Response modality and spatial location:
the effect of temporal delay on response accuracy
in adults and children

Thesis submitted for the degree of Master of Philosophy
by
Joanna Kate Garner

Department of Psychology
University of Surrey
Guildford, Surrey.

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Abstract

Neurological and clinical evidence suggests that specialised processing pathways differ functionally in the way visual information is processed, whether the goal is perceptual representation or action, (Milner & Goodale, 1995). These pathways may differ in emphasis on the same information. While the visuo-motor pathway may need to represent aspects of the environment in relation to the self, the visuo-perceptual pathway may need to form enduring representations in such a way as to overcome changes in item appearance due to self-motion. A second point of difference concerns temporal durability within each pathway. The visuo-motor pathway may rapidly update information in order to “keep up” with changes in the relationship between self and environment but the visuo-perceptual pathway may not operate under such constraints. In normal subjects a two-second critical parameter on visuo-motor accuracy has been noted, (Elliott & Madalena, 1987) as have spatial dissociations between visuo-motor and visuo-perceptual errors, (Gentilucci & Negrotti, 1994).

Three experiments further investigate temporal and spatial parameters surrounding response accuracy in normal adults and 6- to 10-year old children. Experiment one suggests that a two second pre-response delay induces a systematic distortion in the extent of visuo-motor responses while perceptual judgments retain accuracy. A loss of sensitivity accompanied all responses with delay, suggesting processing common to both pathways also occurs. The provision of reference lights in an otherwise dark workspace significantly reduced the effect of exceeding visuo-motor capacity, suggesting that pointing responses can utilise allocentric information where necessary.

Experiment two focuses on response-modality differences in relation to continuous information of the target location, and finds that reliance on this information varies with eccentricity for visuo-motor but not visuo-perceptual responses. These results are consistent with requirements of force-control specific to visuo-motor behaviour and suggest that continuous visual information regarding target position crucially supplements proprioception in a manner distinguishable from
. the effect of pre-movement delay. The finding augments understanding of differences in the use of visual information between visuo-motor and visuo-perceptual modalities.

Experiment three investigates visuo-motor accuracy in children and finds that a one-second delay systematically distorts accuracy but in a manner akin to that noted in adults. For children, distortion precedes loss in sensitivity and extent of response is more fragile than directional components. Seven to eight year olds' particular difficulties suggest deficits in movement force compensation which operate independently of visuo-motor processing.
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1.0 Introduction: Functional Modularity in Visual Processing - Two Visual Systems?

The nature of visual perception and visual information processing has long been a topic of contention among philosophers, psychologists, anatomists and vision scientists. Various accounts of form and function have been grounded in anatomy, physiology and behaviour. For example, according to Gibson (1986), vision and visual processing is best studied in the natural environment, where the brain is but one (albeit central) part of an organic system for perceiving. What is the goal of such perceptual processes? For Gibson, it is the guidance of action, of locomotion and interaction with the environment: “how do we see how to do things, to thread a needle or drive an automobile?” (Gibson 1986, p1). Natural or “ecological” vision involves movement and, in particular, movement of the observer. From this ecological perspective vision drives action and action is an integral and central part of the process of perceiving. Any account of vision should therefore consider the dynamic nature of the perceiver-environment relationship.

How might one recognise the needle, or automobile, in the first place? Studying visual perception thus may also be seen to require an understanding of those processes which not only allow interaction with objects in the environment, but also of those which facilitate the identification of, for example, the needle to be threaded. Marr’s (1982) computational account of visual perception acknowledges the importance of studying vision at many levels, including that of describing the way in which incoming information (in the form of varying intensities of light and shading gradients) may be interpreted so as to permit object identification and the formation of enduring representations. From this computational perspective, then, one of the most important products of the process of vision and visual perception is the ability to identify, learn about and recognise objects in the environment.

Distinguishing between the above points of emphasis in two such influential accounts of the nature and purpose of visual processing may be artificially and exaggeratedly divisive, but it nevertheless serves to illustrate two “problems” facing
visual processing mechanisms (and consequently those who seek to study them). Stated simplistically, these problems are that organisms must be able to see in order to identify and learn about aspects of the environment regardless of superficial changes in their appearance due to viewpoint, occlusion or level of illumination, but that they must also be able to co-ordinate their actions for interaction with objects and other features of the environment. These abilities may require the neural system to place emphasis on different aspects of incoming information, depending upon whether the task requires perception for representation or perception for action.

1.1 Anatomical distinctions

The notion that distinct visual pathways carry information from retina to brain dates back almost one hundred years, (Cajal, 1909, cited in Jeannerod, 1997). Attempts to account for processing distinctions by tracing separable anatomical connections have grappled with the dichotomy between cortical and sub-cortical paths. Theories vary in the degree of emphasis placed upon this dissociation, and in the function to which any dissociation is ultimately attributed to serve. Taken together, however, these accounts lead to an understanding of recent proposals which discuss functional, rather than anatomical, modularity in visual information processing.

Schneider (1969) demonstrated visuo-motor functions for sub-cortical connections in hamsters. After ablation of retino-tectal pathways (a homologue of the superior colliculus in humans), spatial orientation abilities were lost. In contrast, disruption of retino-cortical projections by way of lesion to the visual cortex, resulted in a loss of pattern discrimination. The two visual functions were concluded to be derived from independent anatomical paths, and comprise an early distinction between processing “what” (object identification) from “where” (spatial location).

Primate experiments by Trevarthen (1968) added detail to this hypothesis in higher-level organisms. Lesion techniques revealed a dissociation between object location behaviours, (reaching), from object identification and manipulation behaviours, (discrimination followed by grasping). Anatomical distinctions were, in this case, thought to arise from peripheral retina-superior collicular connections and
central retina-geniculo-striate connections subserving "ambient" (object/spatial location) and "focal" (object discrimination/manipulation) abilities respectively. Like the residual spatial orientation abilities in decorticalized hamsters, Humphrey and Weiskrantz (1967) observed preservation of object-directed movements in monkeys with equivalent lesions. These behaviours included residual reaching abilities. Comparable results in human subjects following lesion injury to these visual areas were found by Perenin and Jeannerod (1978), who elicited reaching behaviours to stimuli presented within the scotoma region, i.e. where the patient reported blindness.

These findings suggest strong sub-cortical input to areas subserving visuo-motor function. Other research, however, has presented evidence to suggest that the spatial orientation versus object discrimination dissociation derives from differences in cortico-cortical pathways.

Retinal ganglion differentiation of spatio-temporal processing across the central and peripheral retina was proposed to account for modularity in visual processing by Livingstone and Hubel (1988; Livingstone, 1990). In tracing distinct magnocellular and parvocellular cells through to the lateral geniculate nucleus (LGN) and subsequently to the primary striate cortex and beyond, form versus motion processing was proposed to remain segregated until the execution of "what" versus "where" behavioural responses. Livingstone (1990) traced magnocellular input through area V1 to the "thick stripes" of area V2, and from there to area MT, where stereo and movement information is derived. Parvocellular input, on the other hand, passes through area V1 to the "blob/thin stripes" and "interblob/pale stripes" regions of V2. The thin stripe areas are then thought to connect to area V4, concerned with colour processing (and not movement), while the pale stripes connect to (as yet unspecified) areas concerned with the derivation of static form and object outline (see Figure 1.1). In this sense the parvocellular system was thought to form the basis for object discrimination abilities, while the magnocellular system related to localization.

Although extra-striate processing pathways have been noted whereby projections relay information dorsally to the posterior parietal cortex (PPC) and ventrally to the inferotemporal cortex, the magno/parvo distinction does not remain in such a clear-cut fashion within these processing streams. For example, significant connections exist
between the thick and thin striped areas of V2, suggesting a combination of magnocellular and parvocellular activity reaches structures thereafter (Lachica, Beck & Casagrande, 1992). Furthermore, temporary cooling of the striate cortex does not prevent activity in the areas within either the dorsal or ventral streams, as would happen if either one depended entirely on cortical input (Girard, Salin & Bullier 1991a, 1991b), and V4, an area proposed to be connected with the infero-temporal processing stream, receives both magnocellular and parvocellular input, (Ferrera, Nealy & Maunsell 1992).

It therefore appears that if any processing distinction is to be made on anatomical grounds, both cortical and sub-cortical connections to ventral and dorsal areas should be considered. However, evidence from clinical studies in humans, and from lesion experiments in animals, suggests instead that progress in understanding the two systems may be more satisfactory if functional output, not anatomical input, is studied.

Rather than distinguishing between dorsal and ventral processing streams by “analysis of what” versus “analysis of where,” more recent formulations such as that proposed by Jeannerod, (1997) and Milner and Goodale, (1995) argue for a functional distinction based on analysis of visual information for the purpose of “perceptual representation” versus “visuo-motor control.” In other words, analysis occurs according to whether information is to be used to perceive and identify objects within the environment, or to act within it. The rationale for determining connections for functional output rather than anatomical and physiological input originates from an evolutionary perspective and encapsulates the issues addressed by both the ecological and computational arguments put forward earlier; vision may have evolved primarily to guide action in phylogenetically older organisms but must also allow for the formation of enduring representations of the environment, such as those utilised in the later-developing visual systems of ontogenetically “newer” species.

There are several implications of considering functional rather than anatomical modularity. Firstly, separable action-specific areas may exist within the visuo-motor, dorsal processing stream (Jeannerod, 1997). Secondly, representations derived within each pathway (in terms of the frame of reference around which representations are
derived) may be specifically tailored to the functions that each stream subserves. Investigation of neuronal populations response properties in various cortical portions has suggested that modular spatial representation processes occur in each stream, (Milner & Goodale, 1995). Finally, evidence to support separable action-specific areas and response-specific representations should be available subject to studying clinical populations and normal human subjects, under appropriate experimental conditions.

1.2 Visuo-motor and visuo-perceptual processing

Milner and Goodale's (1995) formulation develops the previously discussed distinction between a dorsal processing stream reaching the posterior parietal cortex, and a ventral stream reaching the infero-temporal cortex. The account acknowledges previous findings such as the substantial sub-cortical contributions to processing. However, the distinction of localisation versus identification has been replaced by a division of labour between processing for perceptual analysis and processing for visually guided action. It is the contention that "one stream is concerned only with the world 'out there' independent of the observer, while the other is concerned only with the observer's actions within that visual world." (Milner and Goodale, 1995, p63.)

Figures 1.1. and 1.2. depict models of the anatomical connections between the primary visual areas and dorsal and ventral processing streams.
Figure 1.1. A schematic depiction of the magnocellular and parvocellular inputs into dorsal and ventral stream processing. (Adapted from Milner and Goodale, 1995, p.134 and p.40).

Figure 1.2. Parietal and infero-temporal regions in dorsal and ventral stream processing (adapted from Jeannerod, 1997, p.24).

1.2.1 The ventral stream: processing for representation
The ventral stream appears to derive important enduring features of objects in a manner which is object-centred, i.e. independent of the position of the self. It has been implicated in the formation of memories and object representations. From its origins in magnocellular and parvocellular pathway connections through the lateral geniculate nucleus to the visual cortex areas V1, the ventral stream may be traced through visual areas V2, V3 and V4 in the inferotemporal cortex. Cells in this region show selective preferences for visual stimuli and code intrinsic features of an object, independent of either illumination, object location or observer viewpoint. These characteristics suggest that the inferotemporal cortex (thought to comprise the ventral stream) is involved in encoding and identifying the enduring characteristics of objects within the visual array. Furthermore, the ventral stream appears to be implicated in forming representations of the relationship between objects relative to each other, within a visual scene. Pigott and Milner (1993) found that patients with damage to this area showed poor memory for spatial location within a complex array, whereas damage to parietal areas did not seem to affect identification of spatial relations between objects.

Classic spatial neglect and spatial misperception disorders, such as constructional apraxia or topographical disorientation, where recognition of intrinsic and relational spatial patterns external to viewer-perspective is impaired, are also found when infero-temporal damage is apparent (Milner & Goodale, 1995). Therefore, ventral stream connections appear to be equipped to process important features in an allocentric rather than egocentric manner, such that an object, location or landmark may be identified even when the egocentric position has changed.

1.2.2 The dorsal stream: processing for action

Whereas the ventral stream seems suited to encode and construct information about “the world out there,” the dorsal stream uses information in an “on-line”
manner to compute, from moment to moment, the position of objects etc. relative to
the self, so that successful interaction or avoidance may occur within “the world
which includes me.” From previous discussion it is evident that the apparent ease with
which we accurately execute goal-directed movements betrays little of the complex
neurological processes which plan, guide and control behavior. The dorsal stream
subserves these processes by coding spatial and motion information for action.

The focus of the dorsal stream is the posterior parietal cortical area (PPC),
which, in humans, includes areas 5 and 7 in the superior parietal lobule and areas 39
and 40 in the inferior lobule (see Figure 1.2.). As noted previously, both cortical and
sub-cortical areas project into this stream. Areas MT/V5, V2, V3 and superior
collicular connections meet the lateral, medial and ventral intra-parietal areas (areas
LIP, MIP and VIP respectively in Figure 1.2). Mutual connections have also been
found with pre-motor areas. Such connections suggest that the potential for combining
visual, proprioceptive and motor information lies within the dorsal stream region.

Consideration of the functional modularity for visuo-spatial and motoric-
proprioceptive areas within the dorsal stream maps closely with notions of action- and
response-specific neuronal and spatial representations (see section 1.1).

1.2.2.1 Action-specific representation: reaching

Jeannerod, (1997) proposes the existence of two visuo-motor channels within
the dorsal stream. One channel processes information for, and controls, grasping
responses, while the other is concerned with the information processing required for
reaching. Of course, considerable mutual connections relate reaching and grasping for
a co-ordinated prehension movement, and disruption of either one changes the other,
(Desmurget, Prablanc, Rossetti, Arzi, Paulignan, Urquizar & Mignot, 1995). The
reaching areas are pertinent to the present discussion.

The existence of distinct “reach neurons” was discovered following
Mountcastle’s (1975) observations of cells in the PPC which discharged only during
active reaches towards objects. More recently, MacKay, (1992) found that cells in
area 7a (see Figure 1.2.) discharged with preferences independent of which arm was
moved. That these cells were not responding to visual feedback of the arm during the reach was suggested as the cells remained active when reaches were executed in the dark. Activation of premotor areas 4 and 6 was also noted by Caminiti et al., (Caminiti, Johnson, Galli, Ferraina & Burnod, 1991) during reaching movements. Interestingly, activity in these regions varied with changes to the initial start point of the movement, which suggests that some degree of encoding for proprioception or initial limb configuration is also required before the reaching response is executed.

1.2.2.2 Spatial representation in the dorsal stream

Neuronal representation of a movement in the parietal region thus involves both visual and proprioceptive information. In addition, in the premotor and motor areas, action-specific representations of the kinetics of movements pre-empt responses (e.g. Georgopoulos, 1982). How may the visuo-spatial location be encoded? If the purpose of object localization is the construction of a goal-directed action then the precise position of the object or target must be specified in relation to the current position of the actor. Recent findings suggest the existence of cell populations which encode space relative to eye, head and body position within the visuo-motor system (Jeannerod, 1997).

Area 7a and area LIP encode stimulus position relative to head position, by a process of “re-mapping” (Colby & Duhamel, 1993). This process is even anticipatory of saccades, such that the receptive fields of these cells shifts to compensate for future movement and ensure a smooth perception of spatial location. Area 7 cells also respond to changes in the optic flow, which enables encoding relative to either ego- or object-centred motion. Head-centred and body-centred frames of reference need to be supplemented by a representation of object position in relation to the limb which will reach for the object. Furthermore, this representation needs to be capable of being rapidly updated in order to “keep up with” the moving limb. Area 5 and the primary motor areas also appear to be implicated in the representation of limb-target movements.

The direction of limb movement in a goal-directed action such as reaching has been found to be represented in an anticipatory manner by cell populations in the
primary motor cortex and area 5 of the PPC (see Figure 1.2.). Kalaska and Crammond (1995) found that prior to movement initiation, activity in area 5 corresponded to the direction of arm movement. This representation was found to correlate with kinematic but not kinetic parameters, however. Spatio-temporal planning was found not to vary with changes in external load in terms of opposing forces which would, if not countered, "obstruct" the limb during movement. Motor cortical cell populations do correspond to force compensation requirements, however, (Kalaska 1989), although Georgopoulos (1982) has also noted pre-emptive representation of movements in a vectorial fashion within the primary motor areas. Since Caminiti et al. (1991) noted that activity changes in relation to limb configuration, it may be that primary motor areas represent these movement directions in relation to the current position of the arm, in particular the shoulder.

1.3 Clinical evidence to support modular processing

The PPC and functionally related cortical and sub-cortical areas appear to meet the specifications for visuo-motor processing suggested previously. Anatomical and physiological evidence suggests the existence of distinct mechanisms which allow the visual location of a stimulus in egocentred (and limb-centred) co-ordinates. The infero-temporal areas, in contrast, respond in ways which suggest differences in processing. Representation in a world- or allocentric frame of reference seems to be necessary in order that learning, recognition and identification processes occur. The functional consequences arising from damage to one or other stream would, according to this line of reasoning, result in distinct deficits in either representation for action or representation for identification.

The conclusions of lesion studies mentioned earlier (see section 1.1) have been substantially expanded through case studies of human patients who seem to have acquired precisely these injuries. Clinical examination of these subjects suggests that a fundamental dissociation between the two processing modes is possible.

1.3.1 Visuo-motor deficits
Posterior parietal damage typically results in a syndrome identified as optic ataxia, which includes deficient reaching movements. Spatial and temporal aspects of such actions are disrupted; reaches are both slower and less accurate (Jeannerod, 1997). Depending upon the exact site of injury, grasp capabilities may or may not also be disturbed. A case reported by Jakobsen et al., (Jakobsen, Archibald, Carey & Goodale, 1991) documented this pattern. Following parietal region injury, patient VK was able to make goal-directed reaching but not grasping movements. A similar clinical case study of modularity was also reported by Perenin and Vighetto, (1988) who noted that although prehension movements were impaired, object discrimination and other “perceptual” responses were unaffected by parietal region injury. This peculiar combination would result in the ability to identify an object placed close by, for example a coffee cup, yet the ability to perform the simple (for most people) action of reaching and grasping that same cup would be all but lost.

1.3.2. Visuo-perceptual deficits.

The opposite pattern of response abilities has also been found following lesions of the infero-temporal region which spare posterior parietal functioning. Damage to this area, regarded as central to the ventral processing stream, typically results in an inability to perceive or recognise objects. Visuo-motor function necessary to interact with these objects remains. This pattern of symptoms is termed “visual form agnosia,” and is characterised by severe impairment of recognition through form identification/discrimination. One patient in particular, DF, has received extensive examination (e.g. Milner, Perrett, Johnston, Benson, Jordan, Heeley, Bettucci, Mortara, Terazzi & Davidson, 1991; Goodale, Meenan, Bulthof, Nicolle, Murphy & Racicot 1994; Goodale, Milner, Jakobson & Carey, 1991).

DF suffered diffuse axonal damage to the infero-temporal (ventral stream) region following an anoxic episode due to carbon monoxide poisoning. Examination of low-level visual abilities revealed that high spatial frequency (though not orientation) detection and colour discrimination functions remained unaffected, suggesting that parvocellular cell connections remain. From MRI and clinical examinations, the site of damage has been hypothesized to be situated in magnocellular/parvocellular connections through the interblob regions beyond V2 into the
infero-temporal cortex, (Milner et al., 1991). DF cannot, therefore, make perceptual distinctions between objects on the basis of shape. Discrimination between line drawing of simple objects is at chance level, and she cannot copy such pictures either. From colour and textural cues, however, real objects can be identified. The difficulty in form identification is restricted to visual processing; although DF cannot identify letters or numbers on paper before her, tactile and haptic opportunities result in correct responses. DF thus seems to exhibit a profound impairment in perceptual processing skills. More competent demonstrations are elicited, however, when visuo-motor responses are required.

Milner and Goodale (1995) observed that even within a short time following her accident, DF demonstrated accurate reaching and even catching abilities. Despite persistent visuo-perceptual difficulties, DF demonstrated the necessary processes of relating object location not only to herself but to her moving arm and hand. In contrast to the inability to use form information for recognition purposes, this information appears to be fully accessible in order to guide movement.

An example of this task-specific dissociation was reported in detail by Milner et al., (1991). While DF was unable to report the orientation of a slot presented before her (i.e. whether the slot was vertical or horizontal), she could form a “posting” action to accurately align her hand and arm with the orientation of the slot. Interestingly, the same task has been used by clinicians to demonstrate the opposite combination of abilities in patients with optic ataxia.

A second notable paradigm used to investigate visual form agnosia reveals interesting information with regard to the nature of processes occurring in the two streams. In an instructed delay task, normal subjects show an accurate (though exaggerated) “pantomime” movement, scaling hand opening to the size of an object presented moments earlier but no longer visible. DF, despite being successful in executing a prehension movement given the object’s presence, is unable to maintain accuracy given a delay of more than two seconds between object presentation and movement initiation, (Goodale, Jakobsen & Keillor, 1994b). This finding has been interpreted as evidence for a temporal constraint operating within the visuo-motor processing system only. Such a conclusion is consistent with the hypothesis that the
constraints placed on this system require rapid updating of information in order to maintain accuracy as the relative position of arm and object changes during execution of the movement. The ability to perform deferred actions in normal subjects has also been interpreted as evidence for the role of stored object representations. The difficulty that DF and other visual form agnosics have with this type of delay task suggests a separation between the origin of visuo-motor "on-line" and visuo-perceptual "representational" processing in the ventral stream, the latter being precisely where these patients have sustained injury.

1.4 Functional dissociation of visuo-perceptual and visuo-motor processing in normal subjects.

Visual information processing for visual form agnosics appears to be limited to perception for action and hence also appears to be restricted to "the here and now." These findings illustrate functional differences between dorsal and ventral stream processing and correlate well with physiological evidence and lesion-technique research with primates. Recent work with neurologically intact human subjects also suggests that, under the correct conditions, visuo-motor and visuo-perceptual responses differ markedly in certain features.

In both clinical and normal populations, visuo-perceptual processing is strongly associated with conscious awareness. For example, one interesting finding from studies of "blindsight" and visual form agnosic patients is that subjects are typically unaware of objects when presented within the hemifield or region which corresponds to the damaged cortical area. Claims that they do not see, or neglect attention towards, an object in this location are then juxtaposed with accurate and appropriate object-directed behaviours. A separation of visuo-perceptual, "conscious"
processing from visuo-motor, "unconscious" processing was elicited with normal subjects by Goodale et al., (Goodale, Pelisson & Prablanc, 1986) who showed that changes could made in the location of a target without conscious awareness of this alteration by normal subjects. The smooth trajectory of pointing to meet this location altered appropriately but was not disrupted. This seemingly odd phenomena makes sense within a conceptual framework where the visuo-motor system needs to be able to process and account for such rapid changes, whereas the visuo-perceptual system does not. Bridgeman et al., (Bridgeman, Kirch & Sperling, 1981) created the opposite phenomenon using an apparent motion paradigm. Despite the strong illusory percept of target motion due to lateral movement of a frame surrounding the target, subjects showed no difficulty in pointing to the correct location.

These results suggest that motor re-calibration can occur extremely rapidly and without conscious perception by the actor. Milner and Goodale (1995) conclude that such experiments are indicative of the different frames of reference used by the visuo-perceptual and visuo-motor systems. Whereas the former gives precedence to the relative position of the target in relation to objects which surround it, as was the case in Bridgeman et al.'s experiment, the latter must remain unperturbed by such illusions, and instead continue to compute the position of the target relative to the self if actions are to be accurate. The visuo-perceptual system, therefore, appears to operate in an allocentric frame of reference. This conclusion is in agreement with the functions of such a system discussed previously in section 1.2.1. The visuo-motor system, in contrast, may utilize a frame of reference centred around the self.

This is not to say that the ventral or visuo-perceptual system cannot be used to drive goal-directed actions, as the pantomimed movements of normal subjects following a delay have shown. However, movements made after such a delay, perhaps derived from information within visuo-perceptual processing capacities, differ from those made within a visuo-motor frame of reference in ways which are consistent with the frame-of-reference hypothesis. For example, Wong and Mack (1981) used an illusion plus instructed delay paradigm to measure the accuracy of saccadic eye movements made to target locations. After a delay between target presentation and movement initiation, saccades typically resulted in eye movements to the "perceived" (i.e. incorrect) rather than "actual" location, whereas movements without delay were
concluded to be “driven” by the actual and not perceived location. The kinematic features of delay-induced saccades were altered – slower, less consistent movements were noted.

Pre-movement delay has also been studied with regard to larger movements than simple saccades. Thomson (1983) investigated the duration of information useful in guiding walking, and concluded that subjects were able to use “visual” information for up to eight seconds. Subjects were instructed to close their eyes and walk to reproduce distances previously seen. This type of paradigm can unfortunately confound the distance walked with the time taken to complete the response, and Thomson reported that many subjects used imagery strategies to facilitate their performance. Subsequent investigations of temporal constraints on visuo-motor processing have used smaller movements such as reaching or pointing responses, in an attempt to control for these problems. Elliott and Madalena (1987) asked subjects to point to reproduce visually-located target positions following a number of pre-movement delays. A delay of more than two seconds was found to induce a significant degree of error in the pointing response. This result was especially apparent in terms of the amplitude, or distance of the response, which shortened as pre-movement delay increased. The results of this experiment, conducted on normal adult subjects, correlate extremely closely with the difficulties experienced by DF in producing an object-directed movement following more than a two second delay. However, the systematic degradation of responses made by normal subjects after a delay contrasts with the complete disintegration of performance in responses made by DF.

1.5 Conclusions and predictions

In summary, clinical and experimental data using neurologically injured and uninjured human subjects, seems to converge to suggest that task performance characteristics may depend upon the response modality required. Furthermore, underlying these characteristics may be two distinct processing streams. One, the visuo-motor or dorsal stream, is reliant upon a rapid updating process, and is easily disrupted when a delay is introduced between encoding information and executing an appropriate response. The other, visuo-perceptual or ventral stream, is not so
temporally constrained, and is instead able to encode the relative locations between objects independent of the (dynamic) perspective of the viewer/actor. If this is indeed the case, questions arise as to the precise nature of these processing differences. What are the consequences of exceeding the temporal parameters of the visuo-motor system? What is the nature of information and decay within the two systems? How may the information comprising the spatial features of each type of representation be described? An attempt to examine these questions served as a starting point for the following experiments.
Two

2.0 Introduction

In chapter one it was argued that it is unlikely that the human brain possesses, creates or uses, a single, all-sufficing representation of external space. The dorsal and ventral streams hypothesised to be responsible for visuo-motor and visuo-perceptual responses have been discussed in terms of differences in the importance given to the same information regarding external space. In particular, it was argued that visuo-motor mechanisms operate within a co-ordinate system which emphasises spatial relations in regard to the self. In the visuo-motor system it is more likely that we have a representation for “the rules for how to get there,” (Paillard 1991) than for “what is out there.” According to Arbib (1991),

“There is no one absolute space represented in one place in the brain, only a coupling of sensory and motor spaces in such a way as to yield movement to achieve some goal...There is no one space in the brain where one integrated representation of space plays the sole executive role in linking perception and action...” (p.385, p.399)

Similarly, Stein (1991) describes visuo-motor representation as not consisting of

“...a representation of space, but rather a representation of the rules that must be followed in order to direct attention and hence...limb or body movements, towards objects in space.” (p.216)

Euclidean-like geometric spatial representations for the representation and identification of objects, may operate in allocentric co-ordinates, of the type already hypothesised to arise from processing in the ventral stream. Such a representation would emphasise the relative position of objects and locations in the environment rather than specifying the location in terms of the self. The visuo-perceptual system may have no need for rapidly updating information and may instead seek to maintain perceptual constancy in the face of changes in the environment caused by either the actor, the environment, or both. This form of processing, independent of view-point,
has been argued to be necessary for the processes of recognising and memorising features relating to objects, faces etc., (Marr 1982).

The spatial features within each representation may be broadly classified in terms of direction of the location and the distance between either the self and the location or between two locations in the external environment. Exceeding the temporal parameters for the availability of information may lead to two possible forms of distortion of response. One possibility is that a consistent distortion, or bias, becomes evident in responses. Another is that responses become increasingly spread, as accuracy becomes less sensitive.

It may be possible to illustrate the difference between characteristics of the reference frame employed by each system, by eliciting visuo-perceptual and visuo-motor responses. Gentilucci and Negrotti (1994) highlighted differences in accuracy contingent upon the mode of response. Their task required subjects to reproduce the distance between two previously viewed target locations, either by a lateral open-loop pointing movement (i.e. without vision of the moving arm or hand), or by perceptually matching the position with a laser pointer beam. Pointing and matching responses were found not to differ in terms of the relative accuracy of responses, but whereas pointing responses overestimated target distances of less than 10cm from the start point and underestimated distances of over 10cm, matching responses consistently over-estimated this distance for all target locations (see Figure 2.1. below) The difference between response modes was manifested in terms of the direction of error. This finding was interpreted in terms of differences in the encoding of spatial information used to guide visuo-motor and visuo-perceptual responses.

Figure 2.1 Schematic depiction of experiment by Gentilucci and Negrotti (1994)
Two problematic issues arise from this experiment. The first concerns the fact that subjects were required to estimate the relative distance between two locations, not the distance of a location relative to the position of the self. In this case, egocentric coding, such as that postulated to occur for visuo-motor transformations, was probably not as exclusively required or used as an allocentric coding of the relative distance between the two locations in the environment, such as would be employed by mechanisms underlying the visuo-perceptual response. This may have affected the method by which the distance of the target location was encoded prior to generating a motor response. The visuo-motor pointing response may not have fully utilised egocentric representation and as a result, differences between the mechanisms supporting the two response modes may have been inaccurately achieved.

Secondly, the visuo-motor pointing responses were made without feedback on finger position. Whereas visual information regarding the end-point of the laser beam was available at all times for the perceptual matching condition, the pointing response had to be completely guided by proprioceptive feedback. Open-loop pointing movements of this nature are known to be less accurate than movements made under the guidance of visual feedback, (Carlton, 1981). It may be, therefore, that the difference between response modalities noted by Gentilucci and Negrotti (1994) was due to subjects' inability to estimate the magnitude of their pointing response, rather than due to differences in the spatial characteristics of visuo-motor and visuo-perceptual representations.

The present experiment makes simple but critical alterations to this paradigm in an attempt to address these issues. Firstly, an open-loop pointing condition was
administered but pointing responses were also made with visual feedback on fingertip position in order to ensure that perceptually at least, both pointing and matching response modes involved the same degree of visual feedback. Errors in pointing could not, therefore, be attributed to a loss of information about hand position.

Responses were also controlled for whether the target location was encoded relative to the self or relative to other features of the environment, via the provision of four small, dim reference lights within the workspace. When lit, these four small, dim light points were designed to encourage the utilisation of a frame of reference centred in external, allocentric co-ordinates with the minimum requirement for encoding of space relative to the position of the self. Even in the pointing conditions, therefore, the need for encoding target location entirely as a function of the position of the self, was reduced. In the conditions where reference lights were not illuminated, the only source of visual information available to the subject was either the tip of the pointing stylus or the laser pointer “matching” beam during feedback-condition responses.

The degree to which pointing responses use a frame of reference relative to the self, or relative to other features in the environment, may also be examined via the introduction of pre-response delays. If visuo-motor information used to guide an action response such as pointing must be updated rapidly in order to "keep up with" the positions of the arm relative to the object or target location then mechanisms subserving such a response modality may possess a very short retention interval for guiding such actions. Visuo-perceptual mechanisms, however, may not require this level of rapid processing and may therefore not be subject to such a short temporal constraint on processing capacity.

A pre-movement delay of two seconds or longer has been shown to result in a deterioration in visuo-motor response in a clinical patient who suffered extensive ventral, visuo-perceptual stream but not dorsal, visuo-motor stream damage, (see chapter one). She could not form an appropriate grasp aperture in relation to an object presented just seconds previously. This degree of temporal constraint on visuo-motor processing has also been demonstrated in normal subjects. Elliott and Madalena (1987) required subjects to make fast (200-300msec) or slow (400-500msec) movements to reproduce a midline target location placed at either 25 cm or 35 cm
from their hand, depending upon starting position. The movements were carried out either in full vision, or in complete darkness after delays of zero (immediate response), two, five and ten seconds. Measures of response dispersion (total error) were derived for extent (amplitude) and perpendicular (direction) errors relative to each target.

Dispersion of the extent of pointing responses was found to increase when continuous visual feedback information regarding hand position was denied, even when there was no pre-movement delay. This was noted particularly for slower movements made within the 400-500msec interval, and was not noted for either movement time condition for the directional response measure. The finding suggests that some information regarding hand position is available for up to 400msec after visual information is denied. Response dispersion for both extent and directional measures were found to increase after a pre-movement delay of two seconds, a result which concurs with clinical evidence. No further deterioration was found to occur if response initiation was delayed for longer, since the two and five second delays did not differ significantly from each other. Elliott and Madalena (1987, experiment 1) interpreted the result using the concept of maintenance of visual information in a form of iconic memory but it may be that due to the open-loop nature of the pointing response, deterioration in information for a representation of arm position and not spatial position of the target location per se, may have occurred. Elliott and Madalena's (1987) third experiment illustrated that the two forms of information may be separable. During the delay period, visual information regarding target location was continually available, but the pointing response was still open loop. While amplitudinal and directional errors were reduced in magnitude, they remained a significant source of error. These authors concluded that information other than that provided by visual location of the goal of the movement is necessary for optimal movement accuracy.

A second account for these results is that error in the immediate response condition represents a different type of information loss from that which occurs after longer delays, since all of the longer delays differed from the vision/no-vision-no-delay conditions. But however this finding is interpreted, it illustrates the relative durability of information used to plan and execute the directional component of the
response, and the fragility of the information used to derive the amplitude component of the response. Whereas amplitude information may require visual feedback in order to effect adequate braking onset (e.g. Bard, Hay & Fleury, 1986) directional information may be both pre-programmed and able to remain in the event of a pre-movement delay (Georgopoulos, 1982, see chapter one). The findings are therefore in agreement with neurological evidence.

The present experiment attempts to both illustrate these issues and overcome the aforementioned methodological difficulties, by providing subjects with the opposite combination of information from that described in experiment three above. Instead of reducing the necessity for a visual representation of the location, the current experiment provides feedback on the position of the arm as it moves through space in one pointing condition with a view to reducing the necessity for accurate representation of the position of the arm while maintaining the necessity for accurate representation of information regarding the position of the target respective to the body.

Secondly, by maintaining starting position and altering target position only, the present experimental design reduces the possibility that movements could be learned and reproduced in a learned manner, utilising a large propensity for movement pre-programming. In the task used by Elliott and Madalena, (1987) feedback on terminal error was available after every trial. In conjunction with the single target position, this may have provided subjects with ample opportunity to create a response strategy based on a learned representation of either the target distance or movement characteristics. In addition, the change in start position only would have resulted in a visuo-motor change in the perception of the target location, but perceptually the target position remained the same, irrespective of the initial start position of the hand. Deliberate changes in the relationship between the target and the position of the head and trunk and not changes in the relative position of the target in relation to the hand were thus incorporated into the design of the current experiment.

On the basis of previous findings, it was hypothesised that a pre-response delay of two seconds or longer would affect pointing but not matching responses. Furthermore, if the addition of reference lights to the pointing condition in particular,
was to encourage the utilisation of an allocentric frame of reference such as would be used by the visuo-perceptual stream, then delay would no longer be expected to result in deterioration of accuracy. The difference between the pointing and matching conditions would be minimised with regard to the relative temporal parameters on accuracy.

The following predictions were made:

1. Pointing responses may be less accurate than matching responses. In particular, error is expected to increase from small to large with matching, visual feedback pointing and open-loop pointing responses.
2. The effect of response modality may interact with delay condition. Error is expected to increase from matching error to visual feedback pointing error to open loop pointing error as delay duration increases. For pointing responses only, the introduction of a delay period of more than two seconds may increase error.
3. The addition of reference lights may reduce error. The utility of reference lights may become more apparent in preserving a representation of space after a delay period is introduced. A two second or more delay period may be particularly significant for the utility of reference lights.
4. The position of the target location in the work space, in particular the distance, may affect the accuracy of the response. This is expected to occur to a greater degree for pointing responses than for matching responses.

Measures of both bias and sensitivity were derived for amplitudinal and directional components of the response. This was to examine whether the degradation in information used to guide movements occurred consistently over time, resulting in a change in the mean or bias of the response, and whether these changes were accompanied by a loss in sensitivity or spread of responses. Elliott and Madalena (1987) only reported data in terms of total error, a measure of response dispersion which did not permit the derivation of the direction of the error. In accordance with Elliott and Madalena (1987), Gentilucci and Negrotti (1994) noted that variable error changed across distance or extent of target position from the start point, although the latter authors did not find evidence for a change in the magnitude variable error depending on whether responses were motor or perceptually based. This finding was
interpreted as evidence for a common stage in processing spatial locations for both response modalities. Measures of variable error in the present experiment were thus analysed in addition to constant error measures in order to determine whether these findings could be replicated.
2.1 Method

2.1.1 Design

The experiment employed a 4 (zero/immediate, one, two, and four seconds’ delay) x 6 (open-loop pointing with/without reference lights, visual feedback pointing with/without reference lights, matching with/without reference lights) x 6 (target position) within subjects, repeated measures experimental design. Subjects completed 4 response trials per target position for each delay/response condition combination, giving a total of 576 trials per subject.

2.1.2 Subjects

Four right handed male subjects participated in the experiment, mean age 31 years. All subjects had normal or corrected-to-normal vision.

2.1.3. Apparatus

The subject was comfortably seated before a featureless table top surface, onto which red circular (10mm diameter) targets could be laser-projected in random sequence as controlled by a Macintosh computer. The subject’s head position was controlled using a cup-shaped chin rest, and hand starting position was held constant prior to each trial via a start switch placed directly below the chin rest in the subject’s midline. In the pointing conditions, subjects moved to reproduce the target position using a pencil which, in the feedback pointing conditions, had a luminous tip. For conditions where a perceptual matching response was required, subjects moved a laser pointer beam (10mm in diameter) to match the location of the target before marking this location themselves with a pencil held in the other hand. The laser pointer was in a fixed position at the same height, but 30cm to the side of, the chin rest, in the direction of the subject’s preferred hand (see also Gentilucci & Negrotti, 1994).

Target positions were placed at 24cm and 48cm from the start switch, in the midline and at 40 degrees to the left and right of the midline. Reference lights were LED’s placed at 20° eccentric to the left and right of the midline at 36cm and 72cm
from the start switch and, in the relevant conditions, were dimly illuminated at all times. A heavy black cloth covered the apparatus to prevent any ambient light from entering into the workspace. Neither targets, reference lights or laser beams emitted sufficient light as to illuminate other portions of the workspace. Figure 2.2 below depicts the apparatus as viewed from above, and approximate layout of the targets and reference lights (not to scale).

Figure 2.2. Diagram of experimental apparatus

2.1.4 Procedure

The subject was invited to seat themselves with their chin in the chin rest and their hand on the start switch. They were shown the function of the start switch and laser pointer/or were given the stylus with which they were to point. The subject was invited to read a sheet of written instructions and to clarify with the experimenter, any point which they did not fully understand. The pointing movement and movement of the laser-pointer were demonstrated by the experimenter at the beginning of each block of trials as necessary. Speed and accuracy for each mode of response, were emphasised to the subject.

The experiment was conducted in complete darkness. Each trial began with the projection of the target for one second, followed by the requisite delay. Delay duration was ended by the "go" signal, a computer-generated beep. The subject
responded on hearing the beep. In the perceptual matching conditions, the end of the delay coincided with the flashing activation of the laser-pointer beam. The subject positioned the laser beam to reproduce the target position. When satisfied with that position, a pencil mark was made on the table top to represent the position, then the laser beam was moved to a random position and switched off. Each block of trials consisted of 24 trials. On completion of a block, the room lights were illuminated and, without the subject seeing, the responses were colour coded by the experimenter. Subjects did not receive explicit feedback on accuracy at any time during the experiment. Subjects completed the blocks of trials in random sequence and rested whenever necessary.

2.1.5 Data Analysis

Subjects’ scores were derived in terms of amplitude (under/overshoot) and direction (perpendicular error to the left/right of the target) in millimetres, for each trial and for each target position separately. Errors were recorded in relation to the distance and perpendicular distance from each target position. This resulted in 1,152 data points for each subject, as amplitude and direction scores remained separate throughout the analysis. Bias, or constant error, was calculated as the signed mean of responses for each target position, where under-estimation responses were recorded as negative and over-estimation responses were recorded as positive. For directional error, a negative value denotes bias to the left of target position, and a positive value reveals bias to the right of the target position. Sensitivity, or variable error, was calculated as the standard deviation of responses around a given target, to give an indication of the spread of responses. Separate Analyses of Variance were conducted for each measure of spatial error and also for bias and sensitivity measures. Data are reported in millimetres.

2.2 Results

2.2.1 Response modality and the effect of pre-movement delay.

Predictions were made regarding the interaction between response modality (open-loop pointing, visual-feedback pointing and perceptual matching) and pre-response delay. In particular, it was hypothesised that whereas a delay of greater than
two seconds would disrupt pointing accuracy, matching accuracy would remain stable across conditions. Firstly, tables 2.1 and 2.2 present data relating to the main effects of response modality on amplitude bias, and of delay on amplitude bias and amplitude sensitivity.

Table 2.1 Mean response errors for each modality.

<table>
<thead>
<tr>
<th>Response Modality</th>
<th>Error Measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude Bias</td>
</tr>
<tr>
<td>Open Loop</td>
<td>-23.44</td>
</tr>
<tr>
<td>Feedback P</td>
<td>-12.410</td>
</tr>
<tr>
<td>Vis Match</td>
<td>-0.708</td>
</tr>
</tbody>
</table>

Table 2.2 Mean response errors for each delay condition.

<table>
<thead>
<tr>
<th>Response condition</th>
<th>Error Measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude Bias</td>
</tr>
<tr>
<td>Immediate</td>
<td>-8.53</td>
</tr>
<tr>
<td>1 second</td>
<td>-12.021</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-12.930</td>
</tr>
</tbody>
</table>

Secondly, tables 2.3. (i)-(iv) present the data for response modality across the four delay conditions, for each component measure of responses. The interaction between delay condition and response modality should be noted for amplitude bias only.

Table 2.3.

i. Amplitude bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Standard deviations are not reported since sensitivity measures are the SD of bias measures.
Response modality and spatial location

<table>
<thead>
<tr>
<th></th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td>-16.713</td>
<td>-9.896</td>
<td>1.030</td>
</tr>
<tr>
<td>1 second</td>
<td>-21.767</td>
<td>-11.795</td>
<td>-2.501</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-23.704</td>
<td>-11.325</td>
<td>-3.756</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-31.561</td>
<td>-16.622</td>
<td>2.396</td>
</tr>
</tbody>
</table>

ii. Amplitude sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open Loop</td>
</tr>
<tr>
<td>Immediate</td>
<td>11.237</td>
</tr>
<tr>
<td>1 second</td>
<td>10.636</td>
</tr>
<tr>
<td>2 seconds</td>
<td>11.249</td>
</tr>
<tr>
<td>4 seconds</td>
<td>14.290</td>
</tr>
</tbody>
</table>

iii. Directional Bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open Loop</td>
</tr>
<tr>
<td>Immediate</td>
<td>-4.193</td>
</tr>
<tr>
<td>1 second</td>
<td>-10.186</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-12.550</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-10.700</td>
</tr>
</tbody>
</table>

iv. Directional sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open Loop</td>
</tr>
<tr>
<td>Immediate</td>
<td>9.377</td>
</tr>
<tr>
<td>1 second</td>
<td>8.699</td>
</tr>
<tr>
<td>2 seconds</td>
<td>9.929</td>
</tr>
<tr>
<td>4 seconds</td>
<td>12.576</td>
</tr>
</tbody>
</table>

Although main effects of response modality and delay were noted for amplitude bias, F(2,90)=7.866, p=0.021, and F(3,90)=9.555, p=0.004 respectively,
and delay affected amplitude sensitivity, $F(3,90)=7.814, p=0.001$, it is the interaction between these independent variables which is of most notable interest. There was a significant interaction between response modality and delay for amplitude bias only, $F(6,90)=1.574, p=0.0284$. The nature of this interaction is presented graphically in Figure 2.2. below.

Figure 2.2. Interaction between response modality and delay condition.

The graph shows mean amplitude bias for each delay condition and response mode. Error is shown to decrease in magnitude from open-loop to feedback pointing, and then to perceptual matching. Delay particularly disrupts pointing responses. Further analysis compared the pointing conditions with the matching condition and revealed an effect of delay on the two pointing conditions only, $F(3,9)=6.899, p=0.010$. Bonferroni post-hoc comparisons revealed significant differences in pointing accuracy between two and four seconds, $p=0.027$. No significant effect of delay was noted on matching performance, $p>0.05$. Mean accuracy of the distance component for pointing responses thus seems to deteriorate at a faster rate than for matching responses. Directional accuracy and the overall sensitivity of responses did not show the same significant patterns of interaction, although a decrease in sensitivity of the amplitude response was noted for all three response modalities between the zero and two second delay conditions, $p=0.042$.

2.2.2 The effect of response modality, delay and reference lights on accuracy.
As with response modality and delay condition, the presence or absence of reference lights significantly affected the amplitude bias and sensitivity of responses, $F(1,90)=17.665$, $p=0.025$ and $F(1,90)=40.011$, $p=0.008$ respectively. These data are presented below in table 2.4.

Table 2.4 The effect of reference lights on response error

<table>
<thead>
<tr>
<th>Response Condition</th>
<th>Error Measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude Bias</td>
</tr>
<tr>
<td>No reference</td>
<td>-16.996</td>
</tr>
</tbody>
</table>

It was predicted that the addition of reference lights to an otherwise dark workspace would act to reduce error, and this was found to be the case. However, pointing responses in particular were expected to improve in the presence of reference lights, and thus also following a delay. The three way interaction for response modality, delay condition and reference lights for the measure of amplitude bias is shown in Figure 2.3.
Figure 2.3. Interaction of response modality, delay condition and reference lights on amplitude bias.

The graphs illustrate several results. The first is the powerful effect of reference lights on minimising response error. The second is that whereas perceptual matching responses are not particularly influenced by the presence of reference lights,
the accuracy of pointing responses improves greatly. Thirdly, as delay increases, reference lights appear to prevent visual-feedback pointing accuracy from deteriorating. Whereas open-loop pointing deterioration may be regarded as indicative of information loss regarding hand position in addition to any deterioration of a spatial representation, the reduction of error due to reference lights in the visual-feedback pointing condition between two and four seconds' delay suggests that reference lights prolong accuracy after the initial two second capacity for “visuomotor” representation has been exceeded. Table 2.5 presents data for response modality, delay and reference light conditions for each error measure.

Table 2.5. Mean response error within response modality, delay and reference lights conditions.

i. Amplitude Bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td>-20.61</td>
<td>-10.97</td>
<td>-9.00</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-38.70</td>
<td>-8.30</td>
<td>-13.82</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-48.67</td>
<td>-32.87</td>
<td>0.300</td>
</tr>
</tbody>
</table>

ii. Amplitude sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
</table>


### iii. Directional Bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No reference</td>
<td>Reference</td>
<td>No reference</td>
<td>Reference</td>
</tr>
<tr>
<td>Immediate</td>
<td>-7.25</td>
<td>-2.34</td>
<td>-6.49</td>
<td>0.69</td>
</tr>
<tr>
<td>1 second</td>
<td>-9.56</td>
<td>-9.931</td>
<td>1.33</td>
<td>-0.38</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-12.38</td>
<td>-12.642</td>
<td>-7.47</td>
<td>1.01</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-14.82</td>
<td>-6.774</td>
<td>-3.84</td>
<td>2.41</td>
</tr>
</tbody>
</table>

### iv. Directional sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No reference</td>
<td>Reference</td>
<td>No reference</td>
<td>Reference</td>
</tr>
<tr>
<td>Immediate</td>
<td>15.52</td>
<td>14.57</td>
<td>16.23</td>
<td>9.55</td>
</tr>
<tr>
<td>1 second</td>
<td>19.49</td>
<td>18.30</td>
<td>15.14</td>
<td>10.39</td>
</tr>
<tr>
<td>2 seconds</td>
<td>14.37</td>
<td>15.29</td>
<td>20.78</td>
<td>12.08</td>
</tr>
<tr>
<td>4 seconds</td>
<td>21.33</td>
<td>12.49</td>
<td>16.00</td>
<td>13.72</td>
</tr>
</tbody>
</table>

2.2.3 The effect of target distance on response accuracy.

The effect of target position on response accuracy varied largely as a function of target distance and on the presence of reference lights, and response modality. When all 6 target positions were included in the ANOVA analyses, significant main
effects were found for amplitude bias, $F(5,90)=7.052, p=0.001$, amplitude sensitivity, $F(5,90)=7.814, p=0.001$ and directional sensitivity, $F(5,90)=4.411, p=0.011$. There was no direct effect of target position on directional bias. The main effects of target position can be seen from table 2.6 below.

Table 2.6. The main effect of target position on response accuracy.

<table>
<thead>
<tr>
<th>Target position</th>
<th>Error Measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude Bias</td>
</tr>
<tr>
<td>Far Middle</td>
<td>-20.487</td>
</tr>
<tr>
<td>Near Middle</td>
<td>-6.79</td>
</tr>
<tr>
<td>Far Left</td>
<td>-17.929</td>
</tr>
<tr>
<td>Near Left</td>
<td>-3.81</td>
</tr>
<tr>
<td>Near Right</td>
<td>-4.373</td>
</tr>
</tbody>
</table>

In order to clarify the complex results regarding the effect of target position, scores for the three far (48cm) and three near targets (24cm) were combined together into two groups. Note that data reported here are raw error scores and that the error occurred as a constant proportion of target distance. This effect was established when data were converted to percentage of target distance. Appendix A (p.108) contains these data in tabulated form and a brief summary of the analyses. Data conversion to percentage of target distance did not alter the effects of the other independent variables, namely the response modality, presence/absence of reference lights, and delay conditions. Tables 2.7 (i)-(viii) below present data for errors for near and far targets, for (a) responses made with no reference lights and (b) responses made with the provision of reference lights.

Table 2.7. Response errors for near and far target positions.

(a) No reference lights

i. Amplitude Bias
### ii. Amplitude sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Open Loop Near</th>
<th>Open Loop Far</th>
<th>Feedback P Near</th>
<th>Feedback P Far</th>
<th>Matching Near</th>
<th>Matching Far</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 second</td>
<td>-12.4356</td>
<td>-44.2420</td>
<td>-19.7083</td>
<td>-17.5928</td>
<td>0.0094</td>
<td>-5.0417</td>
</tr>
</tbody>
</table>

### iii. Directional Bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Open Loop Near</th>
<th>Open Loop Far</th>
<th>Feedback P Near</th>
<th>Feedback P Far</th>
<th>Matching Near</th>
<th>Matching Far</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td>-3.0208</td>
<td>-11.7500</td>
<td>-5.2708</td>
<td>-10.7102</td>
<td>-0.117</td>
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<tr>
<td>1 second</td>
<td>-5.9110</td>
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<tr>
<td>4 seconds</td>
<td>-12.7995</td>
<td>-16.6708</td>
<td>-0.008</td>
<td>-7.4083</td>
<td>-0.8292</td>
<td>5.3125</td>
</tr>
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</table>

### iv. Directional sensitivity

<table>
<thead>
<tr>
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<th>Open Loop Far</th>
<th>Feedback P Near</th>
<th>Feedback P Far</th>
<th>Matching Near</th>
<th>Matching Far</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 second</td>
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<td>23.5795</td>
<td>14.8038</td>
<td>15.9017</td>
<td>15.1125</td>
<td>16.9124</td>
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</table>
(b) Reference lights

v. Amplitude Bias

<table>
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<th>Delay Condition</th>
<th>Response Mode</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Open Loop</td>
<td>Feedback P</td>
<td>Matching</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
</tr>
<tr>
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<td>-13.05</td>
<td>-5.73</td>
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<td>-9.44</td>
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<td>-17.04</td>
<td>-3.59</td>
<td>-12.04</td>
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<td>-13.02</td>
</tr>
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<td>2 seconds</td>
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<td>-13.86</td>
<td>-10.07</td>
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<td>1.27</td>
<td>-4.06</td>
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</tbody>
</table>

vi. Amplitude sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Open Loop</td>
<td>Feedback P</td>
<td>Matching</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
</tr>
<tr>
<td>Immediate</td>
<td>8.9281</td>
<td>14.068</td>
<td>9.95</td>
<td>10.60</td>
<td>9.87</td>
<td>10.98</td>
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<tr>
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<td>10.8984</td>
<td>18.3457</td>
<td>8.05</td>
<td>11.00</td>
<td>11.70</td>
<td>13.90</td>
</tr>
<tr>
<td>2 seconds</td>
<td>13.7487</td>
<td>13.1395</td>
<td>10.67</td>
<td>10.37</td>
<td>17.66</td>
<td>12.61</td>
</tr>
</tbody>
</table>
vii. Directional Bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
</tr>
<tr>
<td>Immediate</td>
<td>-1.59</td>
<td>-3.42</td>
<td>-0.11</td>
<td>1.43</td>
</tr>
<tr>
<td>1 second</td>
<td>-4.27</td>
<td>-16.90</td>
<td>-0.75</td>
<td>-0.20</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-6.34</td>
<td>-18.86</td>
<td>0.41</td>
<td>1.59</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-2.82</td>
<td>-11.06</td>
<td>-0.83</td>
<td>5.82</td>
</tr>
</tbody>
</table>

viii. Directional sensitivity

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
</tr>
<tr>
<td>Immediate</td>
<td>8.9315</td>
<td>16.9725</td>
<td>6.81</td>
<td>11.28</td>
</tr>
<tr>
<td>1 second</td>
<td>9.4976</td>
<td>20.9443</td>
<td>8.80</td>
<td>11.68</td>
</tr>
<tr>
<td>2 seconds</td>
<td>12.370</td>
<td>21.9626</td>
<td>10.47</td>
<td>13.50</td>
</tr>
<tr>
<td>4 seconds</td>
<td>11.3260</td>
<td>11.9562</td>
<td>13.88</td>
<td>12.40</td>
</tr>
</tbody>
</table>

A two-way interaction was noted for target distance and reference lights on the amplitude sensitivity measure, $F(1,18)=11.595$, $p=0.042$. The high degree of error associated with far target distance is greatly reduced when reference lights are provided, Figure 2.4. below. Responses to near targets are show less dispersion than to far targets.

Figure 2.4. Reference lights reduce dispersion of responses to far targets.
For raw error scores, a three way interaction between target distance, reference lights and response modality was noted for amplitude bias only, \( F(2,3,18)=26.673, p=0.001 \). This interesting relationship, which did not change significantly over delay conditions, is shown below in Figure 2.5.

Figure 2.5. Response modality, target distance and the provision of reference lights affect amplitude bias.

As can be seen from the graph, the mean or bias of open loop pointing responses is significantly greater for far targets, particularly without reference lights. Reference lights improve the response such that open loop and visual-feedback pointing responses to far targets are similar in bias. Feedback pointing is also less accurate for far targets but this is aided by reference lights. Visual matching responses are notable for consistency across target distances and irrespective of reference lights. Examination of the differences between the pointing conditions revealed the presence of significant differences contingent upon target distance and reference lights, as has already been established. This relationship was also contingent upon delay condition for directional bias, \( F(3,9)=5.479, p=0.020 \). Significant contrasts were found between open loop and visual-feedback pointing between zero and two seconds’ delay, \( p=0.048 \), and between zero and four seconds’ delay, \( p=0.025 \). Specifically, open loop pointing for all four right handed subjects “drifted” to the left of the target position after a one second delay or longer. This pattern can be seen in Figure 2.7 below.
Response dispersion of pointing but not matching responses varied with target distance, as shown by a significant interaction for directional sensitivity, $F(2,18)=5.321, p=0.047$. This is shown below in Figure 2.6. As pointing responses to further away targets are required without vision of the hand or arm, the lateral dispersion of responses over trials seems to increase. There is a loss in sensitivity for the open loop pointing responses, $F(1,9)=11.615, p=0.042$, which is not evident in the visual feedback or matching responses, $p>0.05$, suggesting that the deterioration is due to a lack of feedback regarding arm position which proprioception alone cannot compensate for. This finding is a further indication of how the pointing conditions differed from each other.

Figure 2.6. Dispersion of pointing but not matching responses depends on target
2.3. Discussion.

Based on previous clinical and experimental evidence regarding the features of visuo-motor and visuo-perceptual processes, several predictions were made. Firstly, it was hypothesised that pointing responses would show significant deterioration following a pre-response delay of more than two seconds' duration. Perceptual matching responses were expected to remain consistent. The results showed the appearance of bias in the amplitude component of pointing responses but not matching responses after more than two second pre-movement delay. This result suggests the effective manipulation of either visuo-perceptual or visuo-motor modality required in order to initiate the appropriate response. In addition, comparison of the two pointing conditions revealed that open loop pointing and visual-feedback pointing also differed in the extent of the underestimation of target distance, after more than two seconds' delay. Overall, open-loop pointing was poorer than visual feedback pointing, and both pointing conditions were significantly less accurate than responses in the perceptual matching condition. Following the review of literature from clinical and experimental sources, these results are unsurprising. But they are nevertheless fascinating, since the only overt difference between the feedback-pointing and perceptual matching conditions is the nature of responses to identical target locations under otherwise identical conditions. The results suggest that visuo-motor representation used to guide pointing is constrained to two seconds, after which a consistent bias or distortion of the distance component of the representation appears. The visuo-perceptual process underlying matching responses is significantly more durable.

The results are in agreement with previous literature. However, the experiment provides an extension of findings reported by, for example, Elliott and Madalena (1987), due to specification of the nature of response deterioration. In particular, the extent of the response in pointing only, becomes biased following delay. Sensitivity error, which may reflect "noise," is no more apparent in pointing than matching responses and appears in the amplitude component after a two second delay regardless of response modality condition. The bias and loss of sensitivity is also found in the
visuo-perceptual representation but the interaction result shows the significantly larger effect of pointing responses than matching responses on amplitude bias. This finding suggests that distinguishable aspects of information processing are common (amplitude sensitivity decreases with delay) and specific (amplitude bias decreases for pointing only) to the different response modalities.

The directional component of the response is relatively “robust.” It appears that only in the open-loop pointing condition, where no visual feedback is available regarding arm/hand position, does the directional component of the response begin to deteriorate. In the present experiment with four right-handed subjects, the nature of this deterioration was in the form of a consistent “drift” towards the left side, which worsened with delay. The directional component of the response was stabilised when visual feedback on finger-tip position was provided. This suggests that visual feedback information is important for both the amplitude and directional components of a pointing response.

The susceptibility of amplitude but not directional response elements to delay is in accordance with previous findings, (e.g. Georgopoulos, 1982). Furthermore, the phenomenon of proprioceptive drift such as was found for directional bias in open-loop pointing is in agreement with experimental inducement of changes in the felt position of the limb as reported by Smyth and Marriott (1988).

Responses were expected to differ according to the provision of reference lights in the otherwise darkened workspace. The improvement in accuracy was particularly notable for after a delay, suggesting that providing information sufficient to construct a representation of the workspace in allocentric and not egocentric co-ordinates was of benefit after the critical retention interval for visuo-motor accuracy was exceeded. Between two and four seconds’ delay, visual feedback pointing error was reduced dramatically with the provision of reference lights. Comparison with responses in visual feedback pointing without reference lights show how it is particularly after two seconds’ delay that reference lights reduce error. It may be that the allocentric representation facilitated by reference lights is a plausible successor in the guidance of action once bias in visuo-motor processing sets in. Reference lights also improved open-loop pointing responses, particularly to far target positions. This
result demonstrates that even in the absence of visual feedback information regarding finger-tip position, other sources of information in the workspace were available to improve the accuracy of an otherwise open-loop response.

Finally, one concern arising from the results of the present experiment is that the nature of the experiment, which employed a repeated measures design, permitted sufficient practice for subjects to learn to reproduce systematic (albeit inaccurate) movements towards the target locations. This may have affected the responses in some way. A between-subjects design was therefore incorporated in to the following experiment.

Three

3.0 Introduction

Results from the previous experiment suggest that the frame of reference for pointing movements was altered when reference lights were added to the pointing conditions. The effect was to improve response accuracy and, for the feedback-pointing condition in particular, to reduce the deterioration in performance when pre-movement delays were introduced. A further significant factor which may differentiate between the visuo-motor and visuo-perceptual information processing systems is the degree to which continuous vision of the target position is required. Not only may pointing responses require continuous vision of the moving hand in order to maintain accuracy, but the visuo-motor response may also be constrained in its reliance on feedback regarding the target location when executing the response, in such a way that the visuo-perceptual system is not.
One issue concerns the necessity for continuous viewing of the target location in order to effectively "hone" the reaching response. The reach trajectory may be divided into two portions, an initial ballistic or pre-programmed phase, and a final approach phase where braking occurs to allow fine-tuning of the movement such that, for example, the selected object is not knocked over (e.g. see Jeannerod, 1997). Visual feedback regarding arm and target position significantly improves the accuracy of such movements (Carlton, 1981), particularly in the final phase of the movement trajectory (Bard, Hay & Fleury, 1986). This may be a feature which is built into the information processing characteristics of the visuo-motor system, such that without this information, the pointing response is not as accurate as it could be. In contrast, the visuo-perceptual system, as it does not make an "active" response, does not have to consider and "update" information with this high degree of accuracy.

What factors may the visuo-motor system be required to control such that visual feedback regarding the arm-target relationship and continuous target location information is necessary while making a reaching or pointing response? Visual feedback of the limb and target position allows control of the temporal characteristics of the response, i.e. the pattern of acceleration and deceleration. The visuo-motor system has to effect the correct pattern of muscle and joint co-ordination and activity, in order that a smooth acceleration/deceleration profile is executed. Part of this requirement, therefore, is controlling joint forces and overcoming inertial forces, to control the muscle forces and braking onset to the target.

When moving the arm through space in order to reach to a specific location, joint torques and movement forces must be taken into consideration such that a smooth acceleration/deceleration profile is effected. If a movement involves a single, isolated joint, the relationship between movement forces and gravitational forces remains a fairly straightforward one. The biomechanical inter-relationship between forces becomes more complex when multi-joint movements (i.e. involving the shoulder, elbow and wrist simultaneously) are examined. Not only does gravity act to assist and/or resist limb movement depending on the spatial configuration of the joints in the limb, but motion of each joint creates velocity- and acceleration-dependent forces which must be controlled when executing the movement at a global level. Forces affect each joint individually and are expressed as torques. Torques at each
joint also interact with one another to affect other joints in a dynamic fashion as the limb moves. The central nervous system must be aware of and act to counter these torques otherwise the movement trajectory is curved, (Ghez, Cooper & Martin, 1996). Visual feedback information and proprioception therefore play an important role in maintaining movement accuracy through the control of joint torques and of interaction torques in particular (Sainberg, Poizner & Ghez, 1993).

The application of Newtonian principles and laws enables a description of the dynamic forces which act upon the limb as it moves through space, and provide clues as to how the nervous system is able to overcome and control these forces. For example, Newton’s third law states that for every force one body exerts on another, the second exerts an equal and opposite force on the first. When applied to the mechanics of limb movement, it may be seen that the force with which the muscle contracts to initiate limb movement, is acting to accelerate the limb against an equal and opposite inertial force. Limbs and limb segments have mass and therefore a moment of inertia, a dynamic (angular) measure of mass. A force must therefore be generated or applied in order to effect a change in acceleration and velocity. The muscle must effect a force to overcome the other, opposing angular forces, known as torques. Torques are thus defined as dynamic loads which must be opposed by the muscle as it contracts, in order to control movement. The application of a torque causes a proportional increase or decrease in angular acceleration in the direction of that torque, (a dynamic or angular statement for Newton’s second law). Therefore, torques become apparent as the limb accelerates and can affect the degree to which muscles and joints contract and rotate throughout the course of the movement.

At any joint, there are several types of movement-dependent torque. The first is an acceleration dependent torque, which is largest at the beginning and ending of a movement. This torque is proportional to the angular acceleration of the joint (according to Newton’s second law of angular motion, angular acceleration is proportional to the torque causing it). The second is a centrifugal torque, which is again dependent upon the acceleration and velocity of the moving limb. The third is coriolis torque, a velocity dependent torque. These torques, when acting on a single joint, are known as self-torques. Most “natural” (i.e. unconstrained) movements, and especially prehension and pointing movements, however, involve the simultaneous
maneuvering of several joints, e.g. the shoulder, elbow, wrist etc. A multi-joint account of movement involves interaction torques, which are torques at a joint related to the angular movement of other joints which affect the movement of that joint as it acts as part of a limb. Gravitational torques, those due to the weight of the limb segments distal to the particular joint, are also important factors since they may facilitate or hinder the ease with which joints move. Interaction torques vary with limb configuration, (Ghez et al., 1996), but as with single joint torques, they vary with acceleration (typically greatest at the beginning and end of the movement) and velocity (typically greatest midway during the movement).

Ghez et al., (1996) found that continuous visual feedback of the limb position increased the ability to control movement-dependent torques. Patients who had undergone large fibre sensory de-afferentation and who therefore were deficient in proprioceptive feedback, showed substantial improvement in movement control under conditions of visual feedback. Interestingly, normal subjects were also helped by visual feedback. This was particularly apparent when the ease of movement was manipulated through increasing and decreasing the inertial load on the limb as it moved to the target position. In particular, for right handed subjects, movement toward the angle of approximately 60° is along the vectorial trajectory of most resistance, and movement toward the right-side angle of approximately 120° is along the vectorial trajectory of least resistance where 90° is the midline. An illustration of this type of task is shown in Figure 3.1. below.

Figure 3.1. Movement-direction dependent errors under open-loop movement conditions.
Continuous visual feedback may be necessary in order to correct for the direction-of-movement-dependent joint torques and inertial forces which operate during the response. Without this information, braking onset may be early, resulting in a more or less universal underestimation of target distance. A consistent underestimation of target distance when vision of the target was occluded was a feature of responses in the experiment described in chapter two.

Proprioceptive information is important for the sense of limb position and limb movement, (Goodwin, McCloskey & Matthews, 1972). However, although derived from physiological sources such as information from muscle spindles and joint, tendon and cutaneous sensory feedback, proprioceptive information alone cannot maintain movement accuracy. Visual feedback information is also necessary to update a calibrated perception of arm position for the maintenance of movement accuracy and the evaluation of whether movement is sufficiently successful in overcoming movement forces. Experiments on movements made under open-loop conditions have found that movement accuracy decreases immediately as feedback of the moving arm towards the target is denied (e.g. Smyth & Marriott, 1981, Ghez et al., 1996). Similarly, without visual feedback information, error in perceived proprioceptive feedback information may be induced experimentally such that the felt position of the limb is incorrect, (e.g. see Jeannerod, 1997).

One significant source of error in open-loop pointing may therefore be an inability to control movement forces due to deprivation of normally dominant visual information, particularly for initiating and controlling the deceleration phase of the movement. Movement forces may be centrally mediated in the sense that a certain portion of the movement is “ballistic” (Georgopoulos, 1986). However, in the motor cortical area (see chapter one) a body of “load-sensitive” cells exist which respond to changes in the force load required to effect the movement. Changes in the direction of movement alter these forces and, significantly, although connected to the posterior parietal cortex, these cells do not become active until after movement has been initiated. While these cells may be responding to afferent feedback from muscle receptors, and not specifically to the sight of the moving arm, it nevertheless remains apparent that at the biological level, a certain degree of control of the movement occurs in an “on-line” manner, is not pre-programmed prior to movement onset and
may require visual information. In effecting a satisfactory braking period as the arm moves closer to the target, therefore, vision of the arm and the target position is required for the maintenance of accuracy. The visuo-motor system thus relies on the provision of information in such a way as is not necessary for the visuo-perceptual system.

The experimental conditions in the current experiment were thus similar to those in chapter two. By manipulating the provision of information, i.e. by removing the target but allowing visual feedback information concerning the moving arm (feedback pointing condition); by removing the target and visual feedback information of the moving limb (open-loop pointing condition); and by removing the visuo-motor response entirely (perceptual matching condition); together with variations in movement direction, it may be possible to examine the relative contribution of continuous visual feedback of the target and arm positions, towards the accuracy of the response.

The provision of feedback regarding hand position should act to reduce the magnitude of the effect of changing the required direction of movement, since the requirement of accuracy in proprioceptive feedback regarding error in joint position is minimised. However, if vision of the target is necessary then some degree of error should still be expected in the feedback pointing condition. Based on the previous experimental results, this effect is expected to occur. More specifically, however, the direction of error would be expected to take the form of an underestimation of the target position. Without visual feedback, error is expected to be larger than with feedback, which would still be less accurate than perceptual matching, especially where the requirement for visual feedback on target location is the greatest, i.e. where inertial forces acting against the limb are also large. Thus, target laterality may interact with response condition.

The current experiment seeks to address these issues and makes the following predictions. Firstly, that the dissociation between response systems can be shown by varying the direction of movement, and, therefore, the demands made upon the visuo-motor system. Perceptually, responding to the left may be no different from judging a response to the right of the midline but motorically these two directions may require a
change in response calculation parameters. This may become evident in the pattern of spatial error which is noted, on comparing the lateral targets for a) pointing and b) perceptual matching responses.

1. It is expected that an interaction will occur between response condition and target position, if target position is examined with regard to movement to the left and right.

2. Open loop pointing may be subject to a larger degree of error than either feedback pointing or perceptual matching. Feedback pointing is expected to be more accurate than open loop pointing but still not as accurate as perceptual matching.

Secondly, it may be that in the previous experiment, the pattern of results reflects the fact that subjects conducted many trials and therefore that the effect of practicing movements to the target positions reduced the observed effects of pre-movement delay. This was almost certainly the case for analyses of lateral target positions, whereby practice was sufficient in masking the effects of movement direction. A between subjects experimental design was therefore employed in order to examine in more detail, the effects of varying pre-response delay. Also, the high repetition of movements in the first experiment may have artificially raised the consistency of responses.

3. It is hypothesised that a two second critical parameter exists, after which response accuracy in the pointing conditions breaks down. Response sensitivity as well as bias may degrade.

4. As with the predictions made in the previous experimental chapter, it is expected that pointing responses shall underestimate target distance and that error magnitude shall vary as a function of target distance.
3.1 Method

3.1.1 Design

The experiment employed a 4 (delay) x 3 (response condition) x 6 (target position), mixed design. As in the first experiment, the delay conditions were: zero/immediate, one, two and four seconds and the response modality conditions were open-loop pointing, feedback pointing and matching. The delay and response conditions were between subjects factors and the target position variable was a repeated measures factor. Subjects completed 4 trials per target position for each of the delay/response type conditions, giving a total of 24 trials per subject.

3.1.2 Subjects

28 males and 64 females (mean age 25.9 years) volunteered to participate in the experiment and were randomly allocated to one of 8 subject groups. In 4 groups there were 8 subjects per group, and 4 groups were made up of 7 subjects.

3.1.3 Apparatus

The apparatus was identical to that described in Section 2.1.3, however reference lights were not included in any of the conditions.

3.1.4 Procedure

The procedure was identical to that described in Section 2.1.4. However, subjects completed one block of trials only.

3.1.5 Data Analysis
Scores were derived in an identical manner to that described in Section 2.1.5. However, only 48 data points were recorded for each subject: 24 data points for amplitude error and 24 data points for direction error.

3.2. Results

All tabulated data are presented in millimetres. Standard deviations of the bias scores are presented as sensitivity scores. Negative amplitude scores reflect underestimation of the target and positive scores reflect overestimation of target distance. For directional measures, a negative score denotes a response to the left of target position and a positive score denotes a response to the right of the target.

Initially, an ANOVA analysis was run with 6 levels of the variable “target position.” Due to the complex interactions which resulted, and in order to give clarity to the results, target positions were collapsed into near and far target positions to reflect target distance, as reported for the results in chapter two. For the analyses on target laterality, target positions were collapsed into left and right. This did not change the effects of delay or response modality except for directional sensitivity, in which the effect of response modality was reduced from significance, $F(2,80)=3.574$, $p=0.033$, to being non-significant.

3.2.1. Pointing and matching responses compared.

Based on the findings of the first experiment, a main effect of response modality on error was predicted. This was found to be the case for amplitude bias only, $F(1,80)=90.335$, $p<0.000$. This is shown below in Figure 3.2. and Table 3.1. presents overall mean error scores for each response modality.

Figure 3.2. The effect of response modality on response accuracy.
Table 3.1. The effect of response modality on response bias and sensitivity measures.

<table>
<thead>
<tr>
<th>Error measure</th>
<th>Open loop pointing</th>
<th>Feedback pointing</th>
<th>Perceptual matching</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude Bias</td>
<td>-51.35</td>
<td>-31.33</td>
<td>-5.96</td>
</tr>
<tr>
<td>Amplitude Sensitivity</td>
<td>34.29</td>
<td>29.22</td>
<td>23.64</td>
</tr>
<tr>
<td>Directional Bias</td>
<td>-4.06</td>
<td>-3.18</td>
<td>-2.99</td>
</tr>
<tr>
<td>Directional Sensitivity</td>
<td>18.82</td>
<td>17.20</td>
<td>15.2</td>
</tr>
</tbody>
</table>

Significant post-hoc contrasts (Bonferroni correction) were established between open loop pointing and visual feedback pointing, $p=0.011$, between visual feedback pointing and perceptual matching, $p=0.008$ and between open loop pointing and perceptual matching $p<0.000$.

3.2.2. Temporal constraints on response accuracy.

Hypothesis three concerned the existence of a two second critical retention parameter constraining pointing but not matching responses. Although there was no significant interaction between response modality and delay condition for any of the error measures, a three-way interaction resulted between response modality, delay condition and target laterality for amplitude bias only, $F(6,80)=16.084$, $p<0.000$. This relationship is shown in Figure 3.3. below.
The above graph shows how matching responses remain significantly more consistent across delay conditions and target locations than do either open loop pointing or visual feedback pointing responses. This finding suggests that a requirement of lateral movement places the individual under different constraints than a requirement of localisation of a position lateral to the midline.

3.2.3. Laterality effects on response modality

The first and fourth experimental hypotheses predicted that response accuracy would depend upon both the modality of the response and the position of the target location in the workspace. With regard to target laterality, a 2-way interaction was noted for response modality and target laterality, on amplitude bias only, F(2,80)=4.15, p=0.019 Figure 3.4. shows this interaction while table 3.2. presents the data for all error measures.
The graph shows the discrepancy in target underestimation between contra-lateral and ipsi-lateral target positions, for pointing responses only. Post-hoc Tukey tests revealed significant differences between open-loop and visual-feedback pointing for the far left \( (p=0.011) \) and far right \( (p=0.049) \) targets, between open loop pointing and perceptual matching for the far left \( (p<0.000) \) and far right \( (P<0.000) \) targets, and between visual feedback pointing and perceptual matching for the far left target \( (p<0.000) \) only. These results suggest that responses to targets placed in the contra-lateral workspace were significantly less accurate for pointing than for matching responses. Pointing responses underestimated the extent of the target distance, particularly in the absence of visual feedback information regarding hand position. Perceptual matching responses showed greater accuracy, and were not as vulnerable to the effect of varying target laterality. While the bias within the response varied as a
function of target laterality, however, sensitivity did not. As can be seen from table 3.2. above, sensitivity of the amplitude and directional components of the response remains stable whether responses are to the left or to the right.

3.2.4. Distance effects on response accuracy

Hypothesis four predicted that target distance would affect response accuracy. This was found to be the case for amplitude bias, $F(1,80)=111.615, p<0.000$, amplitude sensitivity, $F(1,80)=52.881, p<0.000$ and directional sensitivity, $F(1,180), p<0.000$. Mean error responses for each measure are shown in table 3.3. and table 3.4. (i)-(iv) below presents data responses to near and far targets, for each error measure and delay condition.

Table 3.3. The effect of target distance on error parameters.

<table>
<thead>
<tr>
<th>Target Distance</th>
<th>Error measure</th>
<th>Error measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude Bias</td>
<td>Amplitude Sens</td>
</tr>
<tr>
<td>Near</td>
<td>-14.96</td>
<td>16.942</td>
</tr>
<tr>
<td>Far</td>
<td>-47.55</td>
<td>24.288</td>
</tr>
</tbody>
</table>

Table 3.4. The effect of target distance on response accuracy.

i. Amplitude bias

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Open Loop</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>response modality and spatial location</td>
</tr>
<tr>
<td>------------</td>
<td>---------------------------------------</td>
</tr>
<tr>
<td></td>
<td>63</td>
</tr>
<tr>
<td>ii. Amplitude sensitivity</td>
<td></td>
</tr>
<tr>
<td>Delay</td>
<td>Condition</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Immediate</td>
<td>Near</td>
</tr>
<tr>
<td>1 second</td>
<td>Far</td>
</tr>
<tr>
<td>2 seconds</td>
<td>Near</td>
</tr>
<tr>
<td>4 seconds</td>
<td>Far</td>
</tr>
<tr>
<td>iii. Directional bias</td>
<td></td>
</tr>
<tr>
<td>Delay</td>
<td>Condition</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Immediate</td>
<td>Near</td>
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<tr>
<td>1 second</td>
<td>Far</td>
</tr>
<tr>
<td>2 seconds</td>
<td>Near</td>
</tr>
<tr>
<td>4 seconds</td>
<td>Far</td>
</tr>
<tr>
<td>iv. Directional sensitivity</td>
<td></td>
</tr>
<tr>
<td>Delay</td>
<td>Condition</td>
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<td></td>
<td></td>
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</tr>
</tbody>
</table>
A significant interaction was noted between response condition and target distance for amplitude bias only, F(3.80)=4.921, p=0.003. As can be seen from Figure 3.4. below, there is a large difference in magnitude of the amplitude bias in pointing responses but not matching responses, depending upon target distance.

Figure 3.4. The effect of target distance on response accuracy.
3.4. Discussion

In addition to establishing temporal parameters which dissociate visuo-perceptual from visuo-motor responses, it may be possible to show reliance of visuo-motor response processes on continuous information regarding the location of the target, such as is not required when making visuo-perceptual judgments. In particular, responses in different directions lateral to the midline may elicit modality-dependent error profiles. This was the goal of the current experiment, and consequently several predictions were made.

Open-loop pointing and visual-feedback pointing were predicted and found to result in movement direction-dependent errors, such that the magnitude of amplitude bias for pointing was significantly greater in the contra-lateral direction than for matching responses. This finding suggests two notable implications. The first is that pointing but not matching responses are constrained to make use of continuous vision of the target during execution of the response. In the third experiment reported by Elliott and Madalena (1987), a similar conclusion was reached, although pointing and matching responses were not directly compared. This finding suggests the significant inter-relationship between the features of visuo-motor processing and the elements of a visuo-motor response, such as is required in many actions. Representing a target location in relation to the self may be subject to decay after approximately two seconds in the absence of visual feedback information, but executing an accurate response guided towards the target location requires instantaneous and continuous feedback over the course of the movement.

The second area of interest is that open loop pointing showed a significantly larger tendency to underestimate the distance to the target location, for contra-lateral target positions, when compared to visual-feedback pointing responses. Following on from the previous discussion of the importance of visual feedback information in controlling movement dependent joint torques, one interpretation of this finding is that when making open-loop responses, subjects were unable to utilize proprioceptive information to compensate for the loss of visual feedback information, resulting in an undershoot of the target distance. A parallel finding of shorter movement paths, due to the early onset of braking in the absence of visual feedback information, has been
reported by Ghez et al., (1996). The underestimation of target distance in open-loop pointing for contra-lateral targets is larger than for ipsi-lateral targets, and thus it may be an inability to use visual feedback to control for greater movement forces in this direction which results in the larger degree of error for open-loop than visual-feedback pointing. Of course, this problem is not apparent for visuo-perceptual judgments and this finding again illustrates the inter-dependency between the neural elements regarding accurate perception of the scene for action, and accurate guidance of the response dependent upon that perception, which underpins pointing responses. Dissociation between visuo-spatial processing in the response modalities aside from elements which must be controlled for while executing a response, is evident from the relative consistency in matching responses to the left and right of the midline, compared to pointing responses.

Further emphasis was given to these results by the introduction of pre-response delay. The increase in error for open-loop pointing, particularly for contra-lateral targets, may be due to both proprioceptive drift and a reliance upon visual feedback of the target position. Once again, after a delay visual-feedback pointing resulted in a significant undershoot of target position with delay, particularly for contra-lateral versus ipsi-lateral targets and when compared to perceptual matching responses. This finding further emphasises differences between visuo-motor and visuo-perceptual processes in terms of temporal constraints and the continuous presence of feedback information regarding end-point localization.

Finally, the results parallel those reported in chapter two. Error increased in magnitude from perceptual matching to visual-feedback pointing to open loop pointing, with amplitudinal error consistently higher and less robust than directional error. That bias was a feature of modality-dependent differences supports the results from the first experiment, and suggests that the response consistency noted in the previous experiment was not primarily due to the repeated measures design employed. In addition, the utilization of a between-subjects design in the current experiment resulted in clear target laterality effects not found previously. Finally, juxtaposing the laterality- and delay-dependent effects on pointing with the significant improvement in pointing after a delay with the provision of reference lights illustrates how
manipulating the types of information used to guide movements influences accuracy, particularly after a pre-response delay.
4.0. The development of visuo-motor behaviour

The preceding chapters presented and considered evidence to support the hypothesis that separable information processing streams exist; one for processing visuo-motor information underlying goal-directed actions, and the other concerning visuo-perceptual, non-motor judgements such as those underlying object identification and recognition processes. Experiments with normal and clinical subjects have varied the required response modality to show how the two systems appear to be dissociable. Chapters two and three presented data which examined the parameters surrounding the accuracy of these systems when normal adult subjects execute a response, and suggested that there may be differences in the nature of the representation underlying the generation of responses in each modality, in the temporal constraints which determine the durability of information within each system, and in the information used by each modality to achieve response accuracy. The systems appear to differ in the transformations which take place and therefore in the emphasis which is placed upon incoming information. These conclusions are in agreement with the model presented by Milner and Goodale (1995) and others, as discussed in chapter one.

A two second pre-movement delay affected visuo-spatial information underlying visuo-motor mechanisms and resulted in an increase in error for the amplitude component of the response, while the directional element remained consistent as delay increased. Perceptual matching responses, in contrast, did not show an equivalent deterioration in accuracy for either extent or directional components of the response. In suggesting that the source of deterioration is some sort of representation of target location, an important distinction should be made between the durability of features comprising a representation and durability of proprioceptive information regarding accurate limb-position perception.

In both chapters two and three, depriving the visuo-motor system of visual feedback information regarding the position of the arm was found to result in an increase in amplitude bias, such that underestimation of target distance was
Response modality and spatial location

exaggerated compared to a condition where this information was provided. The importance of visual feedback information regarding limb position was thus demonstrated. However, the result also demonstrated the inaccuracy of proprioceptive information to accurately guide the movement, since this type of "intrinsically generated" biological feedback could not adequately ascertain limb position so as to control the movement trajectory and guide the arm to the target location. The findings were congruent with the effect of changing movement torques. Open loop pointing errors were thus interpreted as a reflection of loss of information regarding arm position in addition to loss of information regarding target location. This interpretation was given support from the substantial improvement in accuracy when feedback on hand position was provided.

Normal adult subjects are, in this sense, reliant upon visual feedback information to "recalibrate" proprioception. However, this is not to say that proprioceptive information is generally inaccurate to a large degree and therefore useless in controlling movement. This is far from being the case but visual perception typically dominates proprioception, especially where the two may be seen to be in conflict (Smyth & Marriott, 1988).

One method of inducing conflict, and thereby demonstrating this phenomenon, is through prism adaptation. Adults require a displacement of more than 3 degrees of visual angle before reporting any disturbance in the co-ordination of visually guided movement (Jeannerod, 1997), and this process of adaptation may even be interpreted phenomenologically as a change in the perceived position of the hand. Sight of the limb in what is actually the wrong position results in the misperception of arm position, despite accurate proprioceptive information. However, providing recalibrated proprioceptive information, for example by allowing the "adapted limb" to contact the rest of the body dissolves the adaptation effect. The effect is therefore transient and fragile but powerful under controlled conditions, i.e. when proprioceptive information cannot be updated in any other manner than through visual perception of the limb position.

Therefore, such is the supremacy of visual feedback information that without it proprioception may be subject to a degree of inaccuracy, particularly over time
"Proprioceptive drift" or inaccuracy, may be reduced by recalibrating the position of the limbs with respect to the rest of the body, which must ultimately utilise a frame of reference which calibrates body position with respect to the environment (or even gravity). Although this may be achieved by providing additional proprioceptive information to the "adapted limb," it may be argued that a function of vision is the more rapid and accurate update of this information for the purpose of action. One simple reason for this is that visual information, unlike proprioceptive information, can relate rapidly and simultaneously to both the environment and the body.

However, throughout development the relative utilisation of visual feedback and proprioceptive information for the guidance of movement undergoes a more complex and variable relationship than is apparent from adaptation studies with adult subjects. For example, developmental literature suggests that important changes in the relationship between visual feedback and proprioceptive information are evident throughout the period of infancy and childhood (e.g. Clifton, Muir, Ashmead & Lockman, 1993). At the behavioural level, such changes affect the accuracy of movements and the level of motor skill achieved. The degree to which feedback on skill level can be integrated to produce subsequent movements, i.e. feedback-based motor learning, also appears to be affected. Determining the developmental profile and cause of such difficulties therefore has educational and paediatric implications.

Examining the level of skill attainment and the nature of errors by manipulating the provision of different sources of information can give an indication of the relative use of the different types of information which may be used to guide movement.
4.1. Infancy

The development of reaching movements in infancy has been debated within theoretical considerations given to the pattern of physical development and to the important relationship between motor development and cognitive development. For example, Piaget and Inhelder (1952) argued that developing motor co-ordination permits exploration of the environment with increasing dexterity and results in examination into the relationships between and the properties of, objects and people. For example, an infant learns about object surface texture by grasping and mouthing objects, and later by banging and waving objects. The weight, size and surface features of a cube are examined in relation to the hardness and durability of another surface merely by banging the two. In performing this action the infant is learning about movement and forces, gravity, and about the limitations of their motor skills.

Bower, Broughton and Moore (1970) elicited reaching movements towards visually presented objects in infants as young as two days old. This controversial finding has not been widely replicated and such movements observed before the age of three months do not conform to the definition of a "mature" prehension movement, which typically consist of a smooth, single segment acceleration or transport phase followed by a second, corrective honing phase during which deceleration and accurate contact with the target occurs. A more mature transport phase of the reach does appear to develop at the age of approximately 16-20 weeks (Fontaine & LeBonniec 1988; Ashmead, McCarty, Lucas & Belvedere, 1993; Clifton et al 1993), but an integrated anticipatory pre-shaping of the hand has not been noted until the infant is 6 months old or more. Certainly by 13 months (Von Hofsten & Ronnqvist 1988), pre-shaping and anticipatory braking becomes evident during the transport phase of the reach, the number of corrective segments is reduced and accuracy is greatly improved.

The use of visual feedback information improves, (but is not necessary for), goal-directed reaching in young infants. Improvements in reaching may be closely related to the development of sensitivity to binocular depth cues which occurs at approximately 16 weeks of age. This information permits the infant to make an accurate judgment of, for example, the distance between themselves and the target object. Convergence errors are made by infants until the age of 16 weeks, (Slater &
Findlay, 1975), and since convergence angle may be taken as a correlate of object distance, this finding suggests that until this age infants may have difficulty using this information to make judgments about object distance. Sensitivity to retinal disparity and the ability to utilise disparity to extract information about the three dimensions of a solid object also seems to develop at around the age of 16 weeks (Yonas, Arterberry & Granrud, 1987). The development of sensitivity to both of these types of depth cue therefore seem to correlate well with the onset of visually guided reaching. Indeed, Yonas and Granrud (1987) found that infants with sensitivity for binocular disparity made more frequent and more successful reaching movements towards an object presented within reaching distance than infants who were not yet sensitive to this information.

Since infants seem to possess adequate perceptual abilities for reaching from around 12-16 weeks, the question remains as to what extent the observed pattern is a function of motoric maturity and the ability to integrate visual with proprioceptive information. The development of visual acuity and sensitivity to binocular information cannot completely account for the onset of reaching. For example, during the first year of life the infant makes considerable improvements in postural control. Importantly, it is not until approximately 24 weeks of age that sitting unaided frees the hands for prolonged exploration of the environment and objects within immediate space, (Illyngworth, 1973).

Manipulating visual information has clarified the relative use of visual and proprioceptive information in the control of posture during infancy, childhood and beyond. The “moving room” paradigm (Lishman and Lee, 1973) introduces conflict between sources of information, by upsetting optic flow. Visual information may be manipulated so as to produce an effect of self-motion as walls of the room move either toward or away from the subject. This paradigm illustrates the power of visual feedback information in the mature body, such that proprioceptive information to the contrary (i.e. that the body is stable) is not favoured. Adults typically sway and take steps even though the floor beneath them remains static. The same effect gradually appears in children. Five month olds, although able to sit unaided, do not sway when seated before a “moving room.” Changing the optic induces postural compensations in infants after the age of 7 months, (Berthental, Proffitt, Spetner & Thomas, 1985).
Not only do infants from 7 months sway to follow oscillations of the “room” around them, but they do so with increasing accuracy in terms of the degree to which their postural alignment matches the room position at a particular point in time. This increasing ability to control the relative lag or “gain” appears to be independent from the ability to match the frequency of the required movement, since it increases steadily from 7 months, unlike the measure of frequency which does not change over the age period sampled by Bertenthal et al., (1985). These findings are important in two respects. Firstly, for postural control in the sitting position, the young infant makes significant use of visual feedback information only after the age of 5 months. Secondly, although certain aspects of corrective movements, such as frequency, are mature at 7 months of age, other aspects, particularly the ability to counteract and manipulate forces in order to ensure movement accuracy, develop later. This conclusion is derived from the finding of variability in both frequency and amplitude of infants’ postural adjustments. The ability to detect and the ability to correct changes in information are thus not necessarily simultaneous or parallel.

The research relating to postural control supports the description of proficient reaching in the dark by 5 month olds, (Clifton et al., 1993). This finding once again illustrates the overarching use of proprioception to guide movements at the age of 5 months but the posture literature suggests a switch in the role of visual feedback at around 7 months. Therefore, the relationship between visual and proprioceptive information in guiding actions and movements appears to be neither set at birth to favour visual information, as appears to be the case in adulthood, nor develops following a simple, linear relationship or parallel between the two sources of information.

4.2. Childhood

In childhood a vasculatory pattern has emerged for the control of postural adjustment and action in the face of conflicting visual and proprioceptive/musculoskeletal cues. Manipulating optic flow to induce postural adjustment has been found
to increasingly induce instability from the ages of 2 to 5 years but the influence declines thereafter. Prism adaptation experiments with children in middle and later childhood exploit conflict between visual and proprioceptive cues, and illustrate how the control of pointing and reaching movements changes from little regard for visual information (i.e. a “ballistic” or “feedforward” strategy) to reliance on visual feedback information.

Hay, (1978; Hay 1979, experiment 2) asked 5,7,9 and 11 year old children to point to a single light target while wearing prisms which laterally displaced the actual position of the target by 17°. While 5 year olds corrected the movement error only towards the end of the movement, 7 year olds detected and corrected error extremely early in the movement trajectory. Nine and 11 year olds performed corrections at a mid-point through the reach. The results were interpreted as non-linear age-related differences in the degree to which visual feedback information is used to monitor and correct movement. Five year olds appeared to show the least, and 7 year olds the most, degree of control through visual feedback information.

These findings illustrate a switch in control strategy from a predominantly “ballistic” or pre-programmed strategy to one where visual feedback information is incorporated to result in “on-line” corrections. Seven year olds appeared to employ a particularly hesitant control strategy, characterised by slower movements and early braking activity.

Von Hofsten and Rosblad (1988)’s pointing task (without prisms) illustrated developmental changes in information use. Children aged 4 to 10 years made movements to visible targets with varying degrees of visual feedback and proprioceptive feedback information. Open loop pointing movements were made with: continuous vision of the target; continuous vision of the target and proprioceptive information regarding target position; proprioceptive information only, and without proprioceptive or visual information (“memory” condition). Visual and/or haptic location of the target on a table-top surface was followed by reproducing the location underneath the table with the other hand. The results showed that at 4 years of age, adding proprioceptive information to visual information actually meant that performance deteriorated, whereas the opposite case was noted in 5 year olds. This
was found for measures of both bias and sensitivity. For the later age groups, a linear trend of decreasing error was noted with age, especially where the feedback conditions provided rich sources of information. This finding suggests developmental change in the ability to integrate or “map” visual and proprioceptive information regarding a single point in space.

Hay et al., (e.g. Hay, Bard & Fleury, 1986; Hay, Bard & Fleury, 1991) described in further detail, the non-monotonic trend in the accuracy of open-loop movements. Hay, Bard and Fleury (1986) employed a manual, multi-joint aiming task where vision of the aiming limb could be either permitted or occluded. Children aged 6, 8 and 10 years were asked to hold a lever mounted on a universal joint and make an aiming movement from the initial start point close to their chest, towards targets presented at eye level in front of them. Three tasks conditions were presented and the distance and eccentricity of the targets varied depending on the purpose of the task. In the direction only task, children matched the direction (eccentricity) of the target, deliberately overshooting the distance deliberately. In the amplitude only task, midline targets of varying distances were presented and children moved the lever in to position directly beneath the target. In this condition, the lever was laterally locked so that it would only move in one plane. The third condition required the specification of directional and amplitudinal parameters simultaneously. Children matched the eccentricity of the targets as well as stopping precisely underneath the target (absolute target distance did not vary with eccentricity). Each task was carried out with and without visual feedback of arm position.

The results for the open loop movement conditions revealed that little improvement in directional accuracy was evident across the three age groups, suggesting maturity in “programming” the directional element at an early age. This finding remained for both the direction only task, and the task involving direction and amplitude components. However, analysis for the amplitude only task revealed a non-monotonic trend with regard to movement accuracy and movement evaluation, specifically for the 8 year old group of children. For the task involving amplitude only, 8 year olds showed higher absolute error than either younger or older children by braking early and under-shooting the target position. The early braking phenomenon was also apparent in a kinematic analysis of the responses, whereby 8
year olds showed lower peak velocities, flatter movement profiles in terms of peak acceleration and deceleration, and typically reached peak velocity and peak deceleration sooner than either younger or older children. These findings were interpreted as evidence of an overly cautious, conservative control strategy used by 8 year olds when visual feedback information was not available to guide movement.

Hay et al interpreted these findings as indicative of independence between two motor systems, one concerned with effecting the desired movement through pre-movement programming and one concerned with the evaluation of that movement. However, that reaction times (RT) did not parallel the non-monotonic trend suggested that 8 year old children were not merely attempting to utilise a programming system, since RT has been traditionally thought of as a measure of pre-programming (Georgopoulos, 1988, Hay et al., 1986). RT for the directional only task was found to be larger than for the amplitude only task but since this finding occurred for all children, it may be argued that the 8 year olds were not attempting to utilise a pre-programming strategy for any particular component of the response, and so it is unlikely that such a factor can explain the appearance of the non-monotonic trend.

The “Hay” effect has since been examined in a number of other experiments which have utilised various paradigms to investigate the conditions under which the phenomenon occurs, and its precise features therein. For example, Pellizzer and Hauert (1996, experiment 1) employed a single-joint (flexion/extension) open loop task whereby children aged 6 to 10 years moved a lever with their wrist from a central point (depicted by a single light point) to reproduce the target eccentricity in either the left or right visual field. Errors typically over-estimated the target position but bias was particularly high in 8 year old children for targets in the right visual field, and for movements made with the non-dominant (left) hand.

Fayt, Minet and Schepens, (1993), allowed unconstrained pointing movements to examine whether children aged between 6 and 11 years could utilise feedback given at the end of the movement and incorporate this information into subsequent responses. In this sense, any improvement in accuracy could be taken as a crude measure of visuo-motor learning. Subjects made free pointing movements to targets presented at varying eccentricities in the right hemi-field, with their right (dominant)
The pre-test and post-test trials were open loop, with treatment trials including error feedback once the movement had been made.

Errors tended towards undershooting the target. For 8 year olds, directional, not amplitudinal error was significantly large. This was characterised by curved movement paths when making open loop pointing movements, although the curvature was reduced dramatically when visual feedback was permitted. Learning occurred for all subjects, but was notably slower for the 8 year old group than for other groups. These results may be interpreted as suggesting that 8 year olds have problems correcting the curvature of their movement path when under conditions of proprioceptive guidance with the difficulty manifested in increased directional error compared to older and younger children. This finding is of significance in conjunction with the movement-direction dependent errors found in the open-loop pointing condition reported in chapter three.

While the previous experiments required discrete movements towards target locations and cross-sectional experimental designs, Rosblad (1996) employed a repetitive, multi-joint paradigm to investigate non-monotonic trends in the adequacy of open loop movements. This longitudinal study followed children from 6 to 8 years of age. The task was to transfer beads to and fro between two shallow discs, varying full feedback of target and limb position; vision of the target position only, and no vision of either the target or of the limb. Mean trajectory length of movement under the no vision conditions showed a dramatic decrease at 7 years of age. This pattern had increased to levels above 6 year old scores when the children reached 8 years of age. In contrast, performance in the partial- and full-vision conditions showed linear increases in movement efficiency with increasing age. These results show close parallels to those of Hay et al.

Finally, it is important to note that the non-monotonic trend is not only limited to open loop movements, but is limited to movements and not to perceptual judgements. Pellizzer and Hanert, (1996, experiment 2) used a perceptual localisation task and did not find any age-related differences. Eight year old children performed as well as their younger and older counterparts. When reaction times were examined in a task which did not require the transformation of perceptual information into a motor
response, once again the performance of the 8 year old children was unremarkable. RT decreased linearly with age. These experiments suggest that a particular difficulty is encountered at the age of approximately 8 years, which is specific to some element of the transformation process between incoming perceptual information and the generation of a goal-directed action response. The deficit does not appear to lie within the visuo-perceptual system.

4.3. Introduction to experiment

Integrating the findings of previous developmental literature regarding visuo-motor and visuo-perceptual accuracy, with the neurological and experimental evidence presented in chapters one to three, suggests several points which relate to the existence of a specific visuo-motor difficulty in the middle period of childhood. Firstly, the otherwise mature control of directional components of a movement appears to be disrupted at around the age of 7 to 8 years. The curved movement path resulting in directional bias under open loop conditions reported by Fayt, Minet and Schepens (1993) parallels extremely closely, the movement-direction dependent errors noted in both clinical patients who manifest deficient proprioception and in normal subjects, such as was found in chapter three. Secondly, the noted increase in amplitude underestimation by children of this age, a prominent feature of the results reported by Hay et al., Rosblad (1998) and others, may be indicative of an inability to utilise proprioceptive information in the absence of visual feedback regarding hand position. Visual feedback information increases the accuracy of the final portion of the reach in all individuals but it may be that 7-8 year old children are at a particular disadvantage when making open-loop movements, since at this age visual information is required to guide movement trajectory throughout the entire movement.

Thirdly, differences in movement control may be apparent in relation to temporal parameters on visuo-motor accuracy. This may be examined in much the same vein as described in chapters two and three. The explicit manipulation of pre-response delay has not been an evident part of experimental work with children to date (Graham, Bradshaw & Davis, 1998). Therefore, the final experiment utilises the methodology reported in the previous chapters and seeks to examine questions which
relate to the development of visuo-motor parameters, and in particular to determine the effect of temporal delay in pointing accuracy using children aged 5 to 10 years.

Children may parallel adults in their responses to locations made after a delay, or alternatively may exhibit quantitative and qualitative differences in response accuracy in terms of the bias and/or sensitivity of movements. Additionally, any developmental discrepancy may be particularly pronounced when comparing the open loop and feedback pointing conditions, and 7-8 year old children may encounter particular difficulties with open loop movements relative to older and younger subjects. Finally, with delay, it may be that for all ages, open-loop pointing movements are less accurate due to proprioceptive error.

Therefore, the following predictions may be made:

1. Open loop pointing accuracy may be less accurate than feedback pointing accuracy. The difference in performance may be particularly apparent at 8 years.
2. With increasing delay, pointing performance may deteriorate. A critical temporal parameter of 2 seconds may be derived, after which performance deteriorates significantly.
3. If a specific visuo-motor representational difficulty is apparent at 8 years, as has been suggested, then movement accuracy may differ from that shown by older and younger children.

4.2. Method

4.2.1. Design

The experiment was a 3 (age group) x 4 (zero/immediate, one, two and four second pre-movement delay) x 2 (open-loop pointing, visual feedback pointing) mixed design. Each subject completed three trials per target position for each delay and feedback combination, giving a total of 96 trials.
4.2.2 Subjects

Five boys and 14 girls were allocated to age-appropriate groups as follow: 5;8-6;9 years (n=7, mean 6;5 years), 7;8-8;6 (n=7, mean 8;2 years) and 9;3-10;0 years (n=5, mean 9;8 years). All had normal or corrected-to-normal vision.

4.2.3 Apparatus

The experimental set-up was similar to that used for the experiment with adult subjects as outlined in chapters two and three, except that children did not complete either the reference light conditions as described in chapter two or the perceptual matching task described in chapters two and three. Pilot testing revealed difficulties with the children's attention span which led to unsatisfactory task completion for these tasks and so the conditions were eliminated and the total number of trials were reduced.

Children sat comfortably before a featureless table-top. Head movements were restrained by a chin rest. Their preferred hand was position in the midline directly below the head position. A computer checked, via a pressure-sensitive switch, that the subjects did not initiate a response before the given signal. Two midline and two lateral (40°) targets of 10mm diameter were positioned at 16cm and 32cm from the start switch. The lateral targets were matched for handedness, placed on the same side as the child's preferred hand. Targets were laser-projected for one second and their presentation and the pre-movement interval were controlled by a Macintosh Power PC. The signal response was an audible beep. Children marked pointing responses using a pencil. A luminous pencil-tip was used to provide feedback on hand position during the relevant trials.

4.2.4. Procedure

The experiment was conducted in complete darkness. The pointing movement was demonstrated to the child and the child practiced the procedure to non-target locations until confident. Children were instructed to point quickly but to be careful to maintain
accuracy. The child’s proficiency to comply with these instructions was checked by the experimenter during this practice session. The order of target presentation and delay/pen condition were fully randomised, under computer control, throughout the session. After each block of 12 trials, the child was moved away from the test area and the room and target lights were switched on. The experimenter colour-coded responses for different conditions. Children completed the experiment in two sessions separated by a 15 minute rest period. No explicit feedback on error or target position was given during testing.

4.3. Results

The aims of this experiment were three-fold. They were (i) to determine any age-related differences in pointing accuracy, (ii) to examine the effects of pre-movement delay on children, and (iii) to determine any age-related interactions between open loop and feedback pointing, with particular emphasis on comparing the performance of the middle age group with that of older and younger children.

ANOVA analysis were conducted with target positions collapsed to near and far target distances. Responses to the four target positions were not separated due to the small number of responses to each target in each condition (3 trials).

4.3.1. Age group

No main effects were found for pointing responses across the three age groups of children. The following table 4.1. (i)-(iv) shows the mean error values for each age group, for the delay and response modality conditions. Table 4.2. shows total mean error values for each age group.

Table 4.1.
i. Amplitude bias
### Response modality and spatial location

#### ii. Amplitude Sensitivity

<table>
<thead>
<tr>
<th>Delay condition</th>
<th>Age group</th>
<th>5-6 years</th>
<th>7-8 years</th>
<th>9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td></td>
<td>-21.00</td>
<td>-11.51</td>
<td>-15.88</td>
</tr>
<tr>
<td>1 second</td>
<td></td>
<td>-27.59</td>
<td>-22.05</td>
<td>-19.00</td>
</tr>
<tr>
<td>2 seconds</td>
<td></td>
<td>-21.43</td>
<td>-23.85</td>
<td>-22.78</td>
</tr>
<tr>
<td>4 seconds</td>
<td></td>
<td>-26.21</td>
<td>-30.71</td>
<td>-22.00</td>
</tr>
</tbody>
</table>

#### iii. Directional Bias

<table>
<thead>
<tr>
<th>Delay condition</th>
<th>Age group</th>
<th>5-6 years</th>
<th>7-8 years</th>
<th>9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td></td>
<td>-3.26</td>
<td>-5.05</td>
<td>2.06</td>
</tr>
<tr>
<td>1 second</td>
<td></td>
<td>-4.75</td>
<td>-4.96</td>
<td>-2.55</td>
</tr>
<tr>
<td>2 seconds</td>
<td></td>
<td>-3.87</td>
<td>-9.26</td>
<td>1.37</td>
</tr>
<tr>
<td>4 seconds</td>
<td></td>
<td>-4.06</td>
<td>-11.28</td>
<td>-3.81</td>
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</table>

<table>
<thead>
<tr>
<th>Response condition</th>
<th>Age group</th>
<th>5-6 years</th>
<th>7-8 years</th>
<th>9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Loop</td>
<td></td>
<td>-5.62</td>
<td>-10.40</td>
<td>-1.72</td>
</tr>
<tr>
<td>Lit Pen</td>
<td></td>
<td>-2.35</td>
<td>-4.88</td>
<td>0.26</td>
</tr>
</tbody>
</table>
iv. Directional Sensitivity

<table>
<thead>
<tr>
<th>Delay condition</th>
<th>Age group 5-6 years</th>
<th>Age group 7-8 years</th>
<th>Age group 9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td>8.80</td>
<td>9.41</td>
<td>11.08</td>
</tr>
<tr>
<td>1 second</td>
<td>10.11</td>
<td>9.69</td>
<td>9.39</td>
</tr>
<tr>
<td>2 seconds</td>
<td>13.87</td>
<td>12.21</td>
<td>12.37</td>
</tr>
<tr>
<td>4 seconds</td>
<td>13.68</td>
<td>16.26</td>
<td>13.65</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Response condition</th>
<th>Age group 5-6 years</th>
<th>Age group 7-8 years</th>
<th>Age group 9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Loop</td>
<td>12.72</td>
<td>11.45</td>
<td>11.08</td>
</tr>
<tr>
<td>Lit Pen</td>
<td>10.51</td>
<td>9.41</td>
<td>9.39</td>
</tr>
</tbody>
</table>

Table 4.2. Total mean values for each error measure

<table>
<thead>
<tr>
<th>Response condition</th>
<th>Age group 5-6 years</th>
<th>Age group 7-8 years</th>
<th>Age group 9-10 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude Bias</td>
<td>-24.06</td>
<td>-22.02</td>
<td>-19.92</td>
</tr>
<tr>
<td>Amplitude Sens</td>
<td>15.82</td>
<td>14.85</td>
<td>15.75</td>
</tr>
<tr>
<td>Directional Bias</td>
<td>-3.99</td>
<td>-7.64</td>
<td>-0.73</td>
</tr>
<tr>
<td>Directional Sens</td>
<td>11.62</td>
<td>11.89</td>
<td>11.62</td>
</tr>
</tbody>
</table>

The tables above show how for three of the four measures, children simply demonstrated increasing proficiency in pointing with age. However, the experimental hypotheses predicted an interaction between age group and response accuracy. This
was apparent for directional sensitivity, for far target positions only, $F(2,48)=6.78$, $p=0.007$, and is shown below in Figure 4.4.

Figure 4.4. Non-monotonic trend in movement accuracy

As can be seen from the above graph, target distance appears to affect the spread of directional responses in the middle age group but not for those in the younger and older age groups. Similarly, Figure 4.5 Below shows how open loop pointing appears to be less accurate in 7-8 year olds, for directional bias.

Figure 4.5.
Seven- and eight-year olds seem to make movements to the left of the target when denied visual feedback regarding hand position. Five- and six-year olds tend to point slightly to the left, while 9 and 10 year olds move slightly to the right. A linear developmental trend would have predicted directional bias values between the youngest and oldest groups' values, for the middle age group. However, the non-monotonic trend just failed to reach significance (p=0.055).

4.3.2. Delay

There were no interactions between age group and delay condition. Premovement delay was found to affect amplitude bias, \( F(3,48)=3.708, \ p=0.018 \), amplitude sensitivity, \( F(3,48)=7.256, \ p<0.000 \) and directional sensitivity, \( F(3,48)=10.004, \ p<0.000 \). Post-hoc Tukey contrasts of group mean contrasts for amplitude bias showed significant differences between the immediate and one second delay conditions, \( p=0.010 \), between the immediate and two second delay conditions, \( p=0.028 \) and between the immediate and four second conditions, \( p=0.021 \). Contrasts for amplitude sensitivity showed differences between the immediate and two second delay conditions, \( p=0.041 \) and between the immediate and four second delay conditions \( p=0.003 \). For directional sensitivity, contrasts showed significant differences between the immediate and two second delay conditions, \( p=0.029 \) and between the immediate and four second conditions, \( p=0.001 \). These effects are shown below in Figure 4.6 (i), (ii) and (iii).

Figure 4.6 (i)
Figure 4.6. (ii)

4.3.3. Immediate Response Condition

The immediate response condition was the closest parallel to previous experimental tasks in which a non-linear trend has been reported for control of open loop movements. As can be seen from the graph below, however, responses across age groups are comparatively similar.

Figure 4.6. (iii)

Figure 4.7 (i) Amplitude bias in the immediate response condition
Figure 4.8. (ii) Amplitude sensitivity in the immediate response condition
4.3.4. Response condition.
Response condition significantly affected amplitude bias only, $F(1,48)=6.66$, $p=0.020$. The difference between open loop and feedback-loop pointing are evident in the graph below.

Figure 4.10. The effect of response modality on amplitude bias

![Graph showing mean amplitude bias for open loop and lit pen response modes.]

4.3.5. Target position

Target distance affected amplitude bias, $F(1,48)=38.39$, $p<0.000$, amplitude sensitivity, $F(1,48)=38.39$, $p<0.000$ and directional sensitivity, $F(1,48)=29.29$, $p<0.000$. In addition, there was a significant two-way interaction between target distance and delay condition for amplitude bias, $F(93,48)=6.31$, $p=0.001$. The mean values for near and far targets in each error measure are shown in table 4.3. below. The interaction between delay and target distance is shown in Figure 4.11. below.

Table 4.3

<table>
<thead>
<tr>
<th>Target Distance</th>
<th>Error measure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Amplitude bias</td>
</tr>
<tr>
<td>Near</td>
<td>-9.728</td>
</tr>
<tr>
<td>Far</td>
<td>-34.27</td>
</tr>
</tbody>
</table>

Figure 4.11. The interaction of delay and target distance on amplitude bias
4.12. The effect of target distance on directional sensitivity

From both Figure 4.11. and 4.12. above, it can be seen that with delay, pointing responses to far but not to near targets, deteriorate. The magnitude of distance underestimation, and the spread of the directional component of the response, are poorer at all times for the far target positions. Adding a pre-response delay further contributes to the magnitude of distance underestimation. This result is shows a parallel with the increase in error also shown by adults, when pointing to far target positions.

4.4. Discussion
The experiment sought to investigate the relationship between visuo-motor response accuracy and feedback information in the presence of pre-movement delays, in children aged 5 to 10 years. The results firstly suggest that the 7-8 year old age group show a different profile of errors in their pointing responses, compared to older and younger children. However, unlike the previous findings of Hay et al. and others, non-monotonic trends emerged in the directional and not amplitudinal elements of the response.

The 7-8 year old group showed a larger degree of lateral dispersion in their responses than did older or younger children, particularly when pointing to far target positions. Not only did they demonstrate a loss of sensitivity, however, but bias was also affected. A systematic tendency to point to the left of the target position was noted for this age group in the open-loop pointing condition only. Older and younger children also demonstrated errors but these were smaller in magnitude than those made by the 7-8 year olds.

The present findings suggest that 7-8 year olds did indeed have difficulty controlling movement end-point accuracy, particularly with regard to the direction of the response. This was found both for the sensitivity and bias measures, and relates closely to the findings reported by Fayt, Minet and Schepens, (1993) and by Ghez (1995). An inability to control for movement direction-dependent joint interaction and inertial forces in the absence of visual information typically results in a curvature of the movement trajectory and subsequent end-point error. Although kinematic analysis of movement trajectories was not available in the current experiment, the end-point errors made by 7-8 year old children suggest difficulty with precisely these factors. In this sense, the non-monotonic trend as reported by Hay et al is less likely to be due to a switch in information dominance from proprioceptive to visual information, or due to a deficit in one or other “motor” system for making and evaluating a movement. It is perhaps more likely that visual dominance is required since proprioceptive information cannot provide for accurate “on-line” control of joint forces encountered during movements. Further investigation of the performance of this age group with respect to open-loop movements in specific directions and under conditions of high and low inertial load on the moving limb may serve to test this interpretation.
The experiment was also concerned with establishing the temporal parameters of pointing accuracy in children following the introduction of pre-movement delays. It was found that after a one, two, or four second delay following target extinction children showed a rapid and marked deterioration in pointing accuracy. In fact, accuracy declined significantly after a delay of only one second. This finding is qualitatively similar to those found with adult subjects when data from the pointing conditions only was considered, but children seem to be susceptible to a shorter pre-movement delay.

The nature of any deterioration in performance in terms of the effect of delay on the underlying representation/control structures was also investigated. The dissociation of delay effects on bias (one second) and precision (two seconds) of the amplitude component suggests that pointing performance is consistent with a systematic distortion of space/hand position, and then, with the influence of “noise.” That is, the underlying representation or control structure seems to distort systematically before degrading to the degree that only increasingly imprecise (noisy) movements can be supported.

Thirdly, to distinguish the nature of this deterioration further (in terms of change in the perception of spatial position or hand position), visual-feedback was manipulated. Pointing responses were made either with or without, visual feedback in an effort to assess whether feedback affected children of different ages in different ways. The fact that there was no interaction of feedback with delay overall suggests that children of all ages were affected by the manipulation of delay and by feedback on hand position. Feedback reduced the size of the bias in the amplitude component by a constant amount for each delay, which suggests that its absence leads to a constant error. This is consistent with may previous findings of both developmental and adult studies (e.g. Carlton, 1981; Rosblad, 1996). The increase in error with delay, therefore, may be attributable to the distortion of the representation of near space which is relatively independent of proprioceptive information. This distortion was approximately proportional to distance showing a nonlinear compression of space akin to that noted in many perceptual experiments (Johnston, 1991). However, visual feedback did reduce the bias significantly so, although the primary distortion of space
may be "visuo-perceptual," visual feedback must still place an important role in the reproduction of reaching movements to specific near-space distances.

The effect of delay on the amplitude and direction components of the reaching movement was significantly different. Whereas amplitude error increased significantly following even a one second delay, directional bias was not affected by any of the delay period employed. This finding suggests that a dissociation between the coding/performance of amplitude and direction exists in the visuo-motor system, and that these components are differentially sensitive to the effect of temporal delay. These findings are also in line with results presented in chapter two and three and again suggests that in a qualitative sense, the performance of children of age five years and above does not differ from that of adults in this respect.

Visual feedback reduced the magnitude of the bias in the amplitude of the movements created by the introduction of a pre-movement delay. In contrast, the bias of the directional component did not change, even after a delay of four seconds, and benefited little from the presence of feedback. This may reflect different control strategies in regard to the two components. Direction may be relatively ballistic or set and adjusted at the outset of the reach whereas amplitude may be monitored and adjusted throughout the trajectory. Again, these results is comparable with that found with adult subjects presented in chapters two and three. However, the portions of the reach were not analysed as measures examined spatial error and did not take kinematic factors into account.

Visual feedback has been shown to influence the accuracy of the directional parameter (Ghez, 1995) although Bard et al., (1985) report that it may be incorporated very early in the reach trajectory to correct directional error. The effect of feedback on directional error may have been underestimated in the present experiment because the initial hand start position was always in the midline, situated directly below the chin (and so aligned with line of sight). However, if the centrality or otherwise of hand position was an important factor then the directional error should be greater for the lateral targets when compared to the midline targets. No significant difference, however, was found for this analysis.
In summary, the results suggest that the accuracy of pointing responses made by children are affected by a pre-movement delay of one second. Progressively increasing the duration of the delay affects the bias of the amplitude component and the precision of both amplitude and direction components. This initial deterioration may be the result of systematic distortion of spatial representation such as that discussed previously. Seven and eight year old children tended to experience particular difficulty with open-loop visuo-motor responses although delay affected children equally.
5.0. Summary of results

Three experiments were conducted to investigate the nature of temporal constraints on judgments of spatial location in normal human subjects. Previous anatomical, physiological and clinical evidence has suggested the existence of two parallel processing pathways for effecting visuo-motor and visuo-perceptual judgments of spatial location. These pathways have been postulated to differ functionally with regard to the manner in which the same information is processed. In particular, the visuo-motor processing pathway has been thought to be subject to temporal constraint in terms of the duration for which information is available to guide action. Furthermore, this information may be processed in co-ordinates which emphasise the position of the self with respect to the environment. The visuo-perceptual processing pathway, however, has been thought to retain information for longer periods and to utilise spatial information which is not dependent upon the position of the self in relation to the environment. Therefore, hypotheses were made as to the features of responses made during visuo-motor pointing tasks compared to those made during visuo-perceptual matching tasks.

The nature of visuo-motor and visuo-perceptual processing was examined using four delay conditions, the manipulation of visual feedback information regarding movement position and the position of the target location in the workspace. Experiment one revealed that following a two second delay, amplitude bias increases in pointing but not matching responses. A loss in sensitivity of responses is also noted as delay increases, but occurred for pointing and matching. These results suggest that:

* pointing is indeed constrained in a manner dissociable from matching,
* with delay a consistent distortion is apparent prior to a general deterioration (perhaps due to "noise" or other non-specific factors) in responses,
* the extent, rather than direction, portion of the response is particularly vulnerable to delay.
Therefore, it appears that although common processes in spatial location tasks exist, as was established by the main effect of delay on the bias and sensitivity of all responses, the temporal constraint placed upon this same information differs according to whether the response is a goal-oriented action or a visuo-perceptual judgment only.

Furthermore, the addition of reference lights to an otherwise darkened workspace affected pointing and matching responses in decidedly different ways. Particularly, reference lights reduced amplitude bias in pointing error after a delay of more than two seconds. This finding was interpreted as demonstrating how the visuo-motor response can be manipulated to appear more like a visuo-perceptual response, even after the two-second retention interval has been exceeded. Responses were improved in amplitude, to resemble more closely those elicited in matching conditions, and were more accurate in after a four second than a two second delay period, to a magnitude close to visuo-perceptual error for the equivalent condition.

Experiment two supported the findings of experiment one with respect to response modality, and further investigated the information utilised by visuo-motor processes in executing a response. Target laterality was found to significantly effect pointing but not matching accuracy, suggesting that the direction of movement and not necessarily direction of spatial location of the target, affects response accuracy. Pointing to contra-lateral target positions resulted in significantly greater underestimation of target extent than did matching responses to those same positions. Moreover, this result was not due to a loss of information regarding hand position during pointing. When visual feedback information regarding finger-tip position was provided, responses to contra-lateral targets were still poorer than to ipsi-lateral targets, and also than for matching responses. This result was further magnified by the presence of pre-response delay. The results were interpreted with respect the requirements placed upon visuo-motor processes in effecting an accurate response which overcomes and controls for, direction-dependent joint torques. Without visual feedback of either finger-tip position or target position, error is substantial when movements require overcoming large inertial forces. When only target position is occluded, the effect remains. This finding suggests that continuous visual information regarding the target position facilitates calculation of kinematic movement parameters so as to account for
changes in movement-dependent torques. With delay, deterioration in visuo-motor representation of the target position exacerbates difficulties in movement accuracy. In this sense, the experiment was effective in differentiating between aspects of spatial processing specific to visuo-motor and visuo-perceptual pathways, and between information required by the visuo-motor system for spatial representation versus accurate movement control.

The third experiment examined developmental issues relating to visuo-motor processing parameters and motor control capabilities. It was found that children aged 6 to 10 years demonstrated a qualitatively similar pattern of movement errors to adults, although the amplitude of the response was disrupted after a delay of just one second. In addition, children exhibited an early loss in sensitivity. However, the relatively “robust” directional component of the response was demonstrated in children as with adults, as compared to amplitudinal parameters. This result suggests that in children, as with adults, amplitude and direction elements of movements can be differentiated in terms of processing constraints. The exception to the results regarding directional error was with respect to issues of accurate movement control, and thus was comparable to the movement-direction dependent results noted in adults in the second experiment. Seven and eight year old children seemed to exhibit a reduction in the ability to control movement forces during pointing in the absence of visual feedback. The result augments those previously reported by Hay and others, (e.g. Hay, Bard & Fleury, 1994) but suggests that the difficulty may lie within aspects of movement control and not with visuo-motor processing per se. This conclusion is further supported by the otherwise linear improvement in pointing accuracy shown by 6- to-10 year olds when visual feedback information regarding finger-tip position is provided, and by the consistent effects of pre-response delay on all children.

5.1. Conclusion

The results of the experiments support the model presented by Milner and Goodale (1995) and others, (e.g. Jeannerod, 1997), as discussed in chapter one. It
appears that information processing pathways utilise incoming visual information regarding spatial position in different ways according to the functional output which is required. Whereas the visuo-motor response is constrained to a period of approximately two seconds prior to the onset of systematic distortion of spatial representation, the visuo-perceptual response remains more stable and, in most cases, much more accurate. The visuo-motor system thus also seems to require continuous vision of the target location, although the results of the experiments suggest that this feature of the visuo-motor response may be complicated by kinetic requirements for accurate motor control independent of a representation of location for the purpose of action. Finally, the effect of kinetic and motoric factors has been demonstrated to change the accuracy of visuo-motor responses during middle childhood in a nonlinear fashion.

Further experiments should examine the kinematic features of responses made after a delay is imposed. The experiments reported here did not measure these aspects of responses. In addition, movement direction analysis coupled with kinematic analysis may help to elucidate further, the response-modality differences in accuracy which are apparent in the data presented here. Developmental research could continue in a similar fashion and examine the role of changing kinetic load in conjunction with pre-response delay, in order to describe changes in reaching patterns across middle childhood and changes in the way in which visual information contributes to movement accuracy.
References


**Appendix A**

In experiment one, data on amplitude error were converted to reflect a percentage of target distance. Coding was restricted to amplitude bias as converting measures of sensitivity and directional error as a percentage of target distance would have altered the data in an artificial and non-meaningful way leading to interpretation difficulties (e.g. mean amplitude sensitivity as a percentage of target distance would reduce the magnitude of the measure from near to far target locations, even though the spread or absolute magnitude of responses increased with target distance). Subsequent MANOVA analyses were conducted to establish whether error was a constant proportion of the target distance, or varied as a function of distance in a non-linear manner. Data regarding target distance were collapsed into near and far target positions and the results showed that there was no significant difference between near and far target positions (p>0.05). Therefore, it seems that amplitude bias error increases in a linear fashion, with increasing target distance. There was no interaction between pointing and matching conditions for target distance either, which suggests that these response modalities do not differ in the manner in which error increases with increasing distance. Tables A.(i) and (ii) below provide descriptive information
with respect to each combination of conditions, for mean amplitude bias expressed as a percentage of target distance. Standard deviations are given in parentheses.

A. (i) No reference lights

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
</tr>
<tr>
<td>Immediate</td>
<td>-5.67 (4.40)</td>
<td>-5.55 (4.59)</td>
<td>-2.39 (1.34)</td>
<td>-2.88 (2.62)</td>
</tr>
<tr>
<td>1 second</td>
<td>-5.28 (9.84)</td>
<td>-8.09 (8.58)</td>
<td>-5.97 (1.47)</td>
<td>-6.12 (2.11)</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-10.08 (5.43)</td>
<td>-10.72 (7.93)</td>
<td>-0.65 (5.49)</td>
<td>-1.71 (3.76)</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-12.46 (5.66)</td>
<td>-13.11 (6.22)</td>
<td>-5.27 (4.52)</td>
<td>-8.79 (4.52)</td>
</tr>
</tbody>
</table>

(ii) Reference lights

<table>
<thead>
<tr>
<th>Delay Condition</th>
<th>Response Mode</th>
<th>Open Loop</th>
<th>Feedback P</th>
<th>Matching</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Near</td>
<td>Far</td>
<td>Near</td>
<td>Far</td>
</tr>
<tr>
<td>Immediate</td>
<td>-5.35 (0.92)</td>
<td>-3.155 (1.899)</td>
<td>-2.27 (6.57)</td>
<td>-2.11 (4.16)</td>
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<td>1 second</td>
<td>-5.45 (4.97)</td>
<td>-4.22 (6.08)</td>
<td>-1.46 (1.59)</td>
<td>-2.04 (2.10)</td>
</tr>
<tr>
<td>2 seconds</td>
<td>-1.55 (7.15)</td>
<td>-3.26 (5.75)</td>
<td>-4.17 (3.46)</td>
<td>-3.49 (2.99)</td>
</tr>
<tr>
<td>4 seconds</td>
<td>-4.36 (6.33)</td>
<td>-5.10 (6.58)</td>
<td>3.48 (3.59)</td>
<td>0.58 (1.59)</td>
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