate attacks were launched at the same time.

5(a) Pilot experiment

Apparatus: A dental impression was permanently mounted above a bench top at such a height that a subject could bite upon it while sitting comfortably on a high stool.

Mounted in front of him was a vertical board with one ⅝" hole drilled in a position 4" below the level of his nose and 6" to the right of his median sagittal plane.

Subjects: There was only one subject, the writer.

Procedure:

Preliminary training: This consisted of 100 trials per day in two sets of 50, morning and afternoon. Each trial consisted of an attempt by the subject to put his extended right index finger into the hole in the board with one smooth movement. The eyes were kept closed during each training session, and each movement begun from a position picked at random from an imaginary line drawn just in front of his midriff. Care was taken not to touch his body with his right hand when it was in the starting position. Training was continued until 50 trials could be completed with an error rate of 2% or less. This took 38 days. Such a severe criterion was erected in order that subject variability was cut to a minimum.

Pre-training measures: The subject put his right index finger into a thimble which was packed with plasticine so that it fitted the finger shape perfectly. The front end of this thimble had a ¼" spike mounted in the middle. Ten localisations of the remembered position of the hole were taken just as in the preliminary training, but the original board was replaced with another covered by ⅛" foam procedure was repeated ten times.

Results

Table 12.

Mean lateral errors in tenths of an inch in pointing to a remembered location without knowledge of results (plus indicates to S's right, and is predicted direction of effect)

Trial no.		Before treatment	After treatment
1		-2	+8
2		-3	+9
3		-7	+8
4		-8	+9
5		-1	+9
6		-6	+5
7		-2	+8
8		-4	+9
9		-3	+8
10		0	+6
	Sum	-36	+79
	Mean	- 3.6	7.9

Taking the 'before' measures, we may calculate that the standard deviation is 2.63 whence the standard error of the mean equals 0.83. Hence for the 'before' measures the 95% confidence limits are within the range -3.6 ± 1.96 x 0.83, i.e., lie between -5.3 and -1.97. This is not satisfactory insofar as this does not include zero, and clearly does not match up to the accuracy experienced during the training; it is possible that this result is due to the added length of the finger when wearing the spike ended thimble, (i.e., the finger is hitting the board slightly too early). If this explanation for the asymmetry of initial errors is accepted, then we may go on to test the difference between the two sets of means.

For the 'after' measures the standard error of the mean equals 0.77, and the 95% confidence limits are within the range 3.76 ± 1.96 x 0.77, i.e., within the range 2.25 to 5.27.

The variance of the two sets of means are respectively 6.9 and 3.755, hence $F = 1.835$ which is not significant at the 5% level.

Thus t for for correlated means is appropriate.

$$t = 11.95 \quad df = 9$$

for one tailed test, $p < 0.0005$

Thus there is sufficient evidence to warrant rejection of the null hypothesis that restricted situation prism adaptation does not affect reaching to remembered positions. Great care must be exercised in evaluating this result however, for the fact of statistical significance gives no information as to the <u>relative size</u> of the observed effect vis a vis that which would be observed in the usual situation where the subject points to visual targets. If reference is made to subsidiary experiment 2, it can be seen that 30 seconds exposure to 20 dioptre prisms can produce an after effect of some 66% of the deviation produced by the prism. In the experiment reported above, the prism deviation at arm's length is some 6 inches and the difference between the means is 1.1 inches, thus there is an after effect with a magnitude of only about 16% of the imposed deviation. There seems to be something different about this situation on the evidence of this pilot experiment, but discussion of this will be deferred until after the following experimental evidence.

5(b). An experiment using skilled pianists

This experiment is on a larger scale than the first, the topic under investigation still being a direct attack on the effect of restricted situation prism adaptation on remembered locations. The idea here was to use as subjects a group of people who had apparently overlearnt the positions of objects in their front parallel plane; thus subjects were selected on the basis of their ability to play the piano.

Procedure: The subject was allowed to adjust his position in front of the piano until he was confident that he could locate the middle C key without visual guidance. A platform was placed over that part of the keyboard. The centimetre scale attached to the platform was so positioned that its zero was immediately over the middle C key.

Pre-training measures: The blindfolded subject placed the tip of one finger of his right hand on the platform at the estimated position of the middle C key. The choice of the finger used was left up to the subject, but remained consistent throughout the course of the experiment. After each trial the subject was instructed to move his hand to a differing starting position, and at no time was he allowed to touch any part of his body with his right hand or arm. Ten trials were used, the error of each localisation being measured each time.

Training: The subject wore base right 20 dioptre prisms and sat in front of a horizontal screen at shoulder height. On the top of the screen were six targets symmetical about the objective median plane and spaced 5 degrees apart; each line target was surmounted by a different letter. During the 2½ minute exposure condition, E called out target letters in random order at a rate of one per second. The subject had to shoot his right arm beneath the board in a direction which he thought appropriate to the target called, knowledge of results was obtained when the finger finally appeared from beneath the screen, i.e., the perceived error technique was used.

Post-training measures: The subject shut his eyes, and the board and the spectacles were removed. He then made ten more attempts to place the tip of his finger at the position of middle C on the platform. The errors were measured as before.

A control condition was used which was identical to the above procedure except that the exposure condition was run without wearing the spectacles.

<u>Results</u>

Table 13.

Before and after treatment difference scores
in localising middle C for two conditions
A plus deviation is in the adaptive direction
for base right prisms

Subject	Control	Experimental	Difference
1	-3.3	-2.7	+0.6
2	-3.3	-3.95	-0.65
3	+0.2	-1.85	-2.05
4	-0.4	-0.5	-0.1
5	-1.85	+5.1	+6.95
6	-4.2	+1.2	+5.4
7	+1.7	+0.85	-0.85
8	+0.5	-1.15	-1.65
9	-5.2	-5.05	+0.15
10	-1.5	+3.6	+5.10

The mean of the differences $\doteq 1.29$, and the standard deviation of the mean $= 1.03$, $t = 1.25$ for $df = 9$. $p > 0.20$. This is not significant.

Thus no significant shift occurs in the location of a remembered target as a result of exposure to prismatic displacement, a result which is in accord with that of Efstathiou et al, but not with that of the first pilot experiment.

Discussion: These results are rather puzzling, the more so because they are not consistent. At this point the results of Hamilton and Hillyard, (1965), are of interest, for they highlight the inconsistency. These investigators tested visually directed reaching and reaching for remembered locations. For ten minutes the subject used his dominant arm to learn the position of three pegs, without the aid of vision. Pre-training measures were taken in darkness and consisted in the subject pointing to a luminous spot and to the three remembered positions with both hands. Adaptation procedures were then carried out for ten minutes, followed by post-training measures as above.

The findings were that both visual targets and remembered targets were affected by the adaptation procedure, but that visual targets showed greater adaptive effect than did the remembered ones. Now these are the same sort of observations which were made on the results of experiment 5a above, but are not consistent with the findings of Efstathiou et al, or of experiment 5b.

The writer would wish to interpret this data as follows. Firstly it is not immediately argued that this disposes of the felt position hypothesis, for since there is so much evidence to the contrary, it seems sensible to seek an alternative explanation. For example it is suggested that there is more than one modus operandi for reaching, and that which one is used depends upon the task in hand. It has already been argued that a common 'reaching process' is that whereby a visual object is given a position on some internal scale; the felt position of the arm is also given a position on the same scale and simple subtraction gives the distance to be moved. A decision is made on the speed at which the limb is to move, then the appropriate M.O.T.F.P. is produced to move the limb to the desired position. This hypothetical process clearly relies on felt starting position of the limb, and is appropriate to prism adaptation situations where visual targets are used and the starting position of the hand is not visually monitored.

The results from the above experiment suggest that under some circumstances where limb movement occurs, felt starting position of the limb is ignored. For under such a circumstance restricted situation adaptation can occur, yet it does not show up in the testing situation. It is argued that it is likely that such a class of movement processes may well be involved in movements which are automatic, for example, moving the foot from the accelerator to the brake for an experienced driver. It is easy to demonstrate that if the braking foot is put in an unusual initial position, one cannot be sure where to direct the foot to reach the brake, i.e., it is not the position of the brake which has previously been learned, but the instructions appropriate to moving the foot there. It follows that if the appropriate instructions are known, then felt starting position information is redundant, and need not be used in the overlearnt situation.

The application of this line of argument to the experiments reported above is as follows: Hamilton's and Hillyard's movement situation would not fall into the category of 'overlearnt' movements in that only ten minutes training was used. It follows from the above that the felt starting position of the limb would play what is claimed to be its normal role in pointing in the testing situation, and consequently prism after effects of near normal size were shown when the subject pointed to remembered locations.

Experiment 5a showed a much reduced after effect, it is argued that this reduction is due to the more prolonged training which led to the subject performing in a more nearly automatic fashion, and thus, it is argued that felt limb position played less part in the sequence of events which led to placing the limb in the remembered location. Hence the small after effect.

The experiment of Efstathiou et al, and experiment 5b above used subjects who had sufficient practice to operate in an automatic fashion, and it has been argued that it is under those circumstances that felt position of the limb is ignored, and thus no after effect was shown.

An informal check was made of this finding using a mock-up of the accelerator - brake - clutch assembly of the writer's car. The task was to simulate emergency stops, and to note the position of the braking foot when it had come to rest. (A line on the shoe served to indicate foot position). After taking a number of readings of braking position in this way, adaptation trials were undertaken, attempts being made to kick a target seen through prisms. When kicking was fairly accurate, the prisms were removed, the feet were placed on the 'accelerator' and 'clutch' and another series of 'emergency stops' were undertaken. <u>No adaptive effect</u> was observed under these conditions; whereas if an attempt was then made to kick the training target, <u>a large adaptive shift was shown</u>.

It must be made quite clear that the above analysis is speculative rather than one based on hard experimental evidence. However it fits the experimental evidence we have so far and indicates that certain circumstances can lead to no prism after effects, (i.e., when automatic movements are used in the testing situation). Further work along these lines is desirable; an experiment plotting after effect as a function of number of trials on a single test movement would serve to test the above ideas, for as n got very large, the movement should become more and more automatic, and less and less after effect should be shown.

Section 7

The Free Situation

The distinction between the restricted and the free situation was first made by the writer to describe the two states which gave demonstrably different results after wearing prisms. In the first, only the used limb shows adaptive after effect, and in the second all limbs show this form of adaptation, (see section 3). It is a reasonable hypothesis that the major component in the production of this after effect is a change in the appreciated position of the eyes, though a contaminant may be some effect due to a postural after effect brought about by holding the head to one side while wearing the prisms.

The questions which are the concern of this section are two, namely, a) are the eyes involved in free situation adaptation, and b) what is the essential aspect of the free situation which is instrumental in bringing about the observed after effect?

It will be shown that a change in the appreciation of eye position is the prime cause of adaptation in this situation, and a major component in producing this change is prolonged inspection of the limbs. It can be inferred that 'eye' adaptation is the end point of any lateral deviation prism exposure situation, since as the duration of the exposure condition increases, so will the inspection period of the limbs tend to be 'prolonged'.

From the above it can be seen that the interpretation of the term 'free situation' will be that the subject is free to see his own limbs, movement of the limbs playing no part in producing the adaptation.

Experiment 6

Evidence suggesting eye involvement in adaptation

Introduction:

There was a certain amount of inferential evidence for the implication of the eyes in adaptation which took place when the subject was free to walk around while wearing prisms. For example, pointing with both hands is affected, (Bossom, 1964; Bossom and Held, 1959; Cohen, 1963; Hamilton, 1964; Harris, 1963; Held and Bossom, 1961; Pick and Hay, 1964). Change in egocentric orientation had also been reported, (Bossom, 1959; Bossom and Held, 1957; Held and Bossom, 1961; Held and Mikaelian, 1964; Pick and Hay, 1964).

Harris, (1963), has commented that, 'when a person adapts by walking around while wearing prisms..... the felt orientation of head (or eyes) relative to his body is changed'. Mittlesteadt, (1964), has also argued that since orientation in the visual world consists of a number of subsystems, (eyes, head, body, limbs), then adapting to a disturbance is unlikely to bring into action a unitary mechanism - it will depend upon the subsystem involved. The experiments of McLaughlin and Bower, (1965), and McLaughlin and Rifkin, (1965), may also be interpreted as change in the registered orientation of the eyes, as Harris, (1965), has pointed out.

Wallach, Kravitz and Lindauer, (1963), did an experiment involving inspection of the static body through prisms. This was sound enough in principle, but produced some incomprehensible results, however their main observation was that the technique seemed to produce an altered evaluation of visual direction. Held and Mikaelian, (1964), summarily dispatched the adaptation shown following this exposure technique as unimportant, in that it was not supposed to have 'the generality shown by the involvement of the motor-sensory feedback loop'. This rejection without examination has led to Held failing to realise that it constituted a considerable blow to his theoretical scheme, as also is the case with the findings of Weinstein, Sersen, Fisher and Weisinger, (1964), which were that was repeated 30 times at which time he was instructed to stop and close his eyes.

Post-training measures: The subject kept his eyes closed and was led to the bite on the table top onto which he put himself by feeling with his mouth. The trial frames were removed, the subject opened his eyes and pointed 18 times just as in the pre-training situation.

The null hypothesis was that there would be no shift in pointing due to the treatment.

Results

Table 14

Total errors in cms. before and after training
Pooled results for both arms

Subject		Before	After
1		- 10.5	- 77.0
2		+ 67.0	+ 28.5
3		+ 7.5	- 51.5
4		+ 11.0	- 28.5
5		- 11.5	- 18.0
6		+ 37.5	+ 10.5
7		+ 45.5	+ 9.0
8		- 13.5	- 32.5
9		+ 77.0	+ 60.5
	Sum	+210.0	- 99.0
	Mean	+ 23.3	- 11.0

$\bar{D} = 34.3$; Sum of $D^2 = 14,981$

$t = 4.39$ with df $= 8$

This is significant at $p < 0.005$ for 1 tail test, thus the evidence is sufficient to warrant the rejection of the null hypothesis.

It is now sensible to ask whether eye involvement is a likely explanation. If the observed increase in errors is due to a change in appreciated eye position, it would be predicted that both the right and the left arm would be affected to the same extent, and thus there should be no significant difference between the errors due the right arm and those due to the left. This hypothesis can be tested by treating the data for the two arms separately.

Table 15

Difference in cms. between before and after errors of pointing for right and left arms

Subject		Right arm	Left arm
1		28.5	38.0
2		17.5	21.0
3		30.0	28.5
4		16.0	23.5
5		7.5	5.5
6		15.0	6.0
7		23.0	13.5
8		7.0	12.0
9		7.5	9.0
	Sum	152.0	157.0
	Mean	16.9	17.4

$\bar{D}$ = 3.11 Sum of D^2 = 363.5

An appropriate statistic is t for correlated samples.

$t = 1.68$ with $df = 8$

There is no a priori reason for using only one tail of the distribution. The above result is not significant at the 0.05 level, thus the evidence is insufficient to warrant the rejection of the null hypothesis.

Discussion

The results show directly that adaptation occurs in a situation where the subject only sees his feet and where head and body are immobile. It is a reasonable inference from table 15 that a change has occured in appreciated eye position. The inference is quite a strong one insofar as the head was held symmetrical about the median sagittal plane during both exposure and testing conditions, thus postural after effects would not be expected. Furthermore during the testing the eyes fixated the same three target positions and yet pointing with both arms was affected to the same degree.

There is independant clinical evidence that change in appreciated eye position can occur. Von Noorden, (1963), has reported a case of a patient in which two peripheral retinal areas which would be disparate under physiological conditions, each behaved as the centre of sensory motor orientation under monocular conditions. This suggests that spatial values for a given eye posture are not immutable, though the aetiology of the case is considerably different from that which is being considered here.

There are two points arising from this experiment, and these are: a) Is the saccade of the eyes to fixate the feet a necessary part of the exposure condition?

b) The observed results could equally well be explained on the notion of a change in retinal spatial values.

Concerning a) Following the evidence that tracking movements and saccadic movements may have separate control mechanisms, (Rashbass, 1961), Festinger and Cannon, (1965), have reported that the human orientation system gets more positional information from saccadic movements of the eyes than from tracking movements. This could suggest the importance of eye movement in the adaptive process. Concerning b) The hypothesis sounds a little unlikely, but Cohen, (1963), obtained evidence which may be interpreted this way.

Both these points can be subjected to experimental test. The first by repeating experiment 6 without voluntary eye movements; and the second by asking the subject to position the eyes straight ahead before and after adaptation. Even before performing these experiments, however, it seems appropriate to comment that Harris' (1966) argument that vision modifies limb position sense when the two are in conflict, seems not to hold if the limbs are immobile. If the position information derived from the oculo-motor system is labile as well as that from limb proprioceptors, the further claim made by Harris, that it is likely that humans use built in visual information to calibrate limb position sense, is not true in the strict sense; and there certainly seem to be relativistic problems in using either of these position inputs to calibrate the other.

Experiment 7

Evidence that voluntary eye movement is not needed to produce adaptation compatible with change in appreciated eye position

This experiment follows directly from point a) of the discussion of the last experiment. The null hypothesis is that the exposure condition will not affect accuracy of localisation if voluntary eye movements are not used during the exposure.

Apparatus:

The apparatus is illustrated in figure 4. It consists of a horizontal board 21" long and 3' wide mounted on 8" high legs. The length of the board could be increased to suit any particular subject by means of a sliding panel. Attached to the front of the horizontal board was a rigid vertical board. Half way up this was a slot in front of which a pair of prisms could be swung as required. An inclined board running from the top of the vertical one, to two inches above the far end of the horizontal one, gave the subject a field of view which was restricted to an horizontal band. Below the slot was a solid mounting for a dental wax bite.

The subject could comfortably slide his arm under the horizontal board which served the dual purpose of covering the whole arm except the finger tip, and in the testing condition obscuring the whole arm. Under these latter conditions E could read off errors in pointing from a scale along the edge of the panel. The target was a fine line which could be moved along the front of the sliding panel. The subject could be raised until the horizontal board was at mid-chest height by means of an hydraulic jacking chair.

Method

Subjects: The subjects were ten students in the University of Durham.

Procedure: The prisms were adjusted to the inter-pupilliary distance of the subject, and then swung aside. The subject was then adjusted for height, and asked to bite on the dental wax mouthpiece. Any tendency to body swivel was controlled with a trunk holder. These devices did not interfere with reaching movements of the arm.

Pre-test measures: The single line target was moved into one of five positions symmetrical about the visual axis and five degrees apart. The subject pointed at the target with right and left hands alternately for a total of twenty pointings with each hand. Throughout his arms were under the horizontal board and thus he was without knowledge of results. Viewing took place without prisms.

Training: The 20 dioptre prisms were swung into position and the subject extended his right arm beneath the horizontal board in such a way that the tip of his index finger could be seen to be in the middle of the prism altered visual field. The subject's whole arm was supported on a moulded polyether pad, and strict instruction was given to hold the limb quite immobile during the ensuing inspection period. The subject then inspected his immobile fingertip for three minutes.

Post-training measures: Subsequent to this inspection, the prisms were swung away and five pointings with both right and left arm were taken as in the pre-test. The treatment condition was then repeated, followed by the post-test until a total of twenty post-inspection pointings had been taken for each hand. This procedure was adopted to guard against the possibility of rapid decrement of after effect with time.

All error readings were in degrees, the circular scale, origin between the eyes, being projected onto the straight edge of the board.

Results

Table 16

Mean errors in degrees for right and left hand before and after exposure to prisms

Subject	Mean error on pre-test		Mean error on post-test	
	Right Hand	Left Hand	Right Hand	Left Hand
1	3.2	2.9	6.7	7.2
2	0.6	0.9	6.1	3.9
3	-2.1	-1.5	3.3	4.1
4	1.0	1.7	8.6	8.4
5	1.2	0.3	2.4	6.3
6	-1.9	-1.6	9.1	8.9
7	-2.4	-2.0	5.4	5.0
8	2.6	2.1	8.2	6.6
9	1.3	1.0	5.7	6.0
10	1.1	1.9	9.8	7.2
Sum	5.6	5.7	65.3	63.6
Mean	+0.56	+0.57	+ 6.53	+ 6.36
s	1.836	1.636	2.325	1.588

The 95% confidence intervals of the above means are respectively:- 0.56 ± 3.58; 0.57 ± 3.21
6.53 ± 4.56; 6.36 ± 3.11

Pooling the results for hands before and after exposure, t for 9 degrees of freedom = 8.33 $p < 0.0005$. This level of significance is sufficient to warrant the rejection of the null hypothesis.

An immediate objection to interpreting this result as being due to seeing the finger, is that maybe the whole set of results is due to the subject holding his eyes to one side; as indeed he has to when inspecting a target in the median sagittal plane through prisms. In order to guard against this possibility, the following experiment was carried out with six of the above subjects. The null hypothesis was that the treatment condition would not increase errors of pointing.

Apparatus

The apparatus was that used in the test procedure of experiment 6, namely the horizontal board with the bite mounted above it; all at such a height that the subjects could stand while being tested.

Method

Procedure: The subject bit on the dental impression, and using each arm alternately pointed to two targets standing at arm's length on the table top of the apparatus above. Five readings were taken for each arm, the targets being called in random order by E. The subject was then asked to stay on the bite, but to fixate a small object placed at arm's length 30 degrees to the left of the subject's median sagittal plane. This asymmetric fixation point involved the subject in holding the eyes in the same direction as in the treatment condition of the previous experiment, but at nearly three times the deviation.
The supposition being that if the after effect of the last experiment was due to holding the eyes to one side, this

procedure should show it up even more clearly.

At the end of the 3 minute fixation period, a further five readings of the subject's accuracy in pointing to the targets was taken. After a period of anti-adaptation, this procedure was repeated, each subject therefore gave two sets of 10 readings.

Results

Table 17

Mean errors in pointing before and after 30 degree asymmetrical convergence
Positive errörs are to the subject's left

Subject		Before	After
1		-1.05	-1.85
2		-2.1	-1.8
3		-2.9	-2.7
4		-2.0	-1.9
5		2.5	4.3
6		4.2	5.2
	Sum	-1.35	1.25

$\bar{D} = 0.43$ Sum of $D^2 = 5.02$

t for correlated means is appropriate.

$t = 1.23$ df = 5

$p > 0.15$

This difference cannot be considered statistically significant, and the evidence is insufficient to warrant rejection of the null hypothesis.

Discussion

It seems quite clear from the two experiments above that voluntary saccades of the eyes are not a necessary prerequisite to a change in appreciated eye position, and nor is any of the observed after effect on pointing due to the subject having to hold the eyes to one side during the inspection period.

The idea of I. P. Howard, that what adapts depends upon type of training is perhaps not so useful a predictor as it at first seemed. It certainly would not be immediately evident that the eye would show an adaptive effect after inspecting the immobile fingertip.

Perhaps a more useful way of thinking about this form of adaptation is as follows. When the subject looks at his feet or his fingertip through prisms, the positional information available to him via his limb proprioceptors, and that via the proprioceptors of the neck and the position system of the eyes, are in conflict by an amount equal to the displacement minus any slackness there is in the total localising system, (i.e., the amount of imprecision with which the eye can localise the finger tip).

Now it has already been argued that the evidence for adaptation in the felt position of limbs is consistent with there being a motor component; more specifically, it has been suggested that the felt position of the limb undergoes change as if to preserve the normally appropriate M.O.T.F.P. of the command of the limb. If this is accepted, then it follows that the immobile limb will not show adaptation to the position conflict, for the immobile limb shows no muscular activity, (Basmajian, 1966). The same is true for the proprioceptors of the neck, since the head is kept still in these experiments. It follows further that if any adaptive mechanism exists to remove the conflict, it must involve the visual system. It seems that there is an adaptive mechanism to 'reset zero' within the visual system, and so far it can be said that it is either in terms of appreciated eye position, or change in retinal space values.

A question to be answered is how is it that no 'eye effect' occurs in the restricted situation? A tentative answer is that perhaps the lability of the limb is considerably greater than that of the eye when limb movement is occuring. It is also possible, and pilot experiments tend to confirm, that the 'eye effect' does occur to a certain extent if restricted situation adaptation is prolonged. It cannot currently be said whether the eye would gradually assume the whole of the adaptive shift in very prolonged restricted situation experiments, or whether it would only 'take up the slack' i.e., adapt to the extent that the limb could not adapt to the maximum.

At this stage it is possible to comment about the Held and Bossom experiment, (1961), in which subjects who of an eye centering system systematically, and many parts of the brain can be implicated in the centering function, (Bender, Teng and Weinstein, 1954). Electromyographic evidence supports the idea of a positive centering process, for example, Bjork and Kugelberg, (1953), showed that when the eye looked straight ahead, a given extra-ocular muscle shows a steady tonic discharge; and thus as Davson, (1963), points out, all three antagonistic pairs of muscles are pulling against each other when the eye is at rest.

This sort of evidence quite strongly suggests that the centering process is an active one requiring control rather than a passive event. If this is the case, an experiment requiring pointing of the eyes before and after exposure to prisms is ideally suited to testing for the presence of the hypothesised change in the position controlling mechanism. Thus the null hypothesis was that eye positioning would not be altered by the treatment condition.

Apparatus

For the measurement conditions the subject sat in front of a T.V. camera, the lens of which was behind an 8" x 6" semi-silvered beam splitter placed as close to the eye as possible - some 3", and inclined at 45 degrees to the horizontal. Behind the mirror and 9" from the subject's eyes was a tungsten iodine 100 w bulb. This is shown schematically in figure 5. Reflector spot lamps uniformly his eyes 'straight ahead', (both eyes were open even though readings were taken from only one). There was no target on the viewing surface to denote the straight ahead position, so in one sense this was a judgment, though a judgment based firmly on a physiological mechanism. Craske and Templeton have shown that even when eye centering readings are taken over a number of days the standard deviation of the distribution is only 80 min. of arc, and for a small number of readings taken consecutively they point out that variability was considerably smaller than this, at times zero, (within the limits of the measuring technique). Since the variability of normal eye centering is so low, large numbers of readings were unnecessary. Ten readings of the straight ahead were taken, E continuously moving the cursor to the tangent of the iris, but taking no reading until the subject signified that he was satisfied. When a reading had been taken, the subject looked to one side, after which the procedure was repeated.

Training: In this condition the subject wore trial frames with twenty dioptre base left prisms centered in front of each eye. He stood with his head symmetrical about his median sagittal plane, and inclined in such a manner that his toes could be seen. In order to prevent head movements a dental impression was used, suitably adjusted for height and rake. The subject was asked to clasp his hands behind his back in order that they might not be seen inadvertently. A small light was placed so that only his feet were illuminated and all other room lights were extinguished. The subject inspected his toes for ten minutes, occasionally turning down the light intensity with a variac to counteract dark adaptation, (the hand could not be seen during this operation). No movement of the legs or feet was allowed.

Immediately following the treatment condition, the subject had to reposition himself in front of the T.V. camera, this was done with eyes closed and entirely by touch with E guiding as far as possible. This was in order that the subject should get no viridical position information before any readings were taken. As soon as the subject was seated and on the bite, he was asked to open his eyes and stare at the tungsten-iodine bulb until its grid filament became clearly visible. This was in order that any visual cues that the subject might have found in the pre-test would be masked by the light adaptation to the intense source.

Clearly this procedure produced a strong after-image which was not present in the pre-test; it was found, however, that such an after-image did not impair, and as far as could be determined in pilot experiments, did not affect the subject's eye centering. Ten Doesschate, (1954), has reported that monocular fixation of an after-image produces small amplitude pendular nystagmus, but periodicity was not noted by E in this binocular situation, perhaps because of the rapidity with which the centering judgments could be made and recorded. Certainly repeated measures showed that normal eye centering measures taken with and without after-images were drawn from the same population. It should be pointed out that if the field of view was a ganzfeld the after-image precaution would not be necessary.

Post-training measures: After looking at the intense source for some seconds, ten more measures of the voluntary straight ahead were taken.

Results

Table 18

Mean eye position in mm. taken up before and after treatment as measured at the T.V. monitor (zero is arbitarily the first reading of the pre-test)

Subject	Before treatment	After treatment
1	-1.5	12.6
2	-0.9	9.2
3	1.9	15.95
4	5.75	17.75
5	1.0	13.2
6	-1.9	9.5
7	1.4	14.7
8	-2.1	15.1
	Mean = 0.46	Mean = 13.50

$\bar{D} = 13.04$ Sum of $D^2 = 1421.9$

$t = 9.57$ $df = 7$ $p < .0005$

The above result is statistically significant, and the evidence warrants the rejection of the null hypothesis.

The shift shown above is in the direction appropriate to the adaptive shift shown after inspecting the fingers or the feet.

It would be interesting to calculate the possible effect on pointing which a change in appreciated eye position of this magnitude could bring about. To make this estimate certain other data were required. A subject was asked to scan along a metre scale at a distance of 65 cms. (i.e., arm's length).

A scan of 16 cms. generated a shift of three cms. on the T.V. screen. Using the mean of the above difference readings as an estimate of change in the position signal generated by the eye, it would be expected that a ten minute exposure would give a mean effect on pointing of 1.30 x 16/3 equals 6.7 cms.

Now the results of experiment 7 can be simply converted from degrees to centimetres by assuming arm length to be 65 cms. It can then be calculated that the mean error of 6.45 degrees is equivalent to a displacement of 7.3 cms. on the assumption that the limb reflects the position signal derived from the eye on a one to one basis.

It is readily seen that these two results are by no means incompatible, even though the exposure situation in experiment 7 was somewhat different.

Experiment 8b

Effect of prior asymmetry of gaze on subsequent eye centring

In order to consolidate the finding of a previous experiment, namely that holding the eyes in an asymmetric position does not affect subsequent pointing, two further tests of after effect from asymmetry were performed.
In these two experiments, the procedure was as for the last experiment; pointing eyes straight ahead; treatment; eyes straight ahead again. In the first (i), the treatment consisted of wearing prisms and inspecting a spot on the floor just forward of the feet, the feet not being in view. In the second, (ii), the subject remained on the bite in front of the camera and during the treatment condition fixated a point placed in maximum rightwards asymmetric convergence, in both experiments the treatment condition lasted ten minutes.

Table 19

Mean differences between pre and post-training eye centring for two different treatment conditions
Differences in mm's

Subject	Treatment i	Treatment ii
1	3.0	5.5
2	1.0	0.0
3	-2.5	2.0
4	-1.5	3.5
5	3.0	-4.0
6	-2.5	-1.5

Without the aid of statistics it is quite clear that the 'asymmetric' treatment condition is not producing the change in appreciated eye position shown up so clearly in experiment 8a.

Experiment 8c

Positioning the eye straight ahead after a free movement treatment condition

The experiments of section 7 claim to be aposite to the 'free situation' but so far have not used free moving subjects. It was desirable to perform an experiment to provide evidence directly relevant to the contention that a change in appreciated eye position is the fundamental effect when adaptation takes place when the subject is free moving. On the basis of the previous experiments, a change in the appreciated eye position is expected.

Apparatus

The apparatus was identical to that of experiment 8a.

Subjects: The subjects were six undergraduates in the University.

Procedure: The only difference in the procedure between this and experiment 8a is that the treatment condition lasted two hours and consisted of the subject being asked to roam freely about the psychology building, a locale which was well endowed with stairs and corridors. The treatment condition thus ensured that the subject would see his arms and legs a good deal when negotiating obstacles; a situation which Held and Mikaelian, (1964), have shown to be more effective in producing adaptation than treatment conditions in open spaces, in which the limbs need hardly be seen at all.

Suitably masked 20 dioptre prisms were used in the treatment condition, and were not removed until the subject was seated in front of the T.V. camera, and biting on the dental impression. In this way it was ensured that no accidental view of the viridical body position could be obtained.

The experiment thus consisted of pre-treatment measures of eye centring, followed by the treatment outlined above, and then the post-treatment measures.

Results

Table 20

Mean difference readings in mm's at T.V. monitor
in positioning the eye straight ahead
All readings are in the direction of the adaptive shift

Subject	Mean difference
1	16.8
2	18.0
3	9.7
4	6.4
5	22.0
6	14.8
	Sum 87.70

$\bar{D} = 14.61 \quad D^2 = 1444.3$

$$t = 6.213 \quad df = 5$$

$$0.0005 \quad p \quad 0.001$$

Thus the mean differences between the two situations are statistically significant, and the evidence is consistent with the hypothesis that the prism adaptation which occurs when the subject moves about freely is the same as that which occurs when he inspects his immobile limb.

Discussion

Subsequent to these experiments being carried out, Kalil and Freedman, (1966a and 1966b), have presented evidence that there is eye involvement in what has become a conventional prism-adaptation situation, namely the subject pointing to a visual target while wearing prisms, and only getting knowledge of results when the movement is complete. Until their paper it had been accepted that there was no significant 'inter-manual transfer' of adaptation, (Harris, 1963; Mikaelian, 1963; Hamilton, 1964), and hence, by inference, no involvement of the eye-positioning system. However, experiments carried out by Mr. A Johnston in the psychological laboratory at Durham have confirmed that a change in pointing of the unused arm does occur in this conventional situation, and that this is related to the magnitude of the change in appreciated eye position as directly observed with the T.V. hook-up described here. This finding is in line with that of

Rock, Goldberg and Mack, (1966), who have shown significant correction to prismatic distortion when the exposure condition is limited to mere inspection of a prismatically distorted scene. This eye-involvement in a situation which primarily changes the felt position of the limb, (Harris, 1963; Craske, 1966a), clearly cannot be very great. Adaptation in the eye positioning system *can be of an order no greater than is necessary to 'take up the slack'*, that is, can be no greater than that necessary to adapt to any residual error after the very rapid adaptation at the joint.

To elaborate this point further evidence is being gathered in this laboratory that the population of subjects is not uniform with respect to the readiness with which appreciation of the eye position will change. This is only to be expected, but so far no account has been taken of this in the explanation of adaptation to prisms. Remembering this, it would be expected that degree of eye-involvement after exposure to a prism situation would depend upon the readiness with which both joint and eye will modify position data; which of these systems is being favoured by the exposure situation; and the degree to which the system and sub-systems can tolerate discrepant positional information. Such a proposal would explain why Pick and Hay, (1966), found no changes in appreciated eye position subsequent to a prism treatment condition system of the eye, but it seems quite clear from the above work that such a controller requires input from the limb proprioceptors to correlate highly with its own fedback position information. Certainly without this it rapidly loses stability, a conclusion which is surprising, for it leaves the question as to the candidate for the position system's fixed referent.

Section 8

The Subsidiary Experiments

SE 1. Evidence that limbs are normally moved from felt positions.

SE 2. The efficiency of adaptation using the perceived error technique.

SE 3. Evidence for adaptation to prisms with kinaesthetic error feedback.

SE 4. Adaptation with delayed feedback.

SE 5. The technique of anti-adaptation.

SE 6. To determine the effect of prism adaptation on the judgment of 45 degree arcs.

SE 7a. The variability of 'straight ahead' judgments of the head.

SE 7b. Variability of positioning the eyes 'straight ahead'.

These subsidiary experiments are on a small scale and illustrate points made in the argument. Sometimes what is reported is a matter of common observation by those working in the field, but has not appeared in the literature, other items are easily tested hypotheses not requiring elaborate experimentation.

By their intention these experiments do not require a protracted theoretical introduction, for each one has been introduced in the main argument.

The practice will be observed of reporting these experiments in the most concise way possible. Results will take the form of graphs, significance levels or observations.

Subsidiary experiment 1

Evidence that limbs are normally moved from felt positions

When a limb is moved from one position to another it would seem likely that the internal information as to limb position, (kinaesthesis from joints), would normally be used to indicate starting position. This is argued from the fact that we are always aware of limb position, and it would seem that this could be the prime use of this information. Position information from kinaesthesis is very nearly as accurate as that from vision, (Merton, 1961), thus it can be argued that moving from a felt position to a seen position is a very efficient use of available information. Lastly, common observation would indicate that most movements made by humans take place with no visual checking on the starting position.

Utilising the ideas on ballistic movement already discussed, namely that moving from position A to position B is performed via an appropriate M.O.T.F.P. to the musculature, an experimental technique was applied whereby

The task was to point at the target once per second for 30 seconds while wearing 20 dioptre base right prisms. Since the plate glass sheet was covered to within two inches of the target, the subject obtained knowledge of results only on completion of the limb excursion. The arm was swung from the side and was semi-pronated throughout.

Before and after the exposure period ten measures of the subject's accuracy of pointing were taken, no knowledge of results being permitted.

Results

For the five subjects used, the error in pointing before the treatment condition was minus 1 degree. The mean error after the treatment was plus 6.5 degrees.

Full adaption for these prisms is 11.3 degrees, thus the adaptive shift of 7.5 degrees represents 66% adaptation in the 30 second exposure period, double the adaptive shift reported after the arm wagging treatment within one sixth of the time period.

Subsidiary experiment 3

Evidence for adaptation to prisms with kinaesthetic error feedback

The purpose of this experiment is to provide evidence

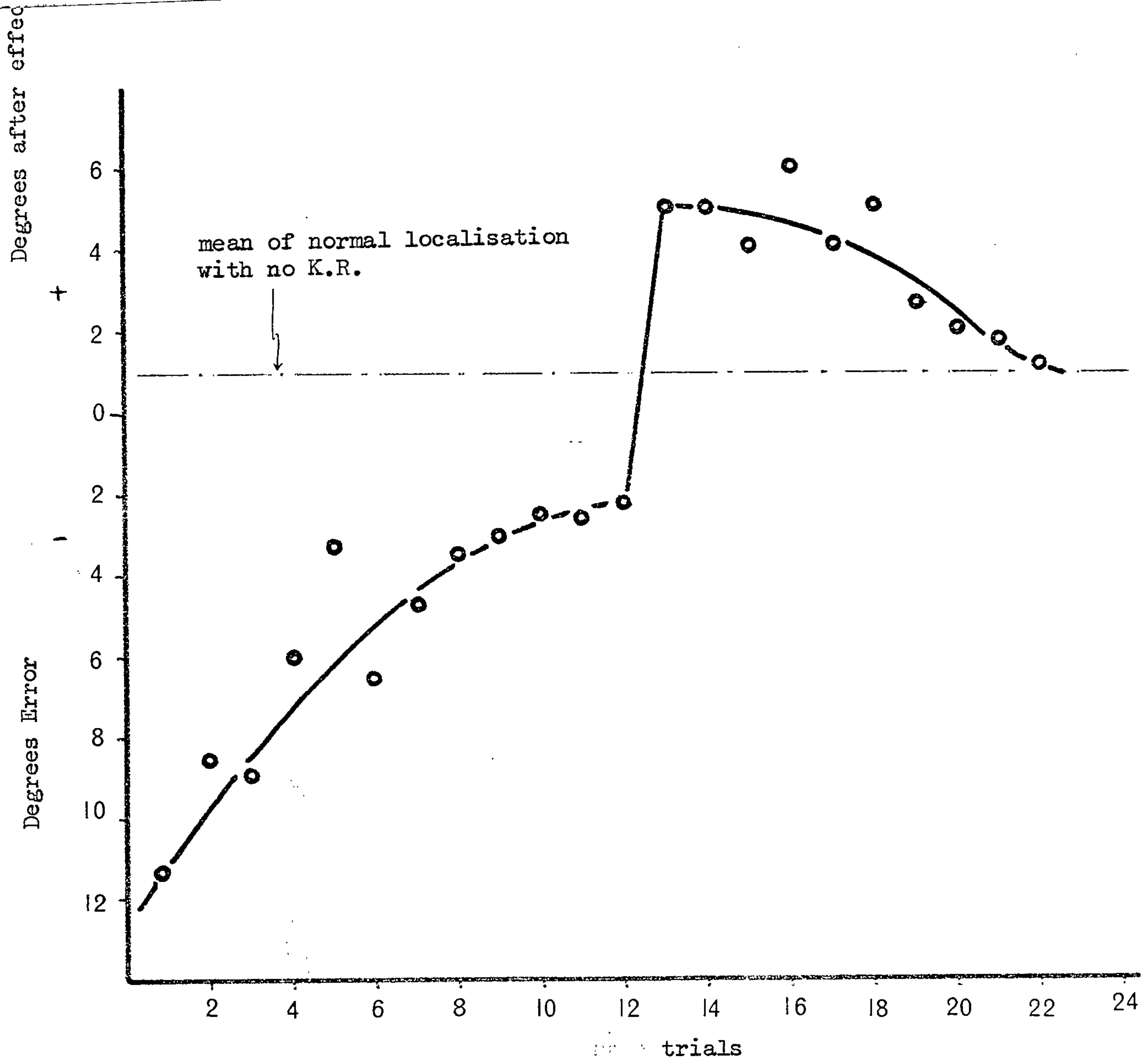

Fig. 6. Time course of adaptation and after effect for adaptation procedure with kinaesthetic K.R.

that adaptation can occur in the localising of visual targets when the knowledge of results is given to the subject by E passively moving the limb to correct any error the subject makes.

With the subject in the restricted situation as in the last experiment, and wearing prisms, he is asked to attempt to point at a single visual target placed at arm's length and in the sagittal plane passing through the point of rotation of his right arm. This is done at the rate of one pointing every 5 seconds, no visual knowledge of results is obtainable, but the E moves the limb to the real target position as soon as the limb excursion is over.

Typical results are illustrated in figure 6 which shows gradual change in pointing with increase in number of trials, and the after effect on pointing after twelve trials which indicates that the modification made is not a conscious one. As in more conventional prism adaptation, the after effect can be seen to decay with time to asymptote with the curve of normal localisation which is plotted on the same graph.

These results are germane to Held's contention that reafference to the distance receptors is a necessary condition to produce this sort of adaptation, for here no such reafference was available.

Subsidiary experiment 4

Adaptation with delayed feedback

Held, Efstathiou and Greene, (1966), used a variant of Held's hand wagging adaptation technique, and showed that delaying the visual feedback associated with the active movement of the hand completely eliminated any prism adaptation. (This experiment is discussed fully in the text).

Their conclusion was that the correlating mechanism which has been hypothesised by Held, 'cannot handle a feedback signal delayed by as little as 0.3 seconds'.

The results of the following experiment illustrate that such general conclusions cannot be sustained, and stem from a misplaced adherence to the theoretical role of reafference via the visual channel in this form of adaptation.

This experiment employed the normal perceived error technique with the subject pointing to a visual target, but the visual feedback as to the position error of the limb was delayed by 30 seconds. The limb was then returned to the subject's side in the normal way, but the onset of the next localising trial was delayed by a further 30 seconds. This procedure was repeated twelve times, which was sufficient to make the point intended, namely that significant adaptation does take place even with 30 second

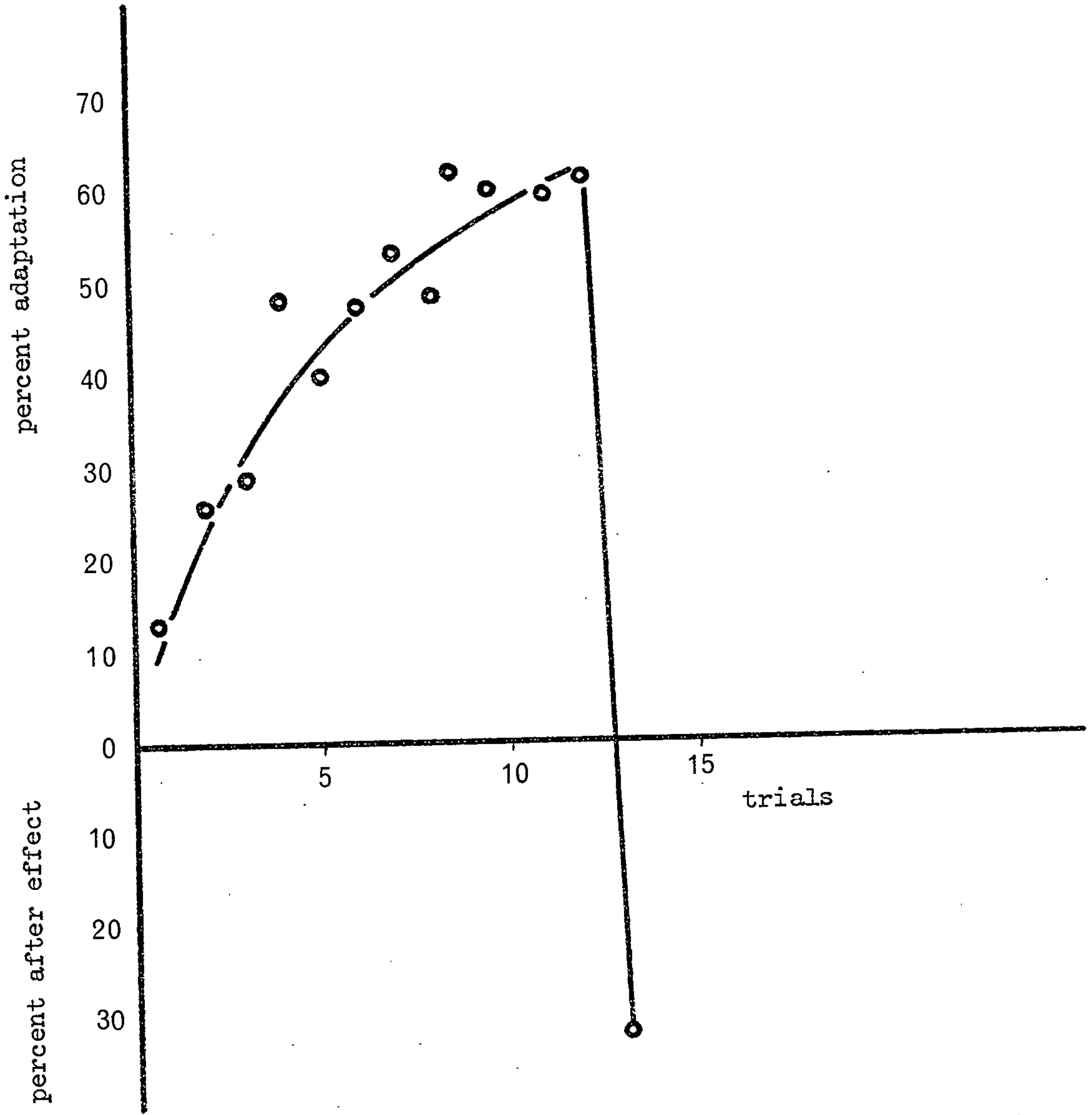

Fig. 7. Adaptation and after effect for perceived error adaptation situation with 30 second delay in K.R.

delay periods between movement and visual feedback. Typical results including initial size of after effect are presented in figure 7.

The reader is referred to the consideration of Held's work in the text, where an explanation of the results of Held et al is presented.

Subsidiary experiment 5

The technique of 'anti-adaptation'

During prism experiments it is often desirable to test the subject under a number of exposure conditions, and in order to do so it is imperative that base line readings for the pre-adapted state should be as similar as possible prior to each part of the experiment.

It is not always convenient or desirable for the subject to come for trials sessions on a number of different days, and for this reason the following procedure was adopted to produce base line readings after a period of prism exposure. Since testing occasions which are separated by hours or days regularly show different base line performance, it is necessary to employ some criterion of the base line; for example one regularly employed by the writer was that the mean of the base line performance on occasion 2 should be plus or minus one degree of that on occasion one. This was quite arbitary, but ensured that subjects with a high level of intrinsic variability were rejected after just a few trials. That is, such people often could not conform to the criterion in the normal state, so were thus not used in experiments.

The 'anti-adaptation' technique is merely to use the same procedure as in the standard adaptation condition for the restricted situation, the only difference being that no prisms are worn. Thus the subject uses the same movements, muscles and joint excursion as in the adaptation procedure, but re-learns to point accurately. This continues until the criterion of accuracy is reached; the practice commonly adopted by the writer was to insist on 4 or 5 consecutive correct localisations.

This technique has been found successful in negating adaptation in the restricted situation, (i.e., adaptation at the level of the joint), about twenty pointings normally being sufficient after normal, short exposure periods.

It must be noted that adaptation of the appreciated position of the eye is more readily destroyed by inspection of limbs without the aid of prisms, see Craske and Templeton, for some observations on the destruction of 'eye effect'.

Subsidiary experiment 6

To determine the effect of prism adaptation on the judgment of 45 degree arcs

Subsidiary experiment 2 illustrated that over 60% adaptive shift was shown in pointing to targets after 30 seconds training using the perceived error technique. Part of this thesis has shown that such adaptation takes place at the level of the used joint, and it has been argued that this form of adaptation takes place 'in order' that the M.O.T.F.P. be preserved, i.e., the motor outflow component definitely does not alter.

An experimental test of this is to show that some judgment likely to depend on the motor outflow alone does not alter after the adaptive procedure has been completed. An appropriate test seemed to be to ask the subject to judge an elbow joint excursion equal to 45 degrees before and after adaptation of this joint. This is the experiment to be reported.

The subject was seated at a bench leaning slightly forward and with his right elbow resting on the bench top. A sliding screen covered the subject's arm, and on the top of the screen along the arc described by his right index finger were marked three line targets. The subject's task was to move his forearm about the elbow joint only until he thought his index finger was pointing at one of the targets which were called out in random order by E.

When he thought his finger was beneath the target, the screen was slid towards the subject so that visual knowledge of results could be obtained. This procedure was continued until the subject reached the criterion of 5 consecutive correct localisations plus or minus one centimetre.

Before and after this treatment condition, the subject was asked to make ten right forearm excursions equal to a judged 45 degrees; again movement took place about the elbow joint. The arm was moved from right to left, and there was no fixed starting position; movement took place without knowledge of results. The distance between the starting and finishing positions of the right index finger was recorded by E.

Results

Whether the acrs measured off by the 8 subjects were in any way accurate is not of concern here. The difference between the before and after measures for each subject is the important datum.

t for correlated means for the data collected equals 0.197; $p \gg 0.15$ for one tail test.

This data does not warrant the rejection of the hypothesis that there is no difference between the two sets of judgments.

The conclusion to be drawn, (assuming that this judgment is based on motor outflow), is that motor outflow undergoes no modification due to the adaptation procedure.

Subsidiary experiment 7

Variability of positioning the head and eyes 'straight ahead'

It is of use to suggest a reason why the head is held to one side when the subject wears prisms in the free situation. If a subject is wearing a pair of base-right prisms, the optics of the situation make it clear that light is bent in such a manner that his visual field is considerably more extensive to the right of his median sagittal plane than to the left. Thus the effect of turning the head is to make the total field of view symmetrical about the median sagittal plane of the body. The thesis that the position of the body median plane is known in some way, and that the eye position is adjusted to this is untenable. The median plane is only real insofar as we can indicate it by pointing with hands or feet or eyes, and in the first two of these situations we are doing nothing more than indicating a place the definition of which we know conceptually. So for example in the case of indicating the median plane with the arm, we can check visually that we have adhered to the definition. In the case of indicating the median plane using a limb without visual checking, the most likely explanation is that we know what M.O.T.F.P. is appropriate to move the limb into this position because we have calibrated the system through time, presumably through knowledge of results.

In the case of indicating points on the median sagittal plane when only the visual channel is used, a likely strategy is that the subject assumes that the head is normally oriented on the shoulders, and then sets his eyes straight ahead by means of symmetrical innervation, Bjork and Kugelberg, (1953), have reported on the electrical activity in the eye muscles, and their data support such an idea.

It would seem from this observation that a case could be made to explain why the head is held to one side in the prism wearing situation. By doing this the prism-wearer puts himself into a position <u>whereby he may maintain his eyes oriented straight ahead</u> with respect to his head when observing objects which are <u>objectively</u> in the median plane of the body. Consider that in the environment in which subjects are normally required to walk about, i.e., corridors, paths, flights of stairs, the point for which the subject is making could be seen by holding the eyes in an asymmetrical manner. Observation indicates that it is clearly preferable however for the subject to innervate the eyes symmetrically and hold the head to one side. In seeking the reason for this, one merely has to perform experiments whereby a non-adapted subject is asked to put his eyes 'straight ahead', and another where he is asked to set his head 'straight' on his shoulders, in both cases without error feedback. As will be seen, the variability of the eyes is extremely low, and that of the head very high indeed. From this it can be inferred that we are not particularly conscious of the direction in which our head is pointing, (even though as a localisation device, the human system must have very accurate knowledge of its orientation, however all this information clearly does not reach consciousness). On the other hand, the straight ahead position of the eyes is known very well. Thus it can be plausibly argued that the head is carried skew on the body in the free prism situation because we are much more aware of the straight ahead position of our eyes than of our head.

Experiment 7a

The Variability of 'straight ahead' judgments of the head

Method

A racing cyclists crash helmet weighing two ounces was fitted with two sighting pins front and back. These were so placed such that when the helmet was worn the point of rotation of the head on the spine was in the vertical plane passing through the sighting pins. In the measurement situation, the subject stood erect and rested collar bones and sternum on three points projecting from a rigid structure in front of him. Sideways movement was prevented by clamps which could be adjusted to shoulder width. Two meters in front of the subject was a circular scale graduated in centimetres. The subject's task was to bring his head in from left and right alternately, and to stop in the 'straight ahead' position. This was done twenty times from each direction, and the stopping position read off by E by looking along the sighting pins to the scale. This whole procedure was carried out with the eyes closed, and no knowledge of results was given. Ten subjects were used.

Results

Mean variance for 10 subjects = 720.2 cms.

Thus mean SD = 26.83 cms.

1° = 3.49 cms.

$\therefore$ SD = 7.68 degrees.

Experiment 7b

Variability of positioning the eyes 'straight ahead'

The following measurements were taken by Craske and Templeton. The T.V. arrangement is identical to that fully reported in experiment 8.

This set-up achieved a times ten magnification of one eye, with the subject only able to see a featureless white surface.

With his head immobilised by a wax bite, the subject's task was to open his eyes every ten seconds, and to voluntarily position them so they were pointing 'straight ahead'. Over a period of days, a series of 121 readings of the horizontal straight ahead position were taken using the left eye of one subject. Vertical changes were ignored. These readings were taken directly from the screen of the T.V. monitor by translating a vertical cursor until its edge formed a tangent to the iris, and then reading off from the millimetre scale attached horizontally to the screen of the monitor.

Results

The results may be conveniently presented as a frequency distribution, with the line of best fit drawn in. (See fig. 8).

Analysis of the data reveals that the distribution is approximately normal, and the standard deviation of the distribution is 0.376 mm. If the appropriate conversion is performed, this is equal to 1.73 degrees at the eye, (see appendix). Now this is the variability in eye positioning over three days and ten occasions. The variability within one set of trials is 0.4 of this value, thus the variability within a short time period is about 0.7 degree, and it is this figure which we should use as a comparison for the variability observed for centering the head on the shoulders, since these results were taken over a comparable period of time, namely some 200 seconds.

Now the variability of positioning the head to straight ahead on the shoulders was seen to be 8 degrees, which is some eleven times as large as the variability of eye positioning.

These data support the hypothesis that the head is carried to one side in the free situation. Given the choice between voluntarily holding the eyes to one side, or voluntarily holding the head to one side, it is the latter which is noticed least, (due to its high intrinsic variability). This being so an asymmetrical head position is adopted in preference to an asymmetrical eye position. It is pointed out that Kohler, (1964), observed that a subject wearing prism spectacles did not notice that his head was carried to one side.

Section 9

Discussion

There are still many problems left in the area of prism adaptation, though the underlying features are better understood than they were. Since each experiment reported here had its major points brought out in its own discussion, and since the General Statement, Summary and Conclusions draw these together, this opportunity will be taken to look at some of the problems and to put forward some largely untested ideas.

The first item to be considered here is the part played in the prism situation by the factors of visual asymmetry and rotation of objectively normally-incident surfaces.

When prism spectacles are worn, the cone of space which can be seen by the subject is asymmetrical about his median sagittal plane. Furthermore if the subject's line of sight is normally incident upon a surface before looking through the spectacles, then subsequent to putting them on, the surface will rotate and appear as if it were slanting with respect to the subject. Harris, Harris and Karsh, (1966), have argued that the negative adaptation, (i.e., maladaptive shift), found by Bauer and Efstathiou, (1965), is due to the subject adjusting his subjective straight ahead in order to unrotate the slanted world. The experimental test employed by Harris et al shows an after effect due to passive inspection of a prism slanted surface; the same effect was also shown by Rock, Goldberg and Mack, (1966), and pilot studies by the writer have also confirmed the observation.

A kindred situation producing change in egocentric localisation is that used by Bruell and Albee, (1955), in which self luminous frames are wrongly positioned by the subject when he is told to adjust one of the verticals to straight ahead. However this and the former variety of asymmetry do not produce the same shift in the subject's behaviour; one is in the opposite direction to the other. In terms of our understanding of eye adaptation, both these situations would repay further study, for they are both affecting the eye positioning system.

It is possible that the observation of 'intermanual transfer' in the restricted training situation used by Kalil and Freedman, (1966a), may be due to the visual asymmetry attendant upon using only one target located along the objective median plane. Though their later report, (Kalil and Freedman, 1966b), would lead the writer to argue that the intermanual transfer is due to a change in the appreciated eye position following sufficient exposure to discordant eye-limb position information. It must be noted however, that it is not known whether the 'Bruell and Albee effect' produces changes in appreciated eye position similar to free situation prism adaptation, and it still remains a possible explanation of their findings. There can be no doubt that those working with prisms should be very careful of the background which their subjects may be able to see, for this may be a source of unexpected error.

Some points raised by a recent review, (Wohlwill, 1966), may be commented upon. For example the contention that, "Harris is forced to rely on changes of the head and eye to account for changes of an apparently visual nature", can now be seen to be unjustified criticism in the light of the work reported and summarised here. He is right however when he argues that the proprioceptive change explanation is difficult to reconcile with the role of visual perceptual variables in adaptation. For example with active movement, adaptation is greater in a corridor than in an open field. This is certainly not a proprioceptive change, but one of appreciated eye position. It is argued that the difference between the corridor and the field lies in difference in liklihood of the subject seeing his limbs. This is far more likely in the corridor, where walls have to be fended off, thus adaptation will be greater.

Wohwill's conclusion that "adaptation effects might be profitably thought of as concerning the system of interrelationships linking.... particular channels rather than changes in any particular channel", does not seem very useful in that distinct changes in the subsystems of the total localising system can be observed.

Some data of Hamilton's, (1964a), present a problem with no ready answer. The problem is that if a subject is asked to locate a target which is viewed through prisms and is allowed no knowledge of results, the error made by the arms is double that made by the legs. Further if the target is looked at, the eyes shut, and then the target approached by walking to it, the error is about that which would be predicted from the prism power. The only possible explanation which occurs to the writer is that maybe some of the differences are accounted for by difference in distance of the prism from the eye in the three cases. The whole question of the relation of prism power to error of reaching has largely been ignored, and parametric studies on the size of the after effect with length of training and number of correct localisations are a big gap, only partially filled by the observations of Rock, Goldberg and Mack, (1966).

Wooster, (1923), made the point that after adaptation the arm felt in the right place. It is now known that there is a change in the felt position of the used arm, so Wooster's point comes to the assertion that there is a change in subjective experience as adaptation progresses. It is now possible to expand this to assert that with change in appreciated eye position, the end point of adaptation results in the eyes pointing in one direction and the subject feeling quite confident that they are pointing elsewhere. It is worth stressing that after adaptation the relation between limb or eye position and the position of objects 'feels right', for in talking about mechanisms, the subjective component is often neglected.

It seems necessary to suggest that Wooster's subjects who showed 47% retention of adaptation after 2¼ years were consciously directing their limb to a place different from that which their visual system defined, for there is no evidence to suggest that any of these effects can survive the constant reality testing of normal experience for any length of time; even Kohler, (1964), after his immensely prolonged experiments did not suffer after effects of this duration.

Kravitz and Wallach, (1966), report an experiment in which the voluntarily relaxed, but passively vibrating arm is inspected through base up or down prisms. Their findings were strange insofar as the ten minute exposure period produced no adaptation reliably attributable to the eye, whereas arm adaptation was quite definite. It would seem that passive vibration of the inspected limb suppresses adaptation in the eye positioning system. A possible though unexplored proposition is that there is adaptation in the limb in this exposure situation due to the volume of positional efference from the limb; if this is so, there should be a gradual change from eye to limb adaptation if a limb were inspected under various levels of vibration from zero upwards. If this proposition were true, then the hypothesis that limb adaptation takes place as if the M.O.T.F.P. had to be preserved would need careful scrutiny.

An experiment by Abplanalp and Held, (1965), uses as a treatment condition a 'negative feedback' situation whereby the subject watches through prisms while his arm is being driven in the opposite direction to the force which he is applying to his limb. No adaptation is observed, and the conclusion drawn from the results is that self-produced movement, where the efferent discharge is highly correlated with the visual and kinaesthetic feedback, is necessary to produce adaptation. That this general conclusion is wrong has been argued previously, but other explanations of Abplanalp's and Held's results on a different basis from Held's theoretical view are difficult to formulate. Furthermore the above exposure situation is merely an unusual variant of eccentric contraction, (the sort of thing which occurs in the biceps when a cup is taken from the lips to the table). When the writer checked for an adaptive effect when just this latter movement was watched through prisms, it was observed that adaptation occured quite readily. It seems to follow that there is a different factor involved when the eccentric contraction is highly unusual. The theoretical significance of this may be that the M.O.T.F.P. has to be calibrated against some kind of distance judgment before adaptation of joint position can take place, Unfortunately no further work of this kind has been done to provide further data.

A problem related to the prism after effects is that of postural after effects, a term used first by Hein, (1965). The effect of posture on subsequent posture has an extensive literature, much of the work having been carried out by Werner, Wapner and their associates. Jackson, (1954), performed an experiment which showed that holding the arm at 45 degrees to the horizontal led to a subsequent upwards effect in judging the limb to be horizontal. This has been 'rediscovered' by Kravitz and Wallach, (1966). Experiments carried out by the writer have indicated that this postural effect takes the form of change in felt position of the limb. The prerequisite condition for this effect seems to be merely holding the limb in some posture different from 'normal'. Apparently related to this is the finding by Wyke, (1965), that with head rotation, pointing error is inversely related to direction of rotation. This area of the effects of posture on localisation is potentially very fruitful, and seems to possess strong links with prism adaptation.

Cohen, (1966), has reported some very intriguing observations. Prism adaptation was undertaken with the subject fixating straight ahead and the training consisted of learning to reach for targets seen only in the periphery. The observed after effect was greater when reaching for targets situated on the same side as those seen in the training. After performing the appropriate control experiments, the most clearly indicated conclusion was that one point on the retina was producing modified position information for a short time. This apparent change in retinal space values has been confirmed by B. P. Moulden. If this procedure does modify retinal spatial values in so short a time, then there is a factor involved in prism adaptation which has not been seriously considered so far, and one so unlikely in view of the clinical findings that further work on this aspect would be highly desirable.

There are a number of experiments which it would be useful to perform, and which may be noted briefly. Concerning adaptation of felt limb position, an informative psychophysiological experiment would be to carry out single unit analysis of the output of monkey joint receptors at various levels up to the post central gyrus both before and after prism adaptation. A change in output at some level would be most interesting and informative.

A more simple experiment stems from the writer's observation that if a subject has adapted and can point to the target using horizontal abduction, then he makes errors when he is asked to move by adducting his limb. Sekuler and Bauer, (1966), showed that the position of the hand during training affected post-training errors. These observations suggested to the writer that it was possible that the limb position sensors might be arranged in sequence, and thus the felt position might be alterable over a limited excursion, and yet not affect some other region of the total possible excursion. The contention of Mountcastle and Powell, (1959), that the evidence indicates a series of receptors with narrow but overlapping excitatory angles lends support to this idea. Put explicitly it is hypothesised that only those sensors subserving the angle of limb excursion used in training are affected by the adaptation procedure. There is further evidence to support this idea. Freedman, Rekosh and Hall, (1965), showed decrement of adaptive shift with different arm movements during adaptation and testing, and Goldstein, (1965), has shown that type of response during exposure affects size of after effect during testing. So far as is known, none of these workers have attributed their findings to what may be called the 'sector hypothesis' proposed above. However, tests of the hypothesis are complicated by the 'direction of movement' implication. Caldwell, (1956), and Caldwell and Herbert, (1956), found that accuracy of arm positioning was dependent on direction of movement. The writer has obtained evidence that the <u>ease of producing adaptation</u> is often different from adductive and abductive movements, as if some threshold for change in position sense were raised for movements in one direction in preference to the other.

So far there has been no rigorous test of either the sector hypothesis or the threshold hypothesis. Pilot experiments on the former using eight subjects and error diminution as an index of adaptation, showed that the total number of errors made subsequent to training followed by testing over one sector (near the limit of horizontal abduction), was zero centimetres, (i.e., full adaptation). When training on the first sector was followed by testing on another, (near the limit of hyperadduction), results showed mean errors of 2.6 cms. It is argued that this result is sufficiently good to justify a rigorous experiment to test the sector hypothesis.

There is an interesting experiment to be performed by someone who has access to a subject with flaccid paralysis of a pectoral limb, but no impairment of afferent pathways. The question is whether such a subject would adapt in the prism situation when his limb was passively moved by E. If he does, then it must be concluded that adaptation of felt limb position can occur with no motor involvement.

Concerning adaptation of appreciated eye position, a similar experiment to that above has yet to be done, namely can a subject with paralysed eye muscles show adaptation subsequent to inspection of the limbs? The inference to be drawn from any result would necessarily depend on the nature and site of the injury causing the paralysis.

The experiments on normal subjects which produce an eye effect suggest that if two base-out prisms were used while the subject inspected his own limbs, the appreciated position of the two eyes would alter in opposite directions.

It follows that the apparent lines of sight would be altered, and thus there should be a change in depth perception, shown up by over-reaching. W. B. Templeton has also expressed such an idea. It also follows that with subsequent monocular vision, errors will be in one direction with one eye open, and in the opposite direction with the other eye open. Once again, pilot experiments suggest that these changes may occur.

Section 10

Summary and Conclusions

The main experiments reported here make it quite clear that in the 'restricted situation' where the subject is not exposed to discordant position information too long, there is adaptation of the felt position of the limb. Furthermore, the part of the system feeding in the error information is argued to be a passive instrument in the adaptive process from the fact that both visual and auditory information can be used to produce this kind of adaptation. It has been shown further that the change in felt arm position is consistent with observed errors of pointing with the adapted limb, both to visual targets, and to the unadapted contralateral limb.

Evidence was gathered which seemed to point to a distinction in the manner in which humans tackle localising tasks. The data was consistent with the hypothesis that as movements become more automatic, (highly overlearned), the limb can be moved to remembered positions without the system using information about felt limb position.

Other experiments have shown that the appreciated eye position is changed when the subject sees his own limb extremities through prisms for a fairly protracted length of time. This is true whether or not voluntary eye movements are used, and both when the limbs have been immobile, and when free unrestricted movement is allowed.

A number of subsidiary experiments were reported. The chief findings from these were as follows. 1. That humans normally move their limbs from felt positions, but need not if the situation demands otherwise. 2. An argument was presented as to the reason why the head is held skew to the body when wearing prism spectacles. Evidence was given supporting the argument, and this showed that the variability of positioning the head straight on the shoulders is considerably greater than that of positioning the eyes. 3. It was also shown that judgment of angle of limb excursion was not affected by adaptation, which provides evidence that motor innervation undergoes no modification in adaptation.

On the basis of the experiments reported and reviewed here, the following four proposals are put forward as germane to the explanation of intermanual transfer of adaptation. The constraints of the situation will determine which of these is relevant at any given time.

1. Postural after effects due to holding the head skew on the shoulders.

2. Normalising to the room slant when looking through prisms.

3. Adaptation due to discordant kinaesthetic information and eye position information; a change in appreciated eye position.

4. Possibly an after effect due to visual asymmetry. There is informal evidence that movement of the head and body are of no importance in the aetiology of the effect.

Added to these, the following proposals are made as to the background to adaptation and the sequence of events in the free situation.

The human animal has a localising system with built-in variability in its various sub-systems. The animal therefore has to be constantly reality testing and modifying parameters in the various sub-systems to compensate for this variability. Positional reality is tested cross-modally by seeing limbs to be where they feel. Support for this comes from Merton, (1961), who has shown that the localisation errors made by the eye and the hand are of the same order of magnitude; this is the sort of result to be expected from such a testing system. Also, Held and Bauer, (1967), showed that infant monkeys displayed poor visually directed reaching with a hand until vision of that hand had been allowed. On being given the opportunity for this visual experience, looking at the hand was 'insistent and prolonged'. It could be argued that this is an example of the necessity for cross modality reality testing.

Now both felt limb position and appreciated arm position can alter, and it is suggested that under free situation prism wearing conditions where limb movement and knowledge of results is allowed, the first occurence will be that the felt position of the used limb will undergo modification in order to rapidly produce appropriate behaviour. This will be followed by more gradual change in appreciated eye position provided sufficient exposure time is allowed. This latter occurs because the eye gets discordant position input from the less used limbs, (which will not be fully adapted). Thus the passing of time will favour adaptation in the registered position of the eyes to the extent to which the subject is capable. This means that the limb effect is transient; a short term rapid response of the system to counter inaccuracy; and change in the internally registered eye position is the end-result of long term exposure.

Now apart from the support for these views embodied in the arguments within the thesis, there is further empirical support. That there are short term limb effects is supported by the evidence of Freedman, Gardos and Rekosh, (1966). Gradual take-up of adaptation by the eye is supported by the experiments of Schaffer and Wallach, (1966). Lastly the paper of Hay and Pick, (1966), provides strong support for the viewpoint above, and a review of the salient points of their experiments seems necessary. In one experiment subjects wore 20 dioptre prisms for six weeks, and were tested on their ability to point to visual targets (eye-hand coordination), and to point to a click (ear-hand coordination) before, during and after adaptation.

It was found that the initial phase of adaptation showed parallel changes in eye-hand and ear-hand coordination. This may be explained as being due to change in felt limb position. The shift in ear-hand coordination was transitory, and by day 2 no marked error of ear-hand coordination was observed; further, eye-hand coordination became very accurate. This was consistent with the idea that the locus of adaptation had changed and there had been a change of appreciated eye positio

A further experiment which measured the course of adaptation through time used four additional experimental test situations. (i) Ear-eye coordination where the subject had to identify the visual direction of a sound source. (ii) Eye-head coordination, in which the subject had to turn his head to face a visual target. (iii) Ear-head coordination, in which the subject had to turn his head to face a concealed sound source. (iv) Head-hand coordination, in which the subject had to point 'straight ahead' with his eyes shut. The six day experiment produced the following results. Test (iii) showed no change throughout, that is, there was no change in auditory localisation. Test (iv) showed the same time course and magnitude of adaptation as did the ear-hand test, and thus a large transient change in felt limb position was indicated; neither test indicated zero adaptation before the end of the experiment however. Tests (i) and (ii) showed between 2 and 3 times the final adaptation level of the previously mentioned pair of tests. These latter tests reflect the take-up of adaptation by change in the appreciated eye position. Finally the eye-hand test reached a stable maximum adaptation which was somewhat higher than shown by tests (i) and (ii), and was consistent with the summed end point effect of eye and limb adaptation as shown independently by the other tests.

May and Pick conclude that 'visual adaptation appears to replace an initial, quick acting proprioceptive adaptation during long-term prism exposure', a view which is in accord with the conclusions drawn by the writer.

Section 11

Appendix

1. The conversion of readings from the T.V. monitor
(millimetres to degrees of eye movement)

The subject was seated in front of the T.V. camera with head immobilised, and a metre rule was placed 66 cms. from the assumed centre of rotation of the eye. (According to Davson, (1963), this is situated 13.4 mm. behind the anterior surface of the cornea). The subject was asked to fixate a point on the rule to one side of his median sagittal plane, and then to fixate another point an equal distance away on the other side of it. By a process of trial and error, it was observed that an eye movement of plus or minus eight cms. produced a movement of three cms. on the monitor. Letting (x) degrees be the total angular excursion of the eye, then tan x/2 equals 0.1212. Whence (x) equals 13.83 degrees.

Thus 3 cms. equals 13.83 degrees, therefore 0.376 mm. equals 0.125 x 13.83 degrees, equals 1.73 degrees, correct to two decimal places.

2. Method used for locating the acromioclavicular joint - the assumed point of rotation of the arm

The subject was asked to stand with his arms hanging loosely by his side. E placed his index and middle fingers on the front surface of the appropriate clavicle, near to the sternum. The fingers were then 'walked' along the clavicle towards the shoulder, moving to the top surface of the clavicle while doing so. If E now palpated firmly, a dip was eventually encountered between the clavicle and the acromion. This was the acromioclavicular joint.

This was chosen as an approximation to the point of rotation on the basis of an X-ray photograph (on page 169, Rasch and Burke, Kinesiology and Applied Anatomy, 2nd Edition). This depicts a shoulder with the arm in the anatomical position. It can be shown from this that a perpendicular from the acromioclavicular joint passes through the head of the humerus at close to its centre point.

3. Definitions

Some terms have been used without definition in the text. These are given below.

Ballistic When referring to a ballistic movement, the meaning is that the segment under consideration is moving fairly rapidly; at greater than one third to one quarter the maximum for the segment according to Hubbard, (1960). Further, it is moving such that the agonist, having initiated movement, plays no further part; the segment continuing its motion by virtue of its momentum.

Horizontal abduction When the arm is flexed to the horizontal, and moved horizontally backward, away from the median sagittal plane.

Horizontal adduction As above, but the arm is moved towards the median sagittal plane.

Kinaesthesis and Proprioception have been used interchangeably, for both are appropriate to describing the sensory afference due to joint receptors, and it is in this restricted context that the terms have been used. Thus, for example, 'kinaesthetic feedback' has been used to mean 'feedback from joint receptors'.

Motor outflow A shorthand term meaning the command signal sent to the limb muscles; the efferent command.

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