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Manual and Oculomotor Control during Tracking and Interception Tasks: Normal Characteristics and Deficits due to Cerebellar Dysfunction

by

Paul van Donkelaar

A DISSERTATION SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF NEUROSCIENCE

CALGARY, ALBERTA JANUARY, 1994

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Abstract

The contributions of visual motion processing, as well as retinal and extraretinal signals were investigated in three experiments in which natural, multijoint tracking and interception movements produced with the hand were directed towards moving targets. The latency of these responses to the onset of target motion was dependent on the velocity of the target. A simple model which assumes that latency is composed of a target velocity dependent threshold time and a subsequent processing time accurately accounted for the data. In addition, the initial trajectory of the hand was independent of target velocity when this variable was unpredictable from trial to trial. These characteristics are analogous to those observed for eye movements produced under similar conditions.

Removing vision of the hand caused increases in positional error but did not influence target velocity matching performance in the tracking task. In contrast, in the interception task this manipulation led to significant increases in the variability of endpoint error. Restricting eye motion caused subjects to overestimate target velocity. In particular, hand gain (hand velocity/target velocity) was substantially increased in the tracking task during visual fixation. Similarly, in the interception task subjects pointed further ahead of the target when eye movements were not allowed. Taken together, these results suggest that retinal information associated with vision of the hand contributes to those aspects of hand movement related to the position of the target, whereas extraretinal information concerning eye motion contributes to target velocity related aspects.

The interaction between signals associated with eye and hand motion was investigated by having subjects with cerebellar dysfunction perform the tracking and interception tasks under these conditions. The normal deficits that are observed in the eye and hand movements of such subjects were exacerbated during the combined motions of these effectors. In particular, hand movements were more smoothly coordinated if the aberrant eye movements were restricted and vice versa. The fact that this interaction is a negative one when eye and hand movements are disrupted suggests that the converse may be the case under normal circumstances. Specifically, information associated with oculomotor and manual motor output may contribute to the high degree accuracy observed in the opposing system. The potential sites within the central nervous system where these interactions may occur are discussed.

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CHAPTER ONE: INTRODUCTION

Reaching for objects is one of the more common movements humans make during everyday life. Information arising from a variety of sources enables us to accurately bring our hand into close proximity to the object to allow grasping and manipulation.. Normally, the visual input related to the spatial attributes of the object and hand both before and during the reach provide the most salient cues required to successfully complete the movement. This visual information is further influenced by any changes in the position or motion of the eyes. Thus, accurate reaching responses require precise eye-hand or visuo-oculo-motor coordination.

The ability of the central nervous system (CNS) to maintain such coordination is further stressed when reaching or pointing movements are made in response to an object that is moving. Under these conditions, information related to the initial position of the object as well as to its subsequent direction and velocity of motion must be taken into account when attempting to generate an appropriate movement with the arm. Because of delays in the system, however, the position of the object at the point in time at which the decision is made to move the arm will not be the same as at the end of the response. Thus, the element of *prediction* becomes very important under these circumstances. This ability to predict relies on information arising from visual and eye motion signals associated with the spatial characteristics of the object's trajectory, as in the simpler static situation described above.

There are at least two ways to direct the hand to a moving target. First, one can attempt to point at or follow the target's movement in a continuous manner. This *tracking* response consists of an initial transient period in which the hand must catch up to the target due to delays associated with the onset of the response. This is followed by a steady-state period during which the hand will normally match both target position and velocity. These tracking responses are analogous in a general sense to tasks such as driving a car or flying a plane. In particular, information about the movement of the target (road, flight path) derived from visual and eye motion signals (among others) is used to produce an appropriate response with the limbs (e.g., steering around a corner). In fact, many of the early studies on tracking were directed towards improving the abilities of pilots flying planes in combat situations.

A second way to interact with a moving target is by reaching forward to intercept it. As with tracking responses, there are examples of interception responses in the real world. The most obvious of these are from sporting situations - for instance, receiving a pass/throw in basketball, football, baseball, or hockey. Interception responses can also occur quite frequently, however, in the home. For example, to stop milk that has just been spilled from spreading over the counter, one has to intercept the trajectory of its advance with a paper towel. Analogous processes are at work when grasping a wine glass that has rolled off a tabletop and is about to hit the floor. In a more general sense gait can be considered to consist of a series of interceptive movements in which the targets for foot placement are moving with respect to the performer. Normally this task does not demand much effort until one attempts to run over rough terrain. Under these conditions it becomes very important to accurately position the foot so that it lands at a location that will provide stability for the purposes of maintaining balance. In each of these cases, as in tracking responses, the characteristics of the target motion, including its direction and velocity, influence the response with the limb. Unlike tracking tasks, however, there is no analogous steady-state portion in an interception movement. Specifically, there does not appear to be a period in which target position

and velocity are matched. Indeed, whereas this matching is an absolute requirement for tracking to be considered error-free, accurate interception responses can be produced using a variety of different strategies. For example, for a target moving at a particular speed, one can initially aim well ahead of it and move slowly, or aim only a short distance ahead but move more rapidly. The mechanisms underlying natural, multijoint tracking and interception movements were investigated in the experiments described in this dissertation. In what follows the relevant evidence from previous studies is reviewed to provide a background for the present studies.

1.1. Limb Movements to Stationary Targets

Perhaps more than moving targets, static or stationary targets are very prevalent in everyday life. We use our hands to grasp many items of interest within peripersonal space throughout the course of the day. Thus, there have been many studies completed over the years in an attempt to understand the mechanisms by which such movements are generated. The actual task of grasping, or prehension, has become an area of study unto itself and will not be dealt with here. Rather, it is the motion of the whole arm which brings the hand into close proximity to the target that is of interest. In particular, a variety of different types of experiments have addressed the issue of how these movements are controlled and what roles various sources of information play in this control.

Pointing and reaching responses made with the arm typically are the result of coordinated rotations about the elbow and shoulder joints. In one of the first studies in which each segment of the arm was measured during the performance of natural, unrestricted reaching movements, Soechting and Lacquaniti (1981) demonstrated that

both the angular displacements and velocities about these joints covary. For example, they showed that as shoulder angle increased so too did elbow angle; furthermore, both joints reached their maximal angular velocities at the same time. The main point being that there was never a period during which the shoulder was being rotated while the elbow angle remained constant or vice-versa (but see Hollerbach & Atkeson [1985] for examples of arm movements in which this was not entirely the case). That the CNS is able to maintain this relatively invariant kinematic coupling between the joints of the arm is remarkable in light of the fact that the forces acting on each segment vary widely during the course of the movement (Smith & Zernicke 1987). For example, the effects of gravitational forces on the forearm and upper arm change as each segment rotates out of the vertical plane. Furthermore, the motion of one segment will produce interaction forces that act on the other segment. The CNS appears to use both feedforward and feedback mechanisms to compensate for the effects of these and other forces by controlling the timing and activation of the appropriate muscles in the shoulder girdle and arm to allow the generation of the smoothly coordinated movements that are observed.

Reaching to targets located at different locations in peripersonal space require subtle to significant changes in the patterns of activity in these muscle groups. Caminiti and colleagues have shown in a series of studies that systematic changes in the timing and magnitude of muscles acting at the shoulder and elbow joints of primates underlie pointing responses in different directions (Caminiti et al. 1990, 1991). Furthermore, this directional specificity is also apparent at the neuronal level in the motor cortex. In particular, individual cells within this area have a preferred direction of motion: their activity is greatest when the arm moves in one particular direction, but it drops off when the arm moves in a different direction. Georgopoulos and coworkers have demonstrated that the activity of the entire population of relevant motor cortical cells can accurately account for the direction in which the arm moves (Georgopoulos et al. 1986). This has also been shown to be true for other areas involved in the generation or modulation of arm movements - including the premotor cortex (Caminiti et al. 1991), area 5 in the parietal cortex (Kalaska et al. 1990), and the cerebellum (Fortier et al. 1993).

To produce an arm movement in a particular direction the CNS must first determine the location of the target with respect to the current position of the arm. The former information is initially realized by the position at which the image of the target falls on the retina. This visual information is further dependent upon extraretinal signals related to the position of the eyes with respect to the head and, in turn, the position of the head with respect to the body. Thus, any sensory information related to eye, head, or body movements can potentially influence the perception of the spatial location of a target as well as any reaching movements directed at the target.

In a sense, the arm can also be considered to be a visual target. As such, retinal and extraretinal signals play a role in determining its current position. In particular, the image of the arm will fall on a certain location on the retina that is dependent upon the position of the eyes. In addition to these signals, proprioceptive and efference copy information associated with recent movements of the arm will also contribute to the determination of its current location in space.

The contribution of these various sources of information to accurate reaching responses have been assessed in a number of different studies. Typically, the signals associated with these sources of information are perturbed in some manner and the effects that these perturbations have on pointing responses are analysed. The influence that retinal signals have on the spatial localization of targets has been assessed in experiments in which subjects view the visual scene through prism goggles (e.g., Thach et al. 1992). These devices shift the retinal position of the target image. When attempting to point at the target immediately after first donning such goggles, subjects produce errors that are dependent upon the amount and direction of the retinal shift. With time, however, adaptive modifications take place such that pointing responses once again become accurate. These modifications persist when the goggles are removed: subjects produce errors in the opposite direction which are reduced to normal levels after several trials.

Another way to perturb retinal information during reaching tasks is by simply restricting vision of the target and/or the limb during the movement. Comparison of these "open loop" responses to those produced under more typical "closed loop" conditions in which vision of the target and/or hand is available provide insight into the role that these signals normally play during reaching and pointing movements. Removing vision of the limb results in significant increases in the degree of endpoint error as well as the variability of this error (Bock & Eckmiller 1986; Chua & Elliott 1993; Prablanc et al. 1979a). If the hand is visible before the response has been initiated, however, but not during the movement itself the amount of endpoint error is substantially reduced (Prablanc et al. 1979b). Thus, it appears that the initial visual information regarding the location of the hand with respect to the target when combined with proprioceptive information concerning the posture of the arm relative to the body is sufficient to allow relatively accurate reaching responses under otherwise open loop conditions.

Removing vision of the target results in analogous increases in error that are dependent upon when the target disappears relative to other critical events within the response. If the target is removed at the onset of the saccade (i.e., approximately 200ms after it appears) then the subsequent hand movement displays a large degree of error (Prablanc et al. 1979a). This error is reduced if the target remains visible until the hand starts moving (i.e., for approximately 300-400ms), and is reduced still further if time is allowed for a corrective saccade (a further 120ms; Prablanc et al. 1986). Finally, error is smallest if the target is visible throughout the response. The fact that pointing responses get more accurate as more time is made available to view the target suggests that corrections are made to the movement in an on-line manner. These corrections appear to be the result of comparisons between the visual information about the location of the target with proprioceptive or efference copy signals related to the position of the moving limb. Taken together, the results of these studies demonstrate that visual information related to the retinal location of the image of the target and/or the limb has a powerful influence on pointing and reaching movements directed to the target.

As mentioned previously, this visual information is dependent upon where the eyes are positioned relative to the target. Because, the eyes can be moved with respect to the head, the head with respect to the body, and the body with respect to the world, a single stationary target can stimulate many different retinal sites. Despite this potential problem, we perceive the target to be stationary during movements of these effectors. This space constancy suggests that information associated with the movement of the relevant body parts is taken into account at a stage before perceptual judgements are made. Traditionally, this information is thought to arise from proprioceptive or efference copy sources. A number of studies have assessed the contributions made by these signals to pointing responses by taking advantage of the fact that they can be dissociated either through artificial perturbations or neurological impairments. Perhaps the simplest way to do this artificially is to deviate the position of the eye. Under these circumstances the proprioceptive information arising from the stretched ocular muscles will be incongruent with the command (or lack thereof) to move the eye. Using a suction lens to deviate one eye, Gauthier et al. (1990) were able to show that pointing responses viewed monocularly through the nondeviated eye were biased in the deviated direction. Thus, they concluded that ocular muscle proprioception contributed in a significant way to the processes underlying the spatial localization of targets as well as to pointing movements directed to such targets.

A second way to artificially dissociate proprioceptive and efference copy information is to vibrate the appropriate muscles. Such vibration stimulates the spindles in the muscle and leads to the illusion that the muscle is stretching (Goodwin et al. 1972). When this vibration is applied to the muscles that rotate the eye in a certain direction (e.g., the lateral rectus), it leads to a similar situation to that described above: the CNS interprets the spindle activity as a signal that the muscle is being stretched and, therefore, that the eye is moving; however, there will be no oculomotor command associated with this activity. When asked to point to targets in peripersonal space under these conditions, subjects mislocalize the targets in the direction associated with the illusory movement of the eye (Roll et al. 1990). Similar errors occur when the appropriate muscles in the neck (Biguer et al. 1988; Roll et al. 1990), or legs (Roll et al. 1990) are vibrated.

There are several naturally occurring oculomotor disorders that result in

analogous effects to those described above: that is, movement or deviation of the eyes independent of a command to do so. The deviation of one eye but not the other as artificially induced by Gauthier and workers also occurs naturally in a condition called strabismus. Strabismic subjects have been shown to exhibit systematic localization errors in the direction of the deviated eye (Gauthier et al. 1985) in agreement with the results described above. Similar observations have been made more recently in subjects with congenital nystagmus, in which the eyes involuntarily oscillate back and forth (Bedell & Currie 1993); and in a case of trigeminal-oculomotor synkinesis, in which movement of the jaw via left lateral pterygoid contraction was aberrantly accompanied by left medial rectus coactivation, and, thus, left eye motion (Lewis & Zee 1993). In each of these cases, the proprioceptive information derived from the movement of the eye was able to have a significant impact on the directional characteristics of subsequent pointing responses.

In contrast to these examples, when eye muscles are partially paralysed either artificially or naturally the reverse situation results. In particular, a command to generate eye movements is present but very little actual oculomotor output results. When reaching for targets under such circumstances, subjects tend to markedly overshoot the distance to the target if an eye movement is generated or attempted at the same time (Stevens et al. 1976). This overestimation is reduced, however, if the subject does not attempt to produce eye movements simultaneously (Perenin et al. 1977). When the eye muscles are partially paralysed the magnitude of the oculomotor command must be increased if the resulting saccadic eye movement is to have the appropriate amplitude. The fact that past pointing occurs in such situations suggests that the signals associated with this command influence the manual motor output as well.

As with retinal signals, the easiest way to assess the influence of extraretinal signals on normal pointing responses is by simply restricting eye motion via visual fixation. It has been demonstrated in a number of studies that the errors in pointing responses systematically increase if the subject is not allowed to move the eves to foveate the target (Abrams et al. 1990; Bock 1986, 1993; Prablanc et al. 1979a). In particular, subjects tend to overestimate the distance to the target when visually fixating compared to the condition in which they are allowed to look at the target. These results have several implications. First, they demonstrate that information derived from the change in gaze direction can contribute to the accuracy of the subsequent limb movement. Alternatively, it may be suggested that the lower acuity of the peripheral retina does not allow the position of the target, or for that matter the position of the limb as it approaches the target, to be accurately determined. The contributions made by these two factors to the observed pointing errors are not easily separated. Prablanc and coworkers (1979a), however, found that pointing accuracy was similar in the condition in which the target disappeared at the onset of the saccade to that observed when the target was visible throughout the response but no eye movements were allowed. Thus, information derived from eye movements in the absence of consequent retinal stimulation is as useful in producing accurate pointing responses as peripheral retinal information in the absence of eye movements. This suggests that the errors that are observed during visual fixation may be due to the lack of extraretinal information rather than the low acuity of the peripheral retina.

Other than the retinal signals associated with vision of the target and the arm and the extraretinal signals related to the position and movement of the eyes, the other relevant source of information that appears to contribute to accurate reaching responses is that arising from limb proprioceptive signals. Again, the role played by this information has been assessed in a number of studies in which proprioceptive signals have been perturbed. This occurs naturally in patients with peripheral sensory neuropathy and artificially in primates in which dorsal root rhizotomies have been performed (e.g. Sainburg et al. 1993; Taub et al. 1975). Such subjects typically have very little deficit if they are allowed to view their limb during pointing and reaching movements. If vision of the arm is restricted, however, their movements become much more erratic and inaccurate. This is also the case in patients with lesions to cortical areas that receive proprioceptive signals (Jeannerod 1986; Jeannerod et al. 1984). Taken together, these results indicate that information derived from the movement of the arm is normally integrated with visual signals concerned with the position of the target to produce accurate reaching responses. If the former signals are not available or can not be processed, the subject will be unable to determine where the hand is located with respect to the target and any on-line corrections that are attempted to reduce this discrepancy will be inaccurate.

In summary, it appears that information derived from a variety of sources contributes to accurate reaching movements directed towards stationary targets. As mentioned earlier the results from experiments that have investigated the mechanisms by which such movements are generated provided a background in which to study analogous processes during reaching movements directed towards moving targets. In particular, the experiments described in this dissertation were designed to allow comparisons between these two types of reaching responses and to assess whether the contributions from some of the specific sources of information described above were similar or analogous when moving targets were used as the stimulus.

1.2. Limb Movements to Moving Targets

As mentioned previously, when a target is moving a subject can either attempt to track or intercept it with the hand. Tracking responses have been studied quite extensively in the past, whereas interception movements have only more recently been investigated. There are at least two general aspects to a tracking response that can be studied. These correspond to the initial catch-up phase immediately after the onset of target motion and the steady-state phase in which the subject attempts to match both target position and velocity with the hand. Somewhat surprisingly, there is relatively little information on the initiation of tracking responses. This is in stark contrast to the large body of literature on the characteristics of smooth pursuit eve movements produced under analogous stimulus conditions (see next section). Thus, other than the fact that increases in target velocity lead to decreased reaction times and increased initial peak velocities in the hand (Beppu et al. 1984; Poulton 1974), little is known about how the various sources of information described above contribute to the initial aspects of a tracking response. Tanaka and colleagues have provided perhaps the only evidence that sheds light on this issue (Beppu et al. 1981; Nagoaka & Tanaka 1981; Tanaka 1984). They have shown in patients with sensory ataxia due to tabes dorsalis or to cerebrovascular lesions confined to the thalamus that the scaling of initial peak velocity with target velocity is left intact. Thus, proprioceptive feedback is apparently not required to produce a normal catch up movement in response to the onset of target motion.

In contrast to the lack of information on the catch-up phase, the steady-state portion of tracking responses has been studied in some detail. These experiments have shown that subjects are able, with practice, to match target position and velocity quite accurately. This ability to predict suggests that information related to the trajectory of the target, presumably from retinal and extraretinal sources, is used in a feedforward manner to produce tracking responses with the required speed and amplitude (Miall et al. 1987). Restricting vision of the target or the limb (or at least the cursor that is driven by limb movement) does not alter this predictive tracking ability for simple ramp target motions in normal subjects (Beppu et al. 1987). At first glance, this lack of effect appears to contradict the findings from studies in which reaching movements were directed to stationary targets under conditions of restricted vision. This difference may be due, however, to the fact that in the tracking studies the target or hand cursors were not removed until well into the response. In this sense, the conditions of Beppu et al. (1987) are analogous to those of Prablanc and colleagues (1979a) in which the hand was initially visible prior to the response. Recall that in this experiment the pointing error was very similar to that obtained under the normal closed loop situation. The influence of proprioceptive information on the ability to maintain an accurate tracking response has also been assessed in subjects who are functionally deafferented (see above). Such subjects show marked increases in tracking error during steady-state portions of the response which are further exacerbated if vision of the limb cursor is removed (Nagaoka & Tanaka 1981).

As noted above interception movements have come under investigation only recently. As such, it is not surprising that the contributions of retinal and extraretinal signals to these responses have not yet been studied. Rather, researchers have concentrated on elucidating the basic mechanisms by which interception movements are generated. Interestingly, some of the first experiments that used an interception task were done on infants (von Hofsten 1979, 1980, 1983; von Hofsten & Lindhagen 1979). These showed that infants as young as 18 weeks of age are able to intercept moving targets using a predictive strategy. In particular, they were able to take the velocity of the target into account and aim in the appropriate direction to intercept the targets relatively accurately. Given that these abilities are present at such a young age, it is not surprising that similar results have been obtained in adults (Bairstow 1987).

Although the relevant experiments have not yet been done that address the issue concerning the role of eye movements and vision of the hand during interception movements, there has been a relatively large number of studies which have analysed the somewhat analogous task of catching balls. Included in these studies have been conditions in which vision of the hand and/or the ball has been restricted. These have shown that the number of successful catches is substantially decreased if the subject can not see the hand during the response (Fischman & Schneider 1985; Smyth & Marriott 1982). In addition, the accuracy of the catches increases as the subject is allowed to view the trajectory of the ball for longer periods of time (Whiting et al. 1970). This result is analogous to findings of Prablanc and coworkers (1979a, 1986) who showed that reaching movements directed towards stationary targets become progressively more accurate as the target remains visible for greater durations.

In summary, compared to the results of experiments using stationary targets, there is substantially less knowledge about the contribution of vision and eye movements to hand movements directed towards moving targets. These issues were addressed in each of the experiments described in this dissertation. Because moving targets were used, it was expected that additional information would be gleaned regarding the interactions between visual motion processing, smooth pursuit eye movements, and the production of tracking and interception responses. The former two processes are considered next.

1.3. Visual Motion Processing and Smooth Pursuit Eye Movements

To accurately follow a moving target with the eyes and reach for it with the hand, the CNS must first determine the target's direction and speed. The processing required to make this determination appears to start as early as the retina (Livingstone & Hubel 1988), and becomes more detailed as the information progresses through the various stages of visual processing. In fact, by the time signals reach the extrastriate areas in the parietal cortex, the processing appears to be uniquely suited for determining the motion of the target with respect to the observer (Saito et al. 1986). In primates, the first area that is specialized for visual motion processing appears to be in the middle temporal cortex, or area MT. Cells within this area of cortex are sensitive to both the direction and velocity of target motion (Maunsell & Newsome 1987). As such, this may be the first stage at which the perception of target motion is realized. Towards this end, it has been demonstrated using random dot displays that the magnitude of activity in individual cells in this area is related to the number of dots moving in the cell's preferred direction, and, consequently, to the ability to correctly identify the direction of motion in the display (Newsome et al. 1989). Furthermore, discrete lesions to area MT lead to substantial increases in the motion direction detection threshold for the preferred direction of the affected cells (Newsome & Pare 1988). In contrast, extracellular microstimulation to a similarly circumscribed region leads to a decrease in this threshold (Salzman et al. 1990).

Area MT projects to area MST which subsequently has connections with area 7a. In both of these latter areas, cells appear to respond to substantially more complex aspects of visual motion. For example, a proportion of cells in area MST are sensitive to rotary but not linear movements of the same visual stimulus (Saito et al. 1986). In addition, there are also cells in this area that respond to changes in the size of the stimulus (Saito et al. 1986). In area 7a there is a subgroup of "opponent vector" cells that are sensitive to the motion of a stimulus either away from or towards the centre of gaze (Motter & Mountcastle 1981). The visual stimuli in each of these cases are similar to those that occur when the animal moves in the environment. These optic flow signals have been shown to be important cues for postural adjustment and the perception of depth (Nakayama 1985).

The role that these areas play in human visual motion processing has been addressed in a number of recent studies. Beckers and Homberg (1992) applied transcranial magnetic stimulation (TMS) unilaterally over area V5 (the human homologue of area MT in monkeys). They found that such stimulation leads to a disruption of the perception of visual motion in the contralateral hemifield. In particular, subjects produced a large proportion of errors when indicating the direction of motion in a random dot display during TMS. This "transitory akinestopsia" has also been shown to exist in a more permanent form in a patient with bilateral lesions to the lateral temporo-occipital cortex (Zihl et al. 1991). This patient has deficits in her ability to perceive target motions exceeding approximately 10% in her central visual field. Responses to either slower moving targets or targets moving in her periphery are less impaired. In contrast, her perceptions of stationary targets are normal. Thus, it appears that analogous structures in the human brain subserve the processing and perception of target motion.

One way to respond to such motion is to follow the target with the eyes. These

smooth pursuit eye movements in some respects are analogous to tracking movements made with the hand. In particular, following the onset of target motion there is an initial transient period during which the eye lags behind the target. A catch up saccade is subsequently generated after which the target remains fairly accurately foveated. As with hand tracking responses the latency of smooth pursuit has been shown to decrease with increases in target velocity (Carl & Gellman 1987; Lisberger & Westbrook 1985). This trend may be consistent with the use of a threshold distance to determine the onset of target motion. In particular, it has been suggested that the target must traverse a certain distance before it is perceived as moving (Carl & Gellman 1987; Collewijn 1972). Obviously, the faster the target moves, the sooner it will cross this threshold, and the sooner its motion will be recognized.

A second aspect of the smooth pursuit response that is of interest is that the initial component is largely independent of target velocity when this variable is unpredictable from trial to trial (Carl & Gellman 1987; Lisberger & Westbrook 1985). This suggests that the direction of target motion is determined and an appropriate response is generated before the exact velocity of the target has been computed. This situation is rectified further into the response, typically following the catch up saccade. In contrast, if the onset of pursuit is delayed by approximately 75ms through alterations in stimulus presentation, the initial aspects of the response are dependent upon target velocity (Carl & Gellman 1987).

The contribution of visual motion processing to the accurate production of smooth pursuit eye movements has been investigated in studies in which the areas subserving this processing have been perturbed. Lesions confined to a small region of area MT in monkeys result in deficits in pursuit initiation in the receptive field of the affected cells (Newsome et al. 1985). In particular, when targets stepped into the affected field then started moving, the velocity of the initial pursuit component and the amplitude of the subsequent catch up saccade were both hypometric. Once the monkey had caught up to the target, however, the steady-state pursuit was normal. In addition, normal responses were also observed for saccades made to stationary targets that stepped into the affected field, as well as for pursuit initiated to targets starting in other locations.

Lesions to area MST lead to the same type of smooth pursuit deficits as those observed following MT lesions: difficulties in initiating pursuit in the affected visual field. In addition, however, such lesions also result in a deficit in steady-state pursuit towards the side of the lesion (Dursteler & Wurtz 1988). This latter problem may be related to the fact that MST neurons receive extraretinal input as evidenced by the continued firing of these cells during periods of smooth pursuit in which the visual target is briefly extinguished (Wurtz et al. 1990). These difficulties in maintaining steady-state pursuit are also apparent following lesions to the parietal cortex (Lynch & McLaren 1982). Comparable deficits are observed in human patients following lesions to homologous regions of cortex. In particular, such patients typically display a low gain for both pursuit and catch up saccades when the target moves towards the side of the lesion (Sharpe & Morrow 1990).

Besides the obvious influence from visual motion processing, smooth pursuit eye movements have also been shown to be modulated by simultaneously produced limb movements. A variety of different studies have demonstrated that smooth pursuit performance improves when the hand is also used to follow the target or the hand itself is used as the target (Steinbach & Held 1968; Mather & Lackner 1981; Vercher & Gauthier 1988). In particular, the delay between target motion and eye motion and the number of catch up saccades are reduced, and the accuracy and maximal velocity of the smooth pursuit system is increased. Analogous improvements have also been observed for vergence eye movements when the hand is used as the target (Erkelens et al. 1989). These results suggest that information derived from the manual motor system, either in the form of proprioceptive or efference copy signals, has access to and is able to influence the oculomotor centres involved in the generation and control of smooth pursuit eye movements. In fact, this influence is strong enough to drive smooth pursuit movements in the absence of a visual stimulus (Vercher & Gauthier 1992).

The issues raised with respect to visual motion processing, smooth pursuit eye movements, and the interactions between these processes and the production of hand movements were addressed in each experiment in this dissertation. In particular, the question put forth was whether there are similarities between the characteristics of eye and hand movements. This was assessed in terms of the response latency - target velocity relationship and the initial kinematic independence with respect to target velocity. The idea being that if these two motor systems displayed similar response characteristics then maybe they were being influenced in the same manner by the mechanisms underlying visual motion processing.

1.4. The Role of the Cerebellum in Eye and Hand Movements

It has long been known that the cerebellum contributes to the control of eye and hand movements (Holmes 1939). Neurophysiological recordings from certain areas of the cerebellum in behaving animals reveal activity related to such movements (e.g.,

Fortier et al. 1989, 1993; MacKay 1988; Marple-Horvat & Stein 1987, 1990; Suzuki & Keller 1988a, 1988b; van Kan et al. 1993). Similarly, stimulating these areas leads to movements of each effector either in isolation or in combination with other body segments (Rispal-Padel et al. 1982). Finally, damage to this structure causes deficits in the output produced by these two motor systems (e.g., Becker et al. 1991; Miall et al. 1987; Sato & Noda 1992; Waterston et al. 1992). One of the more common deficits is dysmetria, characterized by errors in the direction, amplitude, velocity, and force of the movement. For example, when a subject with cerebellar damage attempts to look at and reach for a static object in peripersonal space the eye and hand movements have a tendency to be inaccurate, requiring a series of corrective saccades or submovements to finally achieve the appropriate position (Botzel et al. 1993; Becker et al. 1991). With moving targets the dysmetria manifests itself as an inability to accurately match target velocity. The smooth pursuit eye movements generated to follow the target have a low gain. As a result, a series of catch up saccades must be produced to minimize the retinal image motion. These "saccadic interruptions" can lead to an eve position-time trajectory with a staircase appearance (Grant et al. 1992). Analogously, the hand movement typically consists of a series of saccadic-like pulses during which the hand alternately moves faster and slower than the target (Beppu et al. 1984, 1987; Morrice et al. 1990).

Unfortunately, there is little knowledge of how these deficits interact. However, given what has been reviewed in the previous sections it would not be surprising to find that the aberrant eye movements of subjects with cerebellar damage contribute in some way to the dysmetria observed in their hand movements and vice-versa. Alternatively, because the cerebellum is a site of major confluence for inputs and

outputs related to the control of eye and hand movements it may be that lesions to this structure would lead to a decoupling between these motor systems. This was certainly the finding of Vercher and Gauthier (1988) who showed that the coordination between eye and hand movements during a tracking task was disrupted following discrete lesions to the dentate nucleus in baboons. This issue was addressed in the final experiment of this dissertation.

1.5. Specific Objectives of the Experiments

The general goal of the experiments in this dissertation was to provide a better understanding of the mechanisms by which movements of the hand are directed towards moving targets. More specifically, I was interested in the roles played by visual motion processing and smooth pursuit eye movements in such tasks. In addition, the issue of how these processes interacted was also addressed by taking advantage of the fact that they are disrupted during cerebellar dysfunction. Finally, because both tracking and interception movements were used, it was possible to compare how the different manipulations used in each experiment influenced these tasks. The specific aims of each experiment were as follows:

Experiment One - To assess the normal control strategies by which hand movements are directed to moving targets and compare the characteristics of these strategies to those observed in smooth pursuit eye movements. This would help to clarify how these two motor systems make use of information derived from cortical areas involved in visual motion processing. A second goal was to compare these responses to those produced when static targets are used to see whether there are any differences in the manner in which these movements are generated. Experiment Two - To investigate the contribution of retinal and extraretinal signals to tracking movements performed with the hand. In particular, the signals associated with vision of the hand and eye motion were restricted by various means to determine what role they played under normal conditions. Once again, comparisons were made with the results from previous experiments in which these signals were manipulated during reaching movements directed to static targets.

Experiment Three - To assess the role of the cerebellum in the coordination and interactions between eye and hand movements during tracking and interception tasks. In particular, by using subjects with cerebellar damage in which the normal control of oculomotor and manual motor output is deficient, it was possible to investigate the influence that these perturbations had on the opposing system. In this way, the complex issues concerning the function of the cerebellum in the control of movement as well as how normal interactions between the eye and hand motor systems may occur could be addressed.

CHAPTER TWO: METHODS

2.1. Subjects

2.1.1. Normal Control Strategies

Nine subjects (6 males, 3 females; age range: 23-34) took part in the first experiment, with a minimum of 3 subjects in any one condition. All subjects had normal or corrected to normal visual acuity and were right-handed; none showed signs of neurological deficit. All of the subjects, except one (PVD), were naive with respect to the experimental environment as well as the hypotheses being tested.

2.1.2. Role of Retinal and Extraretinal Signals

In the second experiment there were seven subjects (4 males, 3 females; age range: 23-36 years), again with a minimum of 3 in any one condition. As in the previous experiment all had normal or corrected to normal visual acuity, were right-handed, and showed no signs of neurological impairment. Three of the subjects had participated in the first experiment whereas the other four had no previous experience with the experimental environment. All the subjects, except one (PVD), were naive with respect to the hypotheses being tested.

2.1.3. Effects of Cerebellar Dysfunction

Seven subjects with cerebellar dysfunction (5 males, 2 females; mean age: 52 \pm 13 yrs; age range: 30-70 yrs) and seven age-matched controls (5 males, 2 females; mean age: 55 \pm 17 yrs; age range: 34-70 yrs) with no known neurological deficits participated in the final experiment. None of the subjects had any previous experience with the experimental environment and all were naive with respect to the hypotheses
being tested. Of the cerebellar subjects, four showed unilateral deficits; whereas the other three were bilateral. Figure 1 provides examples of cerebellar MR images showing degeneration, infarct, and resection following hemorrhage from three of the subjects. Table 1 provides a summary of the clinical features of each of the cerebellar subjects.

2.2. Apparatus and Task

In all three experiments subjects were seated in a dimly illuminated room at arm's length (50-70cm) in front of a large (1.1m X 1.1m) vertically oriented translucent display screen onto which the target was back-projected. Target motion was achieved by an orthogonal pair of servo-controlled mirror galvanometers (General Scanning) in the projector beam. The starting position and velocity of these mirrors were controlled by a computer. This computer also triggered data collection by a Watsmart system 300ms before the onset of target motion. The Watsmart tracked and recorded the position of an infrared emitting diode placed on the tip of the index finger of the pointing hand (200 Hz sample rate; static resolution ~1mm; dynamic resolution ~3mm). It also digitized target position (400 Hz) and, in the latter two experiments, eye position (400 Hz). Eye movements were recorded with an infrared corneal reflection device (IRIS). A bite bar attached to a rigid frame on the chair was used to stabilize head movements and facilitate the monitoring of eye motion.

Two tasks were used. In the tracking task, the target appeared on the screen and remained stationary. The subject pointed comfortably at the target with the elbow slightly flexed and index finger extended. In this initial posture the finger was close to but not touching the screen. After an unpredictable delay (500-1500ms), the target



Figure 1. MR images from 3 of the cerebellar subjects. A T2-weighted transverse (axial) image showing area of increased signal intensity compatible with a recent infarct to the right cerebellar hemisphere in subject K.M. B T1-weighted coronal image showing resection of right cerebellar hemisphere in subject L.B. C T1-weighted sagittal image showing atrophy of cerebellar vermis due to diffuse degeneration in subject F.L.

					Hand Movements			Eye Movements	
Patient	Age/Sex	Duration	1 Pathology	Affected Side	Dysmetria	Rapid Alternating Movements	Fine Finger Movements	Smooth Pursuit Impairment	Gaze-Evoked Nystagmus
LB	30F	3 yr	Hemorrhage	Right	2	2	2	1	2
FL	39F	12 yr	Degeneration	Bilateral	1	1	0	2	2
КМ	68M	3 wk	Infarction	Right	2	2	2	1	0
КК	70M	3 wk	Infarction	Left	1	2	2	1	1
RF	60M	3 yr	Infarction	Left	1	1	1	1	0
FC	49M	3 yr	Infarction	Right	0	1	1	1	1
KR	42M	10 yr	Degeneration	Bilateral	1	2	2	1	0

TABLE 1: CLINICAL FEATURES OF THE CEREBELLAR SUBJECTS

0 = normal 1 = mild impairment 2 = moderate impairment 3 = marked impairment

moved in the direction of the pointing hand for 2s. The subject was required to catch up to and follow the target as soon as possible after the cue for responding, which was usually the beginning of target motion.

In the interception task, the target appeared at the same starting position, but the subject started with the index finger placed on the armrest of the chair ~30cm from the screen. The subject was required to reach forward towards the screen and intercept the target as soon as possible after the cue to respond. A small switch attached to a finger casing worn by the subject was closed upon contact with the screen, causing the target to stop.

2.3. Experimental Conditions

A variety of different conditions were used in each experiment in an attempt to uncover the mechanisms by which eye and hand movements are coordinated and what signals are important in this coordination.

2.3.1. Normal Control Strategies

Three experimental variables were manipulated in the first experiment: the type of target motion, the type of cue used for the subject to begin moving, and the randomness of target motion across trials. Unless otherwise noted the target was a circular spot 2cm in diameter and the subjects made both tracking and interception movements with the right hand in each condition.

1. Target motion: Three combinations of changes in target position and velocity were used as stimuli.

Step: The target stepped 25, 100, or 200mm to the right from its starting position for the tracking task, or 50, 100, 200, or 350mm for the interception task. These values were chosen in an attempt to get the subjects to reach to positions similar to those in the ramp condition (see below) so that direct comparisons could be made.

Ramp: The target moved from its starting position to the right at one of five velocities (62, 88, 125, 250, or 500mm/s).

Step-ramp: This was the same as the ramp condition, except that the target first stepped 2 or 5mm to the right immediately prior to the onset of the ramp motion. This condition was used to evaluate the effects of small steps on response latency in the tracking task only.

The variation in arm's length among subjects meant that target motion could be specified in either linear coordinates (distance along the screen) or angular coordinates (visual angle subtended), but not both. For this and subsequent experiments the former was chosen. Therefore, for example, a step of 200mm on the screen was equivalent to an angular displacement of between 18-24° for viewing distances of 70-50cm.

2. The cue to begin movement: For each of the target motions the cue for the subject to begin movement was usually the onset of target motion. For the ramp condition, a second condition was used in which the cue was the last in a series of 4 tones separated by 400ms (after Hening et al. 1988). The last tone occurred either coincident with, 150ms after, or 350ms after the onset of target motion. In this way the duration of the subject's exposure to visual information about target velocity was manipulated and, thereby, the time course of the appropriate specification of a response could be evaluated. For this condition, the starting position of the target was systematically varied to the left or right of its normal starting position as determined by target

velocity and the timing of the final tone. This insured that target position at the onset of hand movement was similar for all cue times to what it was under normal conditions. For example, for the 500mm/s speed the starting position of the target was 112 or 12mm to the left, or 63mm to the right of the normal starting position for the 350, 150, and 0ms cuing times, respectively. Given a latency of 50-100ms after the final tone, target position at the start of arm movement ranged from 88-113mm to the right of the normal starting position *for all cuing times*. This range was similar to that in the normal tracking task (85-95mm). Subjects could not easily predict target velocity or cue time from target starting position because there were 12 separate conditions and for 10 of these the target started within \pm 50mm of the normal starting position.

In the auditory cuing condition the subject's hand was placed in the normal starting position (pointing at the screen for the tracking task or on the armrest of the chair for the interception task). In the tracking task the normal starting position of the target was marked on the screen with a piece of tape.

3. Randomness of target motion across trials: For the step, ramp, and step-ramp conditions, the step amplitude or velocity of the target was varied pseudo-randomly from trial to trial (random condition). In addition, in the ramp condition another set of trials was completed in which target velocity was held constant for 6-10 trials (predictable condition). The subjects were told whether target motion would be random or predictable prior to each block of trials. In all cases the time of onset of target motion was always varied pseudo-randomly.

2.3.2. Role of Retinal and Extraretinal Signals

A total of 7 conditions were used in the second experiment. Unless otherwise

noted the target was a circular spot and only the tracking task was used. In addition, only the ramp target motion with 3 different randomly presented target velocities was used (62, 125, 250mm/s). As in the first experiment, the subjects used the right hand to perform the task.

1. Normal Condition: Full vision of the hand and unrestricted eye movements were allowed. All 7 subjects participated.

2. Restricted Vision Condition: To assess the role of retinal signals concerned with the position and velocity of the hand relative to the target, vision of the hand was restricted throughout the task by covering the arm with an opaque screen (1.0m X 0.5m). The target was a thin vertical line that extended above the screen. This allowed vision of the target without vision of the hand. A small piece of tape was attached to the display screen underneath the opaque screen at the starting position of the target. Subjects aligned their index finger with this tape before each trial to insure that there would be no offset in initial hand position. Eye movements were allowed. All 7 subjects participated.

3. Fixation Condition: The contribution of extraretinal information associated with eye motion was examined by requiring subjects to visually fixate a stationary LED positioned 1cm above the starting position of the main target. Any trials in which there was substantial eye movement (>1°) were discarded from the analysis. Typically, these accounted for <10% of the trials. Vision of the hand was available. All 7 subjects participated.

4. Partially Restricted Vision Condition: To evaluate whether vision of the hand during the initial part of the movement influenced response accuracy the opaque screen was shifted to the right. The distance from the starting position of the target to the leftmost edge of the screen was varied (6.2, 12.5, 25, 50, or 100mm). The target was a thin vertical line and eye movements were allowed. 3 of the original 7 subjects participated.

5. Eccentric Fixation Condition: The possibility of differences between central and peripheral vision on tracking performance were assessed by requiring subjects to visually fixate a stationary LED that was 10, 20, or 30cm to the left of the starting position of the target. Thus, the image of the target at its normal starting position was projected onto eccentric locations on the retina. Vision of the hand was available. 3 of the original 7 subjects participated.

6. Congruent Pursuit Condition: To separate the influences of eye motion and peripheral visual information subjects visually pursued a second target (another circular spot) while pointing at the main target. The two targets were horizontally separated by 10, 20, or 30cm and moved in the same direction and at the same speed. The subjects were required to look at the target on their left and manually track the target on their right. Vision of the hand was available. 3 of the original 7 subjects participated.

7. Incongruent Pursuit Condition: The role of extraretinal information in the control of hand movements was examined by dissociating eye and hand target velocities. This condition was similar to the above except that the velocity of each target was controlled separately. Thus the target being visually pursued moved slower, faster, or at the same speed as the target being manually tracked. The targets were initially separated by 20cm in the horizontal plane and vision of the hand was restricted. 3 of the original 7 subjects participated.

The first 3 conditions comprised the main part of the second experiment. They allowed an assessment of the influence of retinal and extraretinal signals on the ability

of the subjects to accurately track the target with their hand. The last 4 conditions were used to verify certain hypotheses regarding possible control strategies observed in the main part of the experiment.

2.3.3. Effects of Cerebellar Dysfunction

A total of five conditions were used. Unless otherwise noted both tasks and the circular target were used in each condition. As in the second experiment only the ramp target motion with 3 different randomly presented target velocities were used. Because cerebellar subjects sometimes have difficulty generating a prompt response to the onset of target motion, the target velocities were reduced to 50, 100, and 200mm/s. All of the subjects participated in the first four conditions; whereas only the controls completed the fifth condition.

- 1. Normal Condition: As described above.
- 2. Restricted Vision Condition: As described above.
- 3. Fixation Condition: As described above.

4. Eye Movement Only Condition: Smooth pursuit eye movements were generated in isolation to follow the moving target. Comparing the eye movements produced under these conditions with those generated in conjunction with hand movements allowed an assessment of the influence of hand movements on the oculomotor system.

5. Saccadic Pursuit Condition: To directly assess the influence of saccadic interruptions on hand trajectories the control subjects were required to perform the tracking task with their hand while making saccades to 4 equally-spaced stationary targets positioned directly above the path of the moving target. The subjects were

instructed to make a saccade to each stationary target in succession as the moving target passed underneath. Only the 100mm/s target velocity was used and the stationary targets were separated by 6.66cm.

In each condition the cerebellar subjects with unilateral damage used the affected hand, those with bilateral damage used the more severely affected hand, and the controls used the right hand. In addition, in a separate session the 4 cerebellar subjects with unilateral damage completed the normal, fixation, and restricted vision conditions with their unaffected hand. For this session the target moved away from the side of the hand being used (i.e., in the same direction as when the affected hand was used). In addition, the starting position of the target was 17.5cm from the midline toward the unaffected side. This insured that the target would not move out of the subject's peripersonal space during the tracking response to the fastest target velocity.

In all three experiments blocks of 40-160 trials were completed using the same condition, and several blocks were generally completed during one experiment lasting ~30-45 minutes. There was a 3s delay between each trial, a 10s delay between sets of 8-10 trials within each block, and a 45-90s delay between the different blocks. Before each block, subjects received a series of practice trials to acquaint themselves with the task.

2.4. Data analysis

The data were analyzed off-line. The hand and eye position signals were differentiated (FIR 70 Hz cutoff [-3dB]) to yield hand and eye velocities. This high cutoff frequency was chosen based on previous methods in oculomotor research. It was

felt that any error introduced by such a high cutoff frequency would be constant across most of the comparisons of theoretical interest: that is, those between the different conditions rather than the different target velocities. An interactive computer program was used to determine response latency (reaction time) from individual trials: the computer first estimated latency by velocity and acceleration criteria, and indicated this on the velocity trace by a moveable cursor. On some trials, small deviations in the velocity trace led to latency being over- or underestimated. In such cases the user could adjust the cursor to a more satisfactory position using subjective criteria. Trials in which the hand or eye drifted prior to the onset of target motion were excluded from the analysis. In the first two experiments only the response latencies for the hand were analysed; whereas in the third experiment both eye and hand latencies were analysed. Although eye movements were measured in the second experiment the purpose of this was to insure that subjects were *not* moving the eyes in the fixation condition.

Latencies were further broken down according to the model of Collewijn (1972):

latency = threshold time + processing time (1)

where threshold time is the time taken for the target to initially move the threshold distance, and clearly decreases as target velocity increase; and processing time accounts for subsequent central computation, transportation, and electromechanical delays and is independent of target velocity. Thus:

latency = threshold distance / target velocity + processing time (2) This second relationship is equivalent to the equation for a straight line. Therefore, by linearly regressing latency vs. 1/target velocity it was possible to obtain the values of the threshold distance (slope) and the subsequent processing time (y intercept). This procedure was used in all three experiments in an effort to uncover the mechanisms by which target velocity influences the initial processing in each motor system.

In the first experiment the following kinematic measures were made for tracking task responses with the hand: peak hand velocity and time to peak hand velocity were determined for the catch-up phase of the movement; and mean gain (hand velocity/target velocity), within trial standard deviation, and the coefficient of variation (CV=stdev/mean) of hand velocity were determined for the steady-state tracking phase (1000 to 1600ms into the response). In the second experiment the mean acceleration of the hand was determined for the first 100ms of the response. In addition, steady state hand gain and positional error (hand position-target position at each data point) were measured. Finally, in the third experiment these latter two measures as well as steady state hand velocity variability were determined. In addition, hand gain was also quantified for the 100ms periods leading up to and following each saccade under the normal condition for the cerebellar subjects and in the saccadic pursuit condition for the controls.

In the interception task the direction of the hand path was quantified using two related variables: (i) trajectory angle is the direction of hand motion relative to the screen (i.e., where the subject is aiming). By definition, if the subject aimed directly at the screen trajectory angle was 0, if the subject aimed to the right the angle would be positive, and to the left, negative. (ii) Prediction angle is the direction of hand motion relative to the target's current position. If the subject aimed directly at the target, prediction angle was 0, if the subject aimed ahead of it, prediction angle was positive; and behind it, negative. In the first experiment these variables were measured over the first 100ms of the interception responses. In addition, the straightness of the hand path (the average deviation from a straight line), average hand velocity (distance

moved/movement time), and endpoint accuracy (final hand position - final target position) were determined. In the third experiment prediction angle was again measured during the initial 100ms of the response as well as during the 100ms pre- and postsaccadic periods. In addition, movement time, variability of trajectory angle and endpoint error were also determined. Finally, the quality of the eye movements in the third experiment was determined by measuring eye positional error (eye position target position) and the number of catch-up saccades generated during each trial. Where appropriate each measure was subjected to either a t-test or analysis of variance. The ANOVA's were largely of a repeated measures design using target velocity and condition as factors. For the final experiment a mixed design was used to allow comparisons between the different groups of subjects.

CHAPTER THREE: RESULTS

3.1. Response Latency

3.1.1. Normal Control Strategies

In the step condition, response latency was constant across steps of different amplitude and to different positions in relation to the midline of the subject's body. This was the case for both the tracking (group means \pm intersubject SD: 25mm step - 203 \pm 21ms; 100mm step - 190 \pm 22ms; 250mm step - 192 \pm 12ms; F[2,6]=1.09, p=0.39) and interception tasks (50mm step - 197 \pm 6ms; 100mm step - 193 \pm 6ms; 200mm step - 194 \pm 5ms; 350mm step - 194 \pm 5ms; F[3,9]=0.59, p=0.64). The invariance in latency for the different step amplitudes is consistent with previous results from experiments which have used similar step amplitude ranges (Biguer et al. 1982; 1985).

In the ramp condition, in contrast, response latency was dependent on target velocity (Fig. 2A): as target velocity increased latency decreased rapidly then tended to plateau (Fig. 2B). This was true for all four subjects tested in both the tracking and interception tasks, and under random and predictable conditions. For target velocities common to each condition, latency was shorter overall in the tracking task than in the interception task (F[1,3]=35.29, p=0.01); and shorter for the predictable condition than in the random condition (F[1,3]=4.04, p=0.04).

The reduction in latency with increased target velocity is consistent with the use of a threshold distance to determine target motion onset. As mentioned in Methods, by regressing latency vs. 1/target velocity one is able to quantify the values for the threshold distance (slope) and subsequent processing time (y intercept). Figure 3A shows the latency values from the interception task performed under the random



Figure 2. A Average hand velocity traces from four to six trials for a single subject (NB) for tracking movements made to target velocities of 62, 125, and 250mm/s. The vertical lines indicate the onset of the response (determined from individual trials). B Response latency group means for interceptions performed under random (open squares) and predictable conditions (solid squares) and for tracking performed under random (open diamonds) and predictable conditions (solid diamonds). Error bars, 1 intersubject SD.



Figure 3. A Group means for response latency in the interception task performed under random conditions plotted vs. 1/target velocity. The line of best fit is from a linear regression analysis. B Group means for threshold distance and processing time in the random (grey) and predictable (white) conditions averaged across tasks. C Same variables averaged across conditions for the tracking (solid) and interception (hatched) tasks. Error bars, 1 intersubject SD.

condition replotted vs. the inverse of target velocity. The line of best fit is from a linear regression analysis. As can be seen in the figure, this model can account quite accurately for the data: the correlation coefficient for the linear regression analysis was 0.97. Attempts to fit the data with higher order nonlinear functions yielded substantially smaller r values. For this particular condition the threshold distance was 5.3mm and the processing time was 194ms. The group means for these variables from the tracking and interception tasks performed under random and predictable conditions demonstrated that the decrease in response latency observed in the predictable condition was due to a shorter processing time (F[1,3]=33.37, p=0.01, Fig. 3B); whereas the longer latencies in the interception task were the result of increases in both the threshold distance (F[1,3]=10.46, p=0.05) and processing time (F[1,3]=9.68, p=0.05) compared to those observed in the tracking task (Fig. 3C). For both measures the task by target predictability interaction was nonsignificant. This indicates that the influence of target predictability was similar across each task.

It seemed that there might be a simple explanation for this latter effect. In the tracking task the subject initially pointed at the target. Thus, the finger might have served as a reference for detecting target motion. In the interception task, in contrast, the target appeared on the otherwise featureless screen with no stationary landmark nearby. To evaluate the importance of a stationary landmark, three subjects performed the interception task under normal conditions and under conditions in which a reference marker (a piece of black tape 2cm in width) was attached to the screen directly underneath the starting position of the target. Figure 4A shows that the reference reduced latency markedly (F[1,2]=25.33, p=.04). Submitting this data to the regression analysis demonstrated that when a visual reference was provided the threshold distance

:



Figure 4. A Group means for response latency in the interception task performed under random conditions either with (X's) or without (squares) a reference marker attached to the display screen. **B** Group means for the threshold distance and processing time in the normal condition (grey) and in the condition with the reference marker (white). Error bars, 1 intersubject SD.



Figure 5. A Group means for response latency in the tracking task performed under random conditions with simple ramps (*diamonds*) and stepramps with 2 (*crosses*) and 5mm (*inverted triangles*) steps. B Group means for the threshold distance and processing time in the simple ramp condition (grey) and in the 2 (*hatched*) and 5mm (*white*) stepramp conditions. *Error bars*, 1 intersubject SD.

was reduced from 6.3mm to 4.5mm (F[1,2]=19.84, p=0.05) but the processing time was not affected (F[1,2]=1.00, p=0.42, Fig. 4B).

To further explore the relationship between target motion and latency, three subjects performed the tracking task in an experiment interleaving step-ramps with simple ramps. The results showed that trials with step-ramps had shorter latencies than those with simple ramps (Fig. 5A). In addition, the 5mm step eliminated the dependence of latency on target velocity; the 2mm step did not. The regression analysis revealed that for the subjects tested under these conditions the processing time did not vary with the addition of a step prior to the ramp (F[2,4]=0.99, p=0.46, Fig. 5B), however, the threshold distance became progressively smaller as the initial step amplitude increased, being reduced basically to zero with the 5mm step (F[2,4]=31.02, p=0.004, Fig. 5B). Interestingly, when the subjects were asked if they noticed the differences in target motion all replied that they had not.

3.1.2. Role of Retinal and Extraretinal Signals

As in the first experiment, tracking task response latencies decreased as target velocity was increased under conditions in which vision of the hand or eye motion was restricted (F[2,10]=36.74, p<0.001, Fig. 6A). In addition, these manipulations also resulted in increased latencies overall (F[2,10]=8.12, p=0.001). Regressing latency vs the inverse of target velocity showed that these increases were due to inflated processing times in the restricted vision and fixation conditions compared to the normal condition (F[2,10]=7.3, p=0.01, Fig. 6B), whereas the threshold distance remained relatively constant across each condition (F[2,10]=1.06, p=0.37). Thus, after target motion had been detected more time was required to prepare the tracking response



Figure 6. A Group means for response latency in the tracking task performed under random conditions with full vision of the hand and unrestricted eye movements (*diamonds*) or while vision of the hand (*circles*) or eye movements (*squares*) were restricted. **B** Group means for the threshold distance and processing time in the normal (*grey*), restricted vision (*hatched*) and fixation (*white*) conditions. *Error bars*, 1 intersubject SD.

when restrictions were imposed on eye movements or vision of the hand.

In the remaining conditions the values for response latency were in line with expectations. When vision of the hand was made available for the initial aspects of the tracking response in the partially restricted vision condition, latency was not significantly different from the normal condition (F[5,10]=0.63, p=0.68). This was also the case in the congruent pursuit condition (F[3,6]=2.17, p=0.19), in which subjects were required to manually track the main target while visually pursuing a second target moving in the same direction and at the same speed but horizontally displaced 10, 20, or 30cm to the left of the main target. In contrast, latency remained relatively invariant when subjects visually fixated (F[3,6]=1.97, p=0.22), regardless of whether the fixation LED was positioned directly above the starting position of the target ('normal' fixation condition) or 10, 20, or 30cm to the left (eccentric fixation conditions). In each case, however, latency was increased compared to the normal condition in which eve movements were unrestricted. Finally, in the incongruent pursuit condition subjects were required to generate smooth pursuit eye movements with velocities that did not match those produced with the hand (see Methods). Under these conditions the response latency of the hand was more dependent on the velocity of the target being followed by the eyes (i.e., the second target) than that of the target being followed by the hand (i.e., the main target). Statistically, response latency was found to significantly decrease (F[2,4]=31.17, p=0.004, Fig. 7) as a function of eye target velocity. This significant effect was not apparent when comparisons were made as a function of hand target velocity.



Figure 7. Group means for response latency plotted as a function of eye target velocity in the incongruent pursuit condition. Regardless of whether the hand was required to follow a target moving at 62 (*circles*), 125 (*squares*), or 250mm/s (*inverted traingles*) its latency was dependent on the velocity of the target being followed with the eyes. *Error bars*, 1 intersubject SD.

3.1.3. Effects of Cerebellar Dysfunction

In the final experiment, eye and hand responses of both cerebellar and control subjects were measured in the tracking and interception tasks performed under normal, restricted vision, and fixation conditions. In addition, smooth pursuit eye movements generated in isolation were also measured. Thus, a large number of comparisons could be made across the various conditions. For the sake of brevity, however, only those that are meaningful in terms of the hypotheses being tested will be reviewed here. Group means for the hand latencies on the affected and unaffected side of the cerebellar subjects and in the controls are shown for the tracking task in Figure 8A. Figure 8B shows the corresponding eve latencies. In both cases there was a marked decrease in latency as target velocity was increased (Hand: F[2,18]=14.36, p<0.001; Eye: F[2,18]=8.15, p=0.003). Furthermore, hand and eye latencies were significantly larger on the affected side than the unaffected side and were further reduced in the control subjects (Hand: F[2,18]=7.94, p=0.003; Eye: F[2,18]=6.25, p=0.009). These effects were also observed for the latencies of hand and eye motor output in the interception task. In addition, hand latencies were greater overall in this task than in the tracking task (F[1,48]=39.9, p<0.001). When eye motion or vision of the hand was restricted, the latency of the hand movements increased (Tracking task: F[2,18]=8.27, p=0.003; Interception task: F[2,18]=9.12, p=0.002). In each of these cases the effects were similar across each group of subjects. Finally, when the cerebellar subjects used their affected hand in either task there was a significant increase in the latency of simultaneously-produced eye movements (F[2,9]=69.19, p<0.001; Fig. 8C). In contrast, hand movements on the unaffected side and in the control subjects did not influence the eye movement latencies.



Figure 8. A Group means for latency in the tracking task performed under normal conditions by the cerebellar subjects with the affected (*open circles*) and unaffected (*grey circles*) hand and by the controls (*solid circles*). B Latencies of smooth pursuit eye movements under the same conditions. C Comparison of smooth pursuit latencies of the cerebellar subjects when eye movements were generated in isolation (*diamonds*) or in conjunction with affected hand movements in the tracking task (*circles*). Error bars, 1 intersubject SD.



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Figure 9. A Group means for the threshold distance and processing time of the hand averaged across tasks and conditions for the affected (grey) and unaffected (hatched) sides of the cerebellar subjects and for the controls (white). B Same variables for eye latencies. Error bars, 1 intersubject SD.

Application of the latency regression analysis to this data showed that the threshold distance was significantly increased in the cerebellar subjects (F[2,9]=4.95, p=0.04); whereas the processing time was increased only when the affected hand was being used (F[2,9]=8.28, p=0.009; Fig. 9A). This was also true for the eye latencies (Fig. 9B). The greater hand latency in the interception task resulted from increases in both the distance threshold (F[1,12]=7.98, p=0.02) and the processing time (F[1,12]=12.76, p=0.004). Finally, an inflated processing time (F[2,9]=13.31, p=0.005) accounted for the increased hand latency under the fixation and restricted vision conditions. These latter two effects were similar for each group of subjects and reconfirm the findings from the previous experiments.

3.2. Tracking Task Kinematics

3.2.1. Normal Control Strategies

The tracking response in the ramp condition typically consisted of an initial build up in velocity to a peak velocity that was higher than the target velocity (examples in Fig. 10A and B). The velocity then decreased until it approximately matched that of the target, and the subject maintained this velocity until the target disappeared or stopped.

For the random condition (Fig. 10A) a striking feature was the remarkable nonlinearity in the relationship between hand velocity and target velocity. This is apparent in the overlap of the responses to all 5 target velocities for the first ~100ms of the movement. When the target velocity was predictable, in contrast, the overlap was not seen, and the responses to different velocities were distinct nearly from the start (Fig. 10B). This implies that the superimposition noted in the random condition was



Figure 10. Changes in hand velocity in the tracking task depend on the predictability of target velocity. The traces have been aligned so that the onset of movement occurs at 0ms (*dashed vertical line*). A Average hand velocity traces from four to six trials for a single subject (NB) tracking target velocities of 62-500mm/s under random conditions. **B** Traces for target velocities ranging from 62-250mm/s produced under predictable conditions by the same subject. Note the overlap in the initial part of the hand velocity traces in the random condition and the lack of overlap in the predictable condition.



Figure 11. Hand velocity values are plotted against target velocity from single trials 40ms into the response (*left column*) and 160ms into the response (*right column*) for a single subject (MB) performing the tracking task under random conditions in row A and under predictable conditions in row B. Line of best fit in each graph is from linear regression analyses. Note that at 160ms hand velocity is related to target velocity in both conditions, whereas at 40ms only the predictable condition shows a relationship. C The slope of the line of best fit is plotted at 20ms intervals for this subject. The slope became significantly different from zero (*open symbols*, not significant; *solid symbols*, significant) sooner when target velocity was predictable (*triangles*) than when it was random (*squares*).

not due to a nonlinearity at the level of the motor neurons or musculature. If it were, the superimposition should also have been present in the predictable condition.

To quantitatively confirm the graphic impression of superimposition and to determine the time at which the responses to different target velocities separated, the method first described by Cordo and Flanders (1989) was used. Briefly, hand velocity of single trials was measured every 10ms, plotted vs. target velocity, and linear regression analyses were subsequently performed. The 10ms interval at which the slope of the line of best fit first significantly differed from 0 provided an index of when the stimulus (target velocity) started to influence the response (hand velocity). Figures 11A and B show examples of hand velocity values for a single subject measured 40ms after the start of the response (left panel) and 160ms after the start (right panel) for the random and predictable conditions, respectively. Figure 11C shows how the slope of the line of best fit changes as a function of time in each condition. This analysis confirmed the graphic impression of Figure 10A and B: for the predictable target motion the slope became significant at 27 ± 8 ms, significantly earlier than the 77 \pm 20ms for the random condition (t-test, p<0.05, Fig. 12). A similar analysis was done for hand velocity and step amplitude for random steps. It showed that the response was dependent on the stimulus from the onset of the movement.

The above results suggested that when target velocity was unpredictable the hand movement started before visual motion processing was complete. To test this idea, the response was triggered with an auditory cue to dissociate the onset of hand movement from that of target motion. This cue, as described in Methods, was the last in a series of four equally spaced tones. Under these conditions, subjects typically started moving 50-100ms after the fourth tone regardless of target velocity. It was



Figure 12. Group means for separation time (time at which slope became significantly different from zero when regressing hand velocity vs. target velocity for the tracking task). For the ramp target motions, the stimulus started influencing the response significantly sooner under predictable conditions (*white*) than under random conditions (*hatched*). For step displacements (*grey*), the value was also short. *Error bars*, 1 intersubject SD.



Figure 13. Average hand velocity traces from four to six trials for a single subject (PVD) under conditions in which the cue to respond occurred coincident with the onset of target motion (A), 150ms afterward (B), or 350ms afterward (C). In each graph the traces have been aligned so that the onset of movement occurs at 0ms (*first dashed vertical line*). The *second dashed vertical line* represents the point in time at which the velocity traces started to separate from one another as determined by visual inspection.

possible therefore to vary the time available for visual motion processing, by giving the cue (i) coincident with onset of target motion (<100ms of visual information about target movement), (ii) 150ms after onset of target motion (~200ms of visual information), or (iii) 350ms after onset of target motion (>400ms of visual information). The mean responses of one subject to four randomly presented target velocities under these three conditions are shown in Figure 13A-C. The results show that as the time available for visual motion processing increased the duration of the overlap in the hand velocity traces progressively decreased. Using the analysis of slope described above it was possible to determine when the responses separated. This confirmed that responses were distinct from close to the onset of the movement for the 350ms cue time and separated progressively later for the 150 and 0ms cue times, respectively (F[2,6]=23.55, p<0.006, Fig. 14).

To determine whether differences in the position of the target at the start of the response contributed to the amount of overlap that was observed in the initial portion of the movement, subjects performed the tracking task in the auditory cuing experiment with the starting position of the target held constant. This led to wide variations in target position at the onset of hand movement (e.g., 25-225mm [for the 0 and 350ms cue times, respectively] to the right of hand position for the 500mm/s target speed). Nevertheless, the responses produced by the subjects under these conditions were qualitatively and quantitatively similar to those in the condition where the starting position of the target was varied. Analysis of slope as described above confirmed that the duration of superimposition observed at the start of the hand velocity traces progressively decreased as subjects received more time to process information about target motion (F[2,4]=36.83, p<0.001). In addition, these durations were not



Figure 14. Group means for separation time from the auditory cuing experiment. Target velocity started to influence hand velocity progressively sooner as the time avialable to view target motion increased from 0ms (grey), to 150ms (hatched), to 350ms (white). Error bars, 1 intersubject SD.



Figure 15. The timing and magnitude of peak hand velocity suggest that subjects used idiosyncratic strategies to catch up to the target. A Peak velocity means for each of four subjects under random (*open diamonds*) or predictable (*solid diamonds*) conditions. Note the consistency between subjects. **B** Time to peak velocity means for the same four subjects under random (*open diamonds*) or predictable (*solid diamonds*) conditions. For the sake of clarity, error bars have not been included. Intersubject variability ranged from 22-112mm/s for peak hand velocity and 25-87ms for time to peak hand velocity.

significantly different from those obtained previously. This finding suggests that the initial tracking response is largely uninfluenced by target position.

Figure 10A and B show that the hand velocity typically exceeded that of the target. This presumably represented a rapid movement to catch up to the target, and is analogous to the oculomotor catch-up saccade that follows the initial pursuit component in tracking a moving target. The relationship between peak hand velocity and target velocity in the random and predictable conditions is plotted in Figure 15A for each subject. Figure 15B plots time to peak hand velocity from the start of the response. Note the remarkable consistency among subjects for peak hand velocity and the lack of consistency in time to peak hand velocity. Thus, although peak hand velocity was scaled to target velocity, it was reached at widely varying times. In addition, the duration for which hand velocity exceeded target velocity during this portion of the movement also varied widely among subjects. This occurred despite the fact that latency was comparable from subject to subject (i.e., such that target position at the onset of hand movement was similar, for any one velocity, for each subject). This suggests that subjects caught up to the target using idiosyncratic strategies, with the only invariant feature being the magnitude of peak hand velocity.

The steady-state tracking response followed the catch-up component. The values for mean gain, within-trial variability, and coefficient of variance (CV) of hand velocity measured between 1000 and 1600 ms are shown for the random condition in Table 2. Subjects appeared to have the greatest difficulty in maintaining the slowest hand velocity: not only was the gain the lowest in this condition, but the CV was the highest. This latter result may be related to an inability to reduce the variability of steady-state hand velocity below a certain level (see variability values in Table 2).
Measure	Target velocity (mm/s)		
	62	125	250
Gain	0.87	0.97	0.95
Variability	16.9	20.3	35.5
Coefficient of variation	0.33	0.18	0.15

TABLE 2: Group means for the steady-state tracking response (1000-1600ms) performed under random conditions

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Figure 16. The characteristics of the tracking response with the hand depends on the presence of vision of the hand and eye movements. A Average hand position as a function of time for six to eight trials performed by a single subject (BH) tracking a target (*dotted line*) under normal (*solid line*) and restricted vision (*short dashed line*) conditions. Target velocity is 250mm/s. B Average position traces for the same subject performing under normal and fixation (*long dashed line*) conditions. Target velocity is 125mm/s.

Results from the predictable condition were similar.

3.2.2. Role of Retinal and Extraretinal Signals

Restricting vision of the hand or eye movements also had effects on the kinematics of the tracking response with the hand. Figure 16A and B display average hand positions produced under these different conditions by a single subject. The normal condition is compared to the restricted vision condition in A and the fixation condition in B. Two main effects were observed: (1) without vision of the hand the subject lagged behind the target, but matched its velocity; and (2) restricting eye movements caused the subject to move faster than the target. These effects were confirmed statistically for the group. Steady state positional error was slightly positive in the normal and fixation conditions, but negative in the restricted vision condition (F[2,10]=7.98, p=0.02, Fig. 17A). Steady state gain, on the other hand, was close to unity in the normal and restricted vision conditions, but substantially increased in the fixation condition (F[2,10]=5.85, p=0.021, Fig. 17B). In contrast to these findings, the mean acceleration of the hand during the first 100ms of the response was similar in each condition (F[2,10]=0.06, p=0.944, Fig. 17C), although it did increase with target velocity (F[2,10]=42.65, p<0.001).

The fact that subjects failed to catch up to the target in the restricted vision condition suggested that vision of the hand may be required during response initiation to match target position. This notion was confirmed in the condition in which vision was partially restricted. In particular, there were systematic reductions in error related to the duration for which the hand was visible (Fig. 18A). Specifically, as the distance from the starting position of the target to the edge of the screen was increased, the



Figure 17. A Group means for steady-state positional error as a function of target velocity for the tracking responses produced under normal (*squares*), restricted vision (*circles*), and fixation (*triangles*) conditions. Group means for steady-state gain (**B**) and initial acceleration (**C**) performed under the same conditions are also shown. *Error bars*, 1 intersubject SD.



Figure 18. A Average responses produced by a single subject (PVD) tracking the target (dotted line) in the normal (solid line), restricted vision (dashed line), and partially restricted vision conditions in which the hand was initially visible for either 6.2mm (dashed-dot line), or 50mm (think dashed line). Target velocity is 125mm/s. **B** Group means for steady-state positional error plotted for target velocities of 62 mm/s (stars), 125mm/s (diamonds), and 250mm/s (inverted triangles). Allowing vision of the hand during the initial portion of the response led to progressive decreases in error. Error bars, 1 intersubject SD.

steady state positional error became significantly smaller for each target velocity (F[6,12]=6.71, p=0.003, Fig. 18B). In contrast, the initial acceleration and steady state gain of responses produced under these conditions were similar to those produced in the normal condition.

The observation of normal initial acceleration but increased steady state gain in the fixation condition suggested that target velocity was overestimated in the peripheral visual field. This hypothesis was tested directly in the eccentric fixation condition. A comparison of the average hand positions produced by a single subject in the eccentric and original fixation conditions showed that the former appeared to have an effect on the beginning of the movement (Fig. 19A). Indeed, the initial acceleration was significantly greater in the eccentric fixation condition (F[3,6]=28.88, p=0.001, Fig. 19B)], although the steady state positional error and gain were similar to those observed in the original fixation condition. Furthermore, within this condition the eccentricity of the fixation target did not influence the responses. The magnitude of each measure was independent of the distance between the fixation and main targets.

In the congruent pursuit condition the target being manually tracked was projected onto the peripheral retina (as in the fixation conditions) but an appropriate eye motion signal was available. The resulting tracking responses were virtually indistinguishable from those observed in the normal condition: no significant differences were found for any of the measures when comparing the congruent pursuit and normal conditions. Figure 20 provides examples of responses produced by a single subject under each of these conditions.

The incongruent pursuit condition provided an opportunity to more directly assess the influence of extraretinal signals on tracking responses by dissociating eye and



Figure 19. A Average responses of a single subject (SD) tracking the target (dotted line) under the 'normal' eccentric fixation condition (dashed line) and the three eccentric fixation conditions (solid lines). Because of the similarity between the 10, 20, and 30cm eccentric fixation conditions they have not been separately coded. Note the greater acceleration of the hand during the initial part of the response in the eccentric fixation conditions. Target velocity is 125mm/s. **B** Group means for initial acceleration in the 'normal' fixation condition (triangles) and the 20cm eccentric fixation condition (squares). Means from the 10 and 30cm eccentric fixation conditions were similar. Error bars, 1 intersubject SD.



Figure 20. Average hand positions for a single subject (IS) tracking the target (*dotted line*) under normal (*solid line*) and congruent pursuit (*dashed lines*) conditions. The normal tracking response virtually superimposes with those produced when visually pursuing a 2nd target 10, 20, or 30cm to the left of the main target. Target velocity is 125mm/s.



Figure 21. Group means for initial acceleration of the hand during the tracking responses produced in the incongruent pursuit condition. Initial acceleration increased with the velocity of the target being visually pursued with the eyes regardless of whether the target being manually tracked with the hand moved at 62mm/s (*stars*), 125mm/s (*diamonds*), or 250mm/s (*inverted triangles*). Intersubject SD's ranged from 150-298 mm/s/s. *Error bars*, 1 intersubject SD.

hand target velocities. The most consistent effects were observed during the beginning of the response. In particular, in addition to the effect on response latency mentioned earlier this manipulation also influenced the initial acceleration of the hand. Specifically, this measure was found to be more dependent on the eye target velocity rather than the hand target velocity (F[2,4]=67.11, p=0.001, Fig. 21). In contrast to these findings, the steady state measures were found to be variable both within and between subjects. As a result no significant effects were found for either positional error or gain. The high degree of variability for these measures may be attributed to the relatively difficult task of moving the eyes at a different velocity than the hand.

3.2.3. Effects of Cerebellar Dysfunction

Examples of hand and eye tracking movements from single trials produced by a control and cerebellar subject are shown in Figure 22A and B, respectively. Whereas the control subject was able to accurately catch up to the target and subsequently match its velocity with his eyes and hand, the cerebellar subject had difficulty performing this task - producing repeated catch-up saccades and lagging behind the target with the hand. Figure 23A-C provide examples of average hand velocities from the affected and unaffected hand of a cerebellar subject and from a control subject, respectively. Note that the initial extent of overlap in the velocity traces of the affected hand is substantially less than that of the unaffected hand and in the control subject. This subjective impression was quantified using the linear regression analyses described previously to determine the separation times. The group means for this measure demonstrated that the tracking responses of the affected hand became dependent on target velocity significantly sooner than those produced with the unaffected hand or by



Figure 22. Examples from single trials of a control (A) and cerebellar (B) subject attempting to track a moving target (*dashed line*) with the hand (*thick line*) and eyes (*thin line*) under normal conditions. Target velocity is 200 mm/s.

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Figure 23. Average hand velocity traces from eight to ten trials for a single cerebellar subject performing the tracking task under normal conditions with either the affected (A) or unaffected (B) hand in response to targets moving at 50, 100, or 200mm/s. C Similar traces for a control subject.



Figure 24. A Group means for the separation time produced under normal conditions by the cerebellar subjects with the affected (*white*) and unaffected (*grey*) hands and by the controls (*black*). *Error bars*, 1 intersubject SD. *B* Linear regression analysis of the separation time - processing time relation. Each point represents a single subject performing under normal, fixation, or restricted vision conditions.



Figure 25. A Examples from individual trials of steady-state hand velocities produced by a control and cerebellar subject under normal conditions. *Dashed horizontal line* represents target velocity. **B** Group means for hand velocity variability for the cerebellar (*open circles*) and control (*solid circles*) subjects. *Error bars*, 1 intersubject SD.

the control subjects (F[2,15]=17.9, p<0.001, Fig. 24A). Furthermore, there was a significant negative linear relation (r=-0.89) between individual separation times and the corresponding processing times determined in the latency analysis discussed above (Fig. 24B). In other words, increases in the delay between the detection of target motion and the beginning of hand movement enabled the subjects to produce velocity-dependent responses much sooner.

As expected, the cerebellar subjects displayed a greater degree of variability in steady-state hand velocity than the control subjects (F[1,36]=53.4, p<0.001, Fig. 25A,B). The magnitude of hand velocity variability on individual trials was associated with the level of accuracy in the simultaneously-produced eye movements in the cerebellar subjects: regression analyses showed that for each target velocity the variability in hand velocity increased with the number of catch-up saccades (50mm/s: r=0.70; 100mm/s: r=0.78; 200mm/s: r=0.72). Figure 26A shows this effect for 100mm/s target velocity. Furthermore, perisaccadic averaging demonstrated that the saccades typically occurred on the descending limb between local maxima and minima in hand velocity (Fig. 26B). Indeed, analysis of hand gain during the critical periods leading up to and following each saccade showed that this variable was significantly larger during the presaccadic compared to the postsaccadic period (F[1,36]=13.97, p<0.001, Fig. 26C). Thus, the inaccuracy in the eye movements of cerebellar subjects appeared to contribute to the increased variability in their hand movements.

This notion was confirmed in the fixation and restricted vision conditions. In particular, hand velocity variability was substantially reduced in the cerebellar subjects when eye movements or vision of the hand was restricted (F[2,54]=9.4, p<0.001, Fig. 27A). The decreased variability in this latter condition was accompanied by more

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Figure 26. A Number of saccades produced by the cerebellar subjects plotted against hand velocity variability from individual trials during tracking under normal conditions of targets moving at 100mm/s. B Example of perisaccadic average (n=23) of hand velocity from a single cerebellar subject tracking a target moving at 100mm/s under normal conditions. Solid vertical line represents saccade onset and dashed horizontal line represents target velocity. C Group means for hand gain of the cerebellar subjects during the pre-(squares) and post-saccadic (circles) periods. Error bars, 1 intersubject SD.



Figure 27. Comparison of hand velocity variability under normal conditions (*circles*) and when eye motion (*squares*) or vision of the hand (*triangles*) is restricted on the affected (A) or unaffected (B) sides of the cerebellar subjects and in the controls (C). *Error bars*, 1 intersubject SD.

accurate eye movements: both eye error (F[2,54]=30.79, p<0.001) and the number of catch-up saccades (F[2,54]=6.94, p=0.002) decreased. These same manipulations had similar although somewhat less dramatic effects on the variability of movements made with the unaffected hand (F[2,27]=3.88, p=0.03, Fig. 27B). In contrast, the hand velocity variability of the control subjects remained relatively constant across each condition (F[2,54]=2.74, p=0.07, Fig. 27C). Restricting eye movements or vision of the hand had additional effects on the steady-state portions of the responses as shown in the second experiment. During visual fixation hand gain was substantially increased compared to the normal and restricted vision conditions (F[2,18]=6.14, p=0.009). In contrast, covering the hand with a screen caused subjects to lag further behind the target than normal (F[2,18]=8.14, p=0.003).

To more directly assess how saccadic interruptions contributed to hand velocity variability we had the control subjects complete the saccadic pursuit task. Typical responses from the normal (i.e., with smooth pursuit eye movements) and saccadic pursuit conditions are shown in Figure 28A and B, respectively. When the subject made saccades the hand lagged behind the target and tended to be more variable (t-test, p=0.003, Fig. 29A). As with the cerebellar subjects, part of this increased variability was found to be due to systematic changes in hand gain during the pre- and postsaccadic periods: hand gain was greater before than after the occurrence of each saccade (t-test; p=0.02, Fig. 29B). Thus, requiring the control subjects to make cerebellar-like eye movements led to analogous deficits in their simultaneously produced hand movements.



Figure 28. Examples from a control subject tracking the moving target (*dashed line*) with the hand (*thick line*) while making smooth pursuit (A) or saccadic (B) eye movements (*thin line*). Target velocity is 100mm/s.



Figure 29. A The group mean for hand velocity variability was greater when the control subjects performed the tracking task while making saccadic (*white*) compared to smooth pursuit (*grey*) eye movements. **B** Group means for hand gain during the pre- (*black*) and post-saccadic (*hatched*) periods for the control subjects required to make saccadic eye movements. *Error bars*, 1 intersubject SD.

3.3. Interception Task Kinematics

3.3.1. Normal Control Strategies

In the interception task the subjects were required to use information concerning the direction and velocity of the target to generate an arm movement such that the finger arrived at a position coincident with the target as it moved across the display screen. Normal subjects were able to perform this task quite well after a short period of practice. For ramp target motions performed under random conditions, the initial direction of hand movement (trajectory angle) was similar for all target velocities (Fig. 30A). This is best exemplified by the initial overlap in the trajectories in Figure 30A. In the predictable condition, by contrast, trajectory angle was more dependent on target velocity from the beginning of the movement (Fig. 30B). In particular, over the first 100ms of the movement, the mean range for trajectory angle across the different target velocities was significantly larger in the predictable condition than in the random condition (t-test, p<0.05, Fig. 31). For the step condition, this range was similar to that obtained for predictable ramps, although the steps were produced under random conditions.

To determine if interception movements were influenced by the time available for visual motion processing, subjects performed the interception task under the auditory cuing conditions described above (with target starting position determined by target velocity and cuing time). The result was analogous to that for tracking: as the subject was allowed to view target motion for longer times, the extent of overlap in the initial portion of the hand paths decreased (Fig. 32A-C). The range of trajectory angles observed across the different target velocities progressively increased from the 0 to 350 ms cue time conditions (F[2,4]=15.78, p=.013, Fig. 33). This indicates that responses



Figure 30. The initial hand path is more dependent upon target velocity in the predictable condition than in the random condition. Average hand paths from four to six trials for a single subject to targets moving at velocities ranging from 62-500 mm/s in the random condition (A) and in the predictable condition (B). These views of the hand paths are from above - the display screen is at the top of the figure, the targets are moving from left to right, the subject starts in a standard position in the lower left and moves upwards. In each graph, the response to the 62 mm/s target velocity is on the *far left* and that to the 500 mm/s target velocity is on the *far right*.



Figure 31. Group means for the range of trajectory angles averaged over the first 100ms of movement in the interception task. For ramp target motions, subjects used a larger range of trajectory angles in the predictable condition (*white*) than in the random condition (*hatched*). For step displacements (*grey*), this range was also large. *Error bars*, 1 intersubject SD.



Figure 32. The initial direction of movement is dependent upon the duration for which the subject was allowed to view target motion. Average hand paths from four to six trials to target velocities of 62-500mm/s are shown for a single subject (PVD) in conditions in which an auditory cue to respond was given coincident with the onset of target motion (A), 150ms afterward (B), or 350ms afterward (C). Figure orientation is the same as Fig. 30.



Figure 33. In the auditory cuing experiment the range of trajectory angles progressively increased as subjects were allowed to view target motion for greater periods of time. The value for this variable was smallest for the 0ms cuing condition (grey), and largest in the 350ms cuing condition (white), with the 150ms cuing condition (hatched) falling in between. Error bars, 1 intersubject SD.



Figure 34. Group means for prediction angle averaged over the first 100ms of the movement plotted as a function of target velocity. A Prediction angle decreased as target velocity increased in the random condition (*open squares*), increased as target velocity increased in the predictable condition (*solid squares*), and remained constant as step amplitude increased (*circles*). For the steps the x-axis represents step amplitude. B Results from the auditory cuing experiment. Prediction angle decreased as target velocity increased in the 0ms cue time condition (*grey inverted triangles*), remained relatively constant in the 150ms cue time condition (X's), and increased in the 350ms cue time condition (*triangles*). Error bars, 1 intersubject SD.

became more dependent on target velocity as the time available for visual motion processing increased.

Prediction angle is a measure of where the subject aims relative to the target. Like trajectory angle, it was influenced by the subject's knowledge of target velocity (Fig. 34A). Under random conditions the average prediction angle during the first 100ms of the response decreased as target velocity increased (F[3,9]=43.42, p<0.001). In the predictable condition prediction angle increased with increases in target velocity (F[3,9]=19.18, p<0.001). Thus, when subjects did not know how fast the target would be moving, they initially aimed in the same general direction. This strategy led to hand paths which were directed significantly farther ahead of slower moving targets than faster moving targets. For the step condition, in contrast, prediction angle was smaller overall and relatively constant across steps of different amplitude and to different positions in relation to the midline of the body (F[3,9]=1.75, p=0.229). In the auditory cuing experiment the relationship between prediction angle and target velocity depended on the exposure to target motion (Fig. 34B). In the Oms cue time condition, prediction angle decreased with increases in target velocity (F[3,6]=5.46, p=0.038), similar to the random condition in the initial experiment. In contrast, in the 350ms cue time condition, prediction angle increased with increases in target velocity (F[3,6]=3.43, p=0.043). For the 150ms cue time condition, prediction angle did not systematically vary with target velocity.

Average hand velocity increased as target velocity increased in both the random and predictable conditions (F[3,9]=31.17, p<0.001). A similar effect was found in the step condition as step amplitude increased. Fisk and Goodale (1985) demonstrated that reaches made to stationary targets in ipsilateral space are faster than those made into contralateral space. In this experiment, the fastest target velocities and largest target steps led to hand paths which terminated in ipsilateral space. This may have contributed to the differences in hand velocity that were observed.

For moving targets, the average deviation of the hand paths from a straight line was dependent on the predictability of target velocity, but not target velocity itself: hand paths in the predictable condition tended to be straighter $(3.5 \pm 1.35 \text{ mm})$ of deviation) than those produced under random conditions $(5.5 \pm 0.41 \text{ mm})$ (t-test, p<0.05). In the step condition, hand paths to similar endpoints as in the ramp condition had an intermediate amount of deviation $(4.8 \pm 0.25 \text{ mm})$. In the auditory cuing experiment the straightness of the hand path was dependent on the time for which the subjects were allowed to view target motion. The deviation was greatest in the 0ms cue time condition $(9.8 \pm 3.5 \text{ mm})$ and progressively decreased in the 150 (8.2 \pm 4.5 mm) and 350 (6.2 \pm 2.5 mm) cue time conditions (F[2,6]=7.33, p=0.024).

Because these movements were performed under closed-loop conditions (i.e., vision of the hand was not restricted), there was a high degree of endpoint accuracy. On average, the final finger position deviated from target position by ~10mm. For the ramp condition, the accuracy of the movements was influenced by target velocity but not the predictability of target velocity. Subjects had a tendency to undershoot the target (i.e., end up to its left) when it moved at the fastest velocity and overshoot it when it moved at the three slower velocities (F[3,9]=60.21, p<0.001). For similar terminal positions, movements in the step condition were performed with less endpoint error (4.5 \pm 0.92mm) than those in the ramp condition (14.1 \pm 2.4mm) (F[2,6]=66.51, p<0.001).

3.3.2. Role of Retinal and Extraretinal Signals

Although the interception task was not used in the second experiment, the restricted vision and fixation conditions were repeated in the third experiment in which this task was used. Thus, the results reported in this section are from the control subjects' interception responses produced in the third experiment. Requiring subjects to visually fixate during the tracking task resulted in an increase in hand gain. In other words, hand velocity was greater than or overestimated target velocity during the steady-state portion of the response. This overestimation of target velocity was also apparent in the interception task when eye movements were restricted. Figure 35A and B provide examples of averaged hand paths produced under the normal and visual fixation conditions to targets moving at 100 and 200mm/s, respectively. Notice that during visual fixation the subject terminated the movement at a position further to the right (i.e., ahead of) the target. This trend was confirmed for the group in the form of an increase in the magnitude of constant endpoint error (F[2,18]=14.74, p<0.001, Fig. 35C).

Restricting vision of the hand during the tracking task caused subjects to lag behind target position yet still allowed them to match target velocity. Because this effect was restricted to the ongoing positional matching of the moving target, it was difficult to predict what changes, if any, restricting vision of the hand would have on the interception task. Upon analysing the data the most obvious effect appeared to be an increase in the variability of endpoint error. In other words, the subjects on average were able to reach for the target accurately. However, the variable error of their reaches was significantly increased (F[2,18]=4.88, p=0.02). An example of this effect is shown for a single subject in Figure 36A and B, whereas the group means for



Figure 35. Effects of visual fixation on interception task responses. Averaged hand paths from eight to ten trials from a single subject (GMJ) to targets moving at 100mm/s (A) or 200mm/s (B) under normal conditions (*solid line*) or while visually fixating (*dashed line*). Figure orientation the same as Fig. 30. C Group means for absolute endpoint error plotted as a function of target velocity from the normal (*grey circles*) and fixation (*white circles*) conditions. *Error bars*, 1 intersubject SD.



SC/

Figure 36. Effects of restricting vision of the hand on interception task responses. Hand paths from individual trials (n=10) for a single subject (GMJ) performing under normal (A) and restricted vision (B) conditions. Target velocity is 200mm/s. Figure orientation the same as Fig. 30. C Group means for variable error at the end of the movement plotted as a function of target velocity from the normal (grey circles) and restricted vision (white circles) conditions. Error bars, 1 intersubject SD.

variable error are shown in Figure 36C. One possible explanation for the increase in variable error may be related to the fact that the subjects were unable to make visually-based corrections during the final approach to the target with their hand under restricted vision conditions.

3.3.3. Effects of Cerebellar Dysfunction

Figure 37A-C displays average hand trajectories to targets moving at each velocity during interception movements made by a cerebellar subject with the affected and unaffected hand and by a control subject. As with the tracking responses, the extent of initial overlap in the trajectories appeared to be substantially reduced in the affected hand. Quantitatively, when the cerebellar subjects used their affected hand initial prediction angle increased with target velocity (F[2,17]=3.76, p=0.04, Fig. 37D). This velocity-dependence suggests that, as in the tracking task, the cerebellar subjects used the delay in processing time to more fully determine and use information related to the velocity of the target. In contrast, initial prediction angle remained relatively constant across target velocities for the control subjects and when the unaffected hand (F[2,15]=6.28, p=0.01). This appeared to be an appropriate strategy given the fact that movement times were also slower in this hand: if more time is required to reach the target, then one alternative is to initially aim further ahead.

The variability in movement direction was significantly larger in the affected hand than in the control subjects (F[1,30]=43.85, P<0.001, Fig. 38A). As with the tracking task, part of this increase appeared to be related to inaccuracies in the simultaneously produced eye movements. In particular, prediction angle was positive



Figure 37. Average hand paths from eight to ten trials to each target velocity on the affected (A) and unaffected (B) sides of a single cerebellar subject (LB) and from a control subject (YO) (C) performing the interception task under normal conditions. Figure orientation the same as Fig. 30. D Group means for initial prediction angle from the normal condition for the affected (*open circles*) and unaffected (*grey circles*) sides of the cerebellar subjects and from the controls (*black circles*). Error bars, 1 intersubject SD.



Figure 38. A Group means for movement direction variability for the affected hand of the cerebellar subjects (*open circles*) and in the controls (*solid circles*). B Prediction angle of the affected hand during the pre- (*squares*) and post-saccadic (*circles*) periods. Dashed horizontal line indicates prediction angle for movements directed straight at the target. Error bars, 1 intersubject SD.



Figure 39. Comparison of movement direction variability under normal conditions (*circles*) and when eye motion (*squares*) or vision of the hand (*triangles*) is restricted on the affected (A) or unaffected (B) sides of the cerebellar subjects and in the controls (C). *Error bars*, 1 intersubject SD.

during the period leading up to each saccade and negative afterwards (F[1,24]=5.01, p=0.03, Fig. 38B). In other words, the cerebellar subjects alternately aimed ahead then behind the target in relation to the occurrence of a saccade. As expected, restricting eye motion led to a substantial reduction in movement direction variability in the affected (F[2,54]=3.21, p=0.05) and unaffected (F[2,18]=3.53, p=0.05) hand trajectories of the cerebellar subjects but not in the control subjects (F[2,54]=0.99, p=0.38, Fig. 39). In contrast, restricting vision of the hand did not have any significant impact on this measure in either group of subjects. This may be due to the fact that, unlike in the tracking task, eye movement accuracy was not altered under these conditions (F[2,27]=0.11, p=0.89). Finally, the other effects that these manipulations had on the interception responses of the control subjects reviewed above were also apparent in the cerebellar subjects. In particular, requiring the subjects to visually fixate led to endpoint errors that were substantially farther ahead of the target than normal; and restricting vision of the hand caused an increase in the variability of endpoint error.

3.4. Oculomotor Performance

3.4.1. Effects of Cerebellar Dysfunction

Although eye movements were measured in the second experiment the purpose of doing so was to insure that the oculomotor output was appropriate for specific conditions. In particular, it was important that subjects not move the eyes in the fixation conditions and move the eyes at the right speed in the incongruent pursuit conditions. Other than these criteria, however, the eye movement records were not analysed in any detail in this experiment and, therefore, will not be reported on here. In contrast, in the third experiment the effects of producing simultaneous hand


Figure 40. The effects of producing hand movements on the amount of error in the oculomotor output. Group means for eye error are shown from the tracking (A) and interception (B) tasks for the cerebellar subjects producing eye movements in isolation (*open circles*) or in conjunction with an affected (*open squares*) or unaffected (*grey squares*) hand movement as well as for controls making eye movements only (*solid circles*) or combined eye-hand movements (*solid squares*). For the sake of clarity, error bars have not been included. Intersubject variability ranged from 0.2-5mm.

movements on the oculomotor output and how these effects changed with cerebellar dysfunction was of central concern. Therefore, the eye movement records from this experiment were analysed to assess the degree of accuracy and number of saccadic interuptions. The influence that hand movements had on the oculomotor system was assessed by comparing the accuracy of eye movements generated in isolation with those produced in conjunction with hand movements in each task. Figure 40 demonstrates that in the tracking task this influence was positive for the control subjects and when the cerebellar subjects used their unaffected hand: eye movement error decreased when the hand was also used to track the target (F[1,42]=16.75, p<0.001, Fig. 40A). This was also the case for the number of catch-up saccades (F[1,42]=8.40, p=0.006). In contrast, when the cerebellar subjects used their affected hand the simultaneously produced eye movements became worse: both eye movement error (F[1,36]=36.71, p<0.001) and the number of saccadic interruptions (F[1,36]=7.65, p=0.009) increased. In the interception task, in contrast, the accuracy of the eye movements was not influenced by the simultaneously produced hand movement (Fig. 40B). Thus, eye movement error was larger overall in the cerebellar subjects than in the controls (F[1,50]=19.53, p<0.001) but did not change with the addition of either a poorly produced or accurate interception response.

CHAPTER FOUR: DISCUSSION

In the what follows the changes in response latency and movement kinematics that occurred in each task as a result of the various conditions are discussed. In particular, the contributions made by visual motion processing, and retinal and extraretinal signals to the tracking and interception responses are outlined. In addition, the hypothesis that interactions between the oculomotor and manual motor systems can account for some of the discoordination observed in cerebellar subjects is also put forth. Finally, the possible sites within the CNS at which these processes may be taking place are addressed.

4.1. Response Latency

4.1.1. Normal Control Strategies

The finding that response latency decreases toward an apparent asymptote as target velocity increases is comparable to results from previous tracking studies (Beppu et al. 1984), psychophysical experiments investigating the detection of target motion (Tynan and Sekuler 1982), as well as for eye movements in rabbits (Collewijn 1972) and humans (Carl and Gellman 1987; Gellman and Carl 1991). Interestingly, this relationship between target velocity and latency is also apparent for the onset of cell activity in area MT in primates (Movshon et al. 1990). Thus, the behavioral results appear to have their basis in the neuronal limits of areas involved in visual motion processing. For the optokinetic response in the rabbit, Collewijn (1972) demonstrated that a threshold distance model could accurately account for the relationship between target velocity and response latency. Indeed, Smeets and Brenner (1994) have demonstrated that such a model is more appropriate than one based on target velocity

for conditions similar to those used in the present experiments. By using Collewijn's model (see Methods), it was possible to separate out the contributions of the threshold distance and the processing time to response latency.

The results of the present study showed that the different conditions led to changes in each component of response latency. Increases in the magnitude of both the threshold distance and processing time accounted for the inflated latencies in the interception task. Providing a fixed reference marker, however, resulted in a decrease in the threshold distance for this task to a value comparable to that obtained in the tracking task. Thus, it is suggested that the decreased threshold distance during tracking responses may be an artefact arising from the task requirement that the subject be pointing at the target prior to the movement. Under such conditions, the subject appears to make use of visual and proprioceptive information related to the position of the arm to facilitate the detection of target motion onset. The presence of a reference marker in the interception task provided an analogous visual cue that led to the reductions observed in the threshold distance. The processing time, on the other hand, was not influenced by this manipulation. Rather, it remained inflated relative to the tracking task. This may reflect the increased computational difficulty in plotting the course of an interception trajectory compared with simply catching up to a target. In particular, the interception task requires coordinated rotations about the elbow and shoulder joints to project the hand from the starting position to the display screen with a trajectory that results in a high degree of terminal accuracy. In contrast, in the tracking task, the computational load is reduced substantially because the hand is already positioned at the display screen and the movement initially requires rotation about the shoulder joint only.

The predictability of target velocity also had an influence on response latency. In particular, latency was reduced in both tasks if the velocity of the target remained the same from trial to trial. This reduction was due entirely to a decreased processing time. This result is analogous to those of Rosenbaum (1980) who demonstrated that the latencies of pointing movements to static targets are reduced if subjects are given cues prior to the response regarding which arm is to be used or the direction or extent required to reach the target. By keeping target velocity constant for a series of trials, subjects were provided with relevant information that could be integrated into the planned response before the onset of target motion. In this way, it would not cause additional delays during processing time as occurred when target velocity was randomized across trials.

The purpose of the stepramp experiment was to test the threshold distance model. The model predicts that if target motion begins with a step, latency should be reduced. More specifically, if:

step amplitude > threshold distance, then threshold time = 0, and

latency = processing time.

The subjects who participated in the stepramp experiment had a distance threshold of 3.3mm and a processing time of 186ms. As the model predicts, a test with a step of 5mm gave a constant latency (~185ms) for all velocities. In contrast, if:

step amplitude < threshold distance, then

latency = (threshold distance - step amplitude) / target velocity + processing time. Therefore, for the or the 2mm step, therefore, the model predicts latencies of 207, 196, and 191 ms for target velocities of 62, 125, and 250mm/s, respectively. These values provided an accurate estimate of the actual data. Remarkably, the modified threshold distance in the 2mm stepramp condition was in fact equal to the difference between the normal threshold distance and the amplitude of the step: 3.3mm - 2mm = 1.3mm. The fact that latency was still dependent upon target velocity in this condition also shows that the result for the 5mm step was not caused by the discontinuity of the step itself.

This model has also been applied to eye movement latencies in previous studies. In particular, for smooth pursuit the threshold distance was found to be 0.5mm and the processing time was 94ms (Carl & Gellman 1987); whereas for catch up saccades the corresponding values were 1.7mm and 180ms, respectively (Gellman & Carl 1991). These values are considerably smaller in magnitude than those attained in the present study for hand movements. The disparities in processing time are not surprising given the inertial differences between these two effectors. In particular, the eye has a much smaller mass, and thus can be more easily moved upon appropriate muscle activation. In fact, it has been shown during combined eye-hand movements to static targets that the onset of EMG activity is nearly synchronous in each motor system; whereas the overt change in eye position occurs significantly sooner than that of hand position (Bigeur et al. 1982).

The differences in the threshold distance are not as easily explained. If this measure reflects information derived from cortical areas involved in visual motion processing then the large disparities observed for this value in smooth pursuit, saccadic, and manual responses suggest that each system sets its own threshold. This notion appears to be consistent with the functions of the different responses. For example, the goal of smooth pursuit is to maintain a steady foveal image. Thus, any movement of

the image on the fovea requires a response and the threshold is correspondingly small. For the other systems, in contrast, small target movements can be tolerated. Taken together, these results imply that each system follows qualitatively similar rules for responding to target motion, although they do not appear to share a trigger.

4.1.2. Role of Retinal and Extraretinal Signals

The relationship between target velocity and response latency held under conditions in which eye movements or vision of the hand were restricted. This was true for both the tracking and interception tasks. In addition, these manipulations caused an increase in latency compared to the normal conditions in which vision of the hand and unrestricted eye movements were allowed. This increase was found to be due to an inflated processing time. Thus, subjects required more time after detecting the onset of target motion to prepare their responses when they could not see their hand or were not allowed to move their eyes. Similar increases have been shown to occur during these conditions when reaching to static targets (Prablanc et al. 1979a). These authors suggested that visual and proprioceptive information concerning the initial position of the limb must be matched to rapidly complete the processing required to generate the appropriate movement of the arm. When the visual signals are removed, the subject is forced to rely on proprioceptive information alone, and the time required to process the response is increased accordingly. In contrast, the increase in latency when eye movements are restricted was suggested to be due to delays associated with determining the position of the target using only the peripheral retina. While this hypothesis may be satisfactory for stationary targets, it can not explain the analogous result with moving stimuli because under these conditions the target image has not traversed the

distance to the peripheral retina until well into the response. Alternatively, it may be the actual act of visual fixation, or the suppression of eye movements, that results in the observed increases in hand latency. Indeed, the activity of cells in the rostral pole of the superior colliculus has been shown be related to such fixation responses (Munoz & Wurtz 1993a,b). These "fixation" cells have their effect by inhibiting the activity of the brainstem neurons involved in the generation of eye movements. These inhibitory influences may also interact with centres involved in the control of limb movement (see below) to cause the increases in latency that are observed.

As mentioned above, only the processing time was influenced by the restrictions imposed on vision of the hand or eye motion. In contrast, the values for the threshold distance remained relatively consistent. Most importantly, restricting vision of the hand in the tracking task did not cause any changes in this measure. This result is somewhat surprising in light of the importance of visual references in detecting the onset of target motion. In particular, one would expect the threshold distance to increase when subjects could not use the sight of the hand as a stationary landmark to compare any movements of the target. The fact that the threshold distance remained normal under these circumstances suggests that the remaining source of relevant information derived from arm proprioceptive signals was sufficient for this purpose. Indeed, such signals have been shown to contribute to the accurate spatial localization of stationary targets (Levine & Lackner 1979).

4.1.3. Effects of Cerebellar Dysfunction

Damage to the cerebellum has long been known to cause prolonged response latencies (Holmes 1939). This deficit has been thought to be due to a disfacilitation of motor cortical activity leading up to the response resulting from the loss of cerebellar input to this area; or, alternatively, to a disruption in cerebellar-mediated anticipatory postural adjustments (Trouche and Beaubaton 1980). More recently it has been suggested that part of this increased latency may be due to a deficit in the ability of cerebellar subjects to integrate sensory information related to the spatial attributes of the target with the required motor output (Brown et al. 1993). The latency analysis employed in the present study confirmed this notion by showing an increase in both the threshold distance and processing times in subjects with cerebellar damage. Thus, in addition to taking longer to prepare the required response, the cerebellar subjects also had more difficulty in initially determining the onset of target motion. Furthermore, this latter deficit influenced any output that depended on visual motion processing: response latencies of eye movements generated in isolation and hand movements on the unaffected side were also increased, due solely to an elevated threshold distance. These results are reminiscent of the findings of Ivry and Deiner (1991) who showed using psychophysical techniques that cerebellar subjects have difficulties in velocity discrimination tasks. Thus, in general it appears that the cerebellum may be involved in processing information related to target motion for use in both perceptual and motor tasks.

The increase in the latency of the eye movements of the cerebellar subjects when produced in conjunction with an affected hand movement confirms and extends the recent findings of Brown and coworkers (1993). It suggests that even the earliest component of the oculomotor output can be negatively influenced by the processing required to generate a simultaneous hand movement. Thach and colleagues (1992) have speculated that this type of effect may be the result of a more general deficit in which complex multijoint movement sequences incorporating one or more different effectors are preferentially disrupted by cerebellar dysfunction, while simple movements remain relatively unimpaired. With this in mind it is interesting to note that the response latencies of the hand movements were actually shorter if the eyes were also used to follow the target. As discussed above, however, this may be due to inhibitory influences resulting from the act of keeping the eyes fixated.

4.2. Movement Kinematics

4.2.1. Normal Control Strategies

Changes in the magnitude of hand velocity in the tracking task and the direction of movement in the interception task depended on the predictability of target velocity. In the predictable condition, hand velocity and direction of movement depended on target velocity from the beginning of the response. In the random condition, in contrast, the responses were only weakly influenced by target velocity for the initial 60-100 ms. This is similar to findings on the initiation of smooth pursuit (Carl and Gellman 1987; Lisberger and Westbrook 1985). It suggests that, under random conditions, the movement is initiated before visual motion processing is complete. As a result subjects initially produce a "default" response with a magnitude that is intermediate to those that are required for each target velocity (Cordo and Flanders 1989; Flanders and Cordo 1989). When target velocity is predictable, however, an appropriate response can be prepared in advance and released as soon as the target motion is detected.

The auditory cuing experiments allowed the time course of appropriate response specification to be determined by manipulating the time available for visual motion processing before the onset of the hand movement. In both tasks, the duration for which the responses overlapped progressively decreased as more time was available to view target motion. With ~400ms of viewing time (350ms cue time), responses were similar to those produced when target velocity was predictable. When this value was reduced to ~200ms, there was still overlap in the responses (i.e., a default response was initially produced). These results suggest that, when target velocity is unpredictable, subjects require between ~200-400ms to determine target velocity and use it to produce an appropriate response. This was similar to the time required when the onset of target motion was the cue to respond (latency: ~210ms + overlap: ~77ms = 287ms).

Similar results have been obtained for the build-up of isometric force at the elbow (Favilla et al. 1989; Hening et al. 1988), multi-joint reaching movements to stationary targets (van Sonderen and Denier van der Gon 1991), and visually-guided saccades (Stanford et al. 1990). In each of these studies, external cues were used to cause subjects to begin their responses at various times in relation to the change in target position. When the cue caused the response to occur earlier than normal, subjects produced "default" responses that were intermediate to the range of presented target positions. However, in trials in which more time was available to process information about target position, subjects produced progressively more appropriate responses. For these step stimuli the minimal amount of time required to produce the correct response was on the order of 150-200ms. A similar value (140ms) is obtained for correctly specifying the amplitude of the second of two saccades produced in a double-step paradigm (Gellman and Carl 1991). The present findings suggest, therefore, that visual motion processing takes longer than determining the spatial location of a stationary target.

4.2.2. Role of Retinal and Extraretinal Signals

By covering the hand with a screen during the tracking task, the retinal signal associated with the visual perception of hand position relative to the target was removed. Under such conditions, subjects were forced to rely on the remaining sources of feedback: extraretinal signals concerned with eye motion, retinal signals concerned with target image motion, and proprioceptive and/or efference copy information from the moving limb. The inability of subjects to catch up to the target and the subsequent positional errors produced during the steady state portion of the movement suggest that these signals were not sufficient to allow accurate position tracking. In contrast to this difficulty, subjects were able to produce steady state hand velocities that closely approximated target velocity. Allowing vision of the hand only at the beginning of the response led to systematic decreases in the degree of positional error. Specifically, the amount by which the subject lagged behind the target was dependent upon the distance for which the hand was initially visible: the greater this distance, the smaller the error.

Taken together, these results imply that the retinal signal that provides information about the initial position of the hand relative to the target is required to accurately catch up to the target. In contrast, the extraretinal signal concerned with eye velocity combined with proprioceptive information from the moving limb is sufficient to accurately match target velocity, regardless of whether vision of the hand is available. Given the accuracy of hand velocity, it is somewhat surprising that hand position was not also accurate. In theory, the eye velocity signal produced during the pursuit response could be integrated to yield eye position. Assuming the eye is accurately tracking the target, this signal would provide an analogue to target position that could be used by the manual motor system to update hand position after comparison with proprioceptive information. The present results demonstrate, however, that this is not the case. In fact, it has been shown previously that target position is less accurately reproduced by the hand when specified by smooth pursuit than by saccadic eye movements (Festinger and Canon 1965; Honda 1990).

In contrast to the results from the tracking task, when vision of the hand was restricted in the interception task only the variability of the endpoint error increased. The findings from both tasks, however, are similar to those from studies investigating reaching movements directed towards static targets (Prablanc et al. 1979a, b). In particular, such movements contain larger and more variable positional error when subjects can not see the hand. In addition, allowing vision of the hand prior to the response leads to a substantial reduction in the error. Thus, retinal information related to the position of the limb in space must subserve analogous processes during each of these tasks. Taken together, these findings suggest that this process is related to the visual disparities between the positions of the target and the hand. In particular, it appears that the CNS makes use of signals associated with the retinal locations of the images of the target and the hand to initially prepare a response or modify an ongoing one. Indeed, Chua and Elliott (1993) have recently been able to demonstrate that the kinematic adjustments associated with trajectory modifications under normal conditions were substantially reduced in number when vision of the hand was unavailable. That this process is related to positional information is supported by the fact that target velocity was accurately reproduced in the tracking task despite the absence of the visual signal associated with the spatial attributes of the limb.

When visually fixating, the perception of target motion must be extracted from retinal image motion. This leads to an overestimation of target velocity termed the Aubert-Fleischl phenomenon (Dichgans et al. 1975). The present results show that this perceptual illusion also influences the manual motor system. In particular, the steady state gain of the tracking movements produced in the fixation conditions was significantly greater than unity. Two pieces of evidence suggest that this effect was confined to the peripheral visual field. First, the initial acceleration was similar to normal levels when the image of the target started on the fovea, but the subsequent steady state gain was substantially increased. Second, when the image of the target started on the peripheral retina both the initial acceleration and steady state gain were above normal levels. The overestimation of target velocity in the peripheral retina led to similar effects in the interception task. In particular, subjects typically ended their trajectories significantly further ahead of the target when visually fixating compared to when they were allowed to follow the target with their eyes. Analogous findings have been demonstrated for reaching movements made to stationary targets (Bock 1986; Delreux et al. 1991; Prablanc et al. 1979a).

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This result is inconsistent with the findings of Tynan and Sekuler (1982) who showed in a psychophysical task that the estimates of perceived velocity were less for peripherally- compared to centrally-viewed targets. However, this discrepancy may be explained by the fact that different visual stimuli were used in each study. Tynan and Sekuler (1982) used spatially random dots moving upwards in thin vertical strips on the face of a cathode ray tube, whereas a single spot of white light moving horizontally was used in this study. The present results are consistent with the notion that an extraretinal signal concerning eye velocity is not only sufficient but required to accurately reproduce target velocity with the hand. Without such a signal the subjects were forced to rely on the inaccuracy of peripheral retinal image motion to determine target velocity. The advantages of using an eye velocity signal for this purpose were confirmed by having subjects perform the tracking task under congruent pursuit conditions. In particular, although the target and hand were being viewed by the peripheral retina, the accuracy and gain were normal. In other words, furnishing the subject with an eye velocity signal was sufficient to produce an accurate tracking response, even though this signal was not accompanied by the normal foveally-obtained visual information about the position of the hand relative to the target.

The results from the incongruent pursuit condition demonstrated that eye motion signals can have a significant impact on the initiation of tracking responses generated with the hand. Both the latency and initial acceleration of the hand were more appropriate for the velocity of the target being visually pursued rather than that of the target being manually tracked. This suggests that the processing required to generate smooth pursuit eye movements may be shared by the manual motor system. In particular, retinal information about target velocity and extraretinal information about eye velocity may influence the magnitude of the descending command to the limb. As a result the initial response characteristics of the hand movement are dependent on the simultaneously produced eye movement. Analogously, eye motion information appears to influence the direction of hand movement during reaches made to stationary targets (Frens and Erkelens 1991). Alternatively, these results may be explained by the limits in attentional capacity during tasks that require two different types of responses (i.e. moving the eyes and the hand at different speeds). However, such limitations should effect both motor systems in a stochastic manner. In other words, one would predict that the accuracy of the eye and limb movements would be decreased and more variable. The fact that the incongruent pursuit condition led to systematic changes in

the response characteristics of the hand only therefore argues against an explanation that invokes attentional limitations.

The results from the restricted vision condition imply that extraretinal input also influences the ongoing tracking response. If this is the case then one would have expected steady state gain to vary as a function of the eye/hand target velocity ratio in the incongruent pursuit condition. For example, when the eye target velocity was 250mm/s and the hand target velocity was 62mm/s steady state gain should have approached 4. In contrast, when these velocities were reversed steady state gain should have been .25. Despite the variability in the steady state measures these theoretical values were never reached, even on individual trials. Thus it appears that subjects chose to ignore the inappropriate eye velocity signal during the latter portions of the movement; relying instead on feedback from retinal and limb proprioceptive sources in their attempts to accurately reproduce hand target velocity.

In summary, the results from these experiments demonstrate that the manual motor system uses both retinal and extraretinal signals when attempting to accurately track or intercept a target moving at constant velocity. Under normal closed-loop conditions (i.e., both hand and target visible) retinal information concerning disparities between hand and target motions can be used to make adjustments to the hand trajectory to allow an accurate response. In addition, when the head is free to move, signals associated with such movement (from proprioceptive sources in neck muscles and vestibular information) may also contribute to the accuracy of the hand movement. The results of the present study, however, have shown that in the tracking task retinal information related to hand motion was necessary only during the beginning of the response. In particular, subjects required knowledge of the initial position of the hand

relative to the target to accurately catch up to and match target position. However, this information was not required to match target velocity, suggesting that limb proprioceptive and eye motion signals were sufficient for this purpose. As a result, in the partially restricted vision condition, if subjects were given enough time to view the initial motion of their hand relative to the target, they were subsequently able to match both target position and velocity despite the fact that they could no longer see their hand. Thus, while it is likely that visual closed-loop processing is the preferred means by which humans are able to accurately track a moving target with the hand, the present results demonstrate that the system can still accomplish this task with only initial retinal information, and supplementary limb proprioceptive and extraretinal information. By comparison, in the interception task retinal information related to the position of the limb appears to be used to make on-line corrections to allow more consistent response trajectories: removing this signal causes a significant increase the variability of the endpoint error. The influence of extraretinal signals on the ability of the manual motor system to produce target-velocity-appropriate responses was confirmed in the fixation conditions. In particular, when eye movements were restricted subjects were forced to rely on retinal image motion to determine target velocity. This resulted in an overestimation of target velocity as evidenced by a significantly increased steady state gain in the tracking task and substantial past pointing in the interception task. Finally, by dissociating eye and hand target velocities it was possible to show that the processing involved in the generation of smooth pursuit eye movements influenced the initial aspects of a simultaneously produced tracking movement. In each of these cases the contribution of head motion was

4.2.3. Effects of Cerebellar Dysfunction

Damage to the cerebellum results in a variety of motor deficits. As discussed in the section on response latency one of these deficits is increased delays between the detection of target motion and the onset of the response with the affected hand. One advantage of this situation is that the cerebellar subjects were exposed to target motion for a greater period of time before their tracking or interception movement began. As a result, these responses were initially more appropriate than those produced with the unaffected hand or by the control subjects. In a sense, this is similar to the results observed in the auditory cuing conditions in the first experiment. In particular, when more time was given to process information related to the spatial attributes of the target the trajectory of the subject's response becomes appropriate much sooner. This implies that under normal conditions a finite amount of time is required to determine target velocity. Indeed, the y-intercept of the line of best fit for the relation between the processing and separation times (Figure 3.23B) provides an index for this variable: 273ms. As one would expect, this value is remarkably similar to the delay observed in normal subjects between the onset of target motion and the beginning of velocity-dependent responses (287ms).

Unfortunately, this appears to be the only advantage of damage to the cerebellum. Indeed, the main finding of the third experiment was that the kinematic output of the eye and hand motor systems interacts during visuomotor tracking and interception tasks. Furthermore, in subjects with cerebellar dysfunction the output of each system adversely affected that of the other. In particular, in each task the hand trajectories of the cerebellar subjects were influenced by the inaccuracies in the simultaneously produced eye movements. Hand gain and prediction angle were

significantly larger during the presaccadic compared to the postsaccadic period. These systematic changes are consistent with an overestimation of target velocity in the peripheral visual field as occurred in the visual fixation conditions discussed above. It is speculated that the low gain of the smooth pursuit system in the cerebellar subjects mimics the effects of visual fixation in that the image of the target repeatedly moves away from the relatively stationary fovea following each catch-up saccade. Thus, the velocity of the target will appear to increase as it moves further into the peripheral visual field during periods of smooth pursuit. The response with the hand will reflect this overestimation until a saccade is generated and the image of the target that is flashed just before or during the initial aspects of a saccade is similarly overestimated (Honda 1990; Dassonville et al. 1992).

The results from the other conditions confirm this notion. When the inaccurate eye movements were restricted during visual fixation hand trajectory variability was decreased. If vision of the hand was restricted during the tracking task the eye movements of the cerebellar subjects improved and, as a result, hand velocity variability decreased. In contrast, in the interception task the eye movements did not improve under these conditions and, as expected, movement direction variability remained unchanged. These effects were also observed in the unaffected hand of the cerebellar subjects with unilateral damage. This suggests that the inaccurate eye movements influenced even the clinically normal hand. Finally, requiring the control subjects to make successive saccades during the tracking task resulted in increased hand velocity variability. More importantly, as in the cerebellar subjects this increased variability was shown to be partly due to systematic changes in hand gain during the perisaccadic period. Taken together, this evidence strongly suggests that information derived from eye motion (and the resulting changes in retinal stimulation) can have a significant impact on simultaneously produced hand movements. Furthermore, if this information arises from poorly coordinated or inaccurate eye movements then it will adversely influence the hand movements, as recently shown for patients with congenital nystagmus (Beddell & Currie 1993) and trigeminal-oculomotor synkinesis (Lewis & Zee 1993).

Analysis of the oculomotor performance demonstrated that this influence was bidirectional. In particular, during the tracking task the quality of the hand movements had an effect on the accuracy of the eye movements. If the hand movements were smoothly coordinated and contained a low degree of variability then the simultaneously produced eye movements were more accurate than those generated in isolation. This was the case for the control subjects and when the cerebellar subjects used their unaffected hand. In contrast, if the hand movements were highly variable and contained large errors then the eye movements actually became worse, as occurred when the cerebellar subjects used their affected hand. Thus, proprioceptive and/or efference copy information derived from the movement of the hand appeared to have access to and was able to influence the oculomotor system (Gauthier et al 1988). This effect, however, was task-dependent: hand movements generated to intercept the target neither increased nor decreased the accuracy of simultaneously produced eye movements. Thus, hand movements can only have an impact on oculomotor output if the responses produced by each system are analogous. This criterion was satisfied in the tracking task in that the trajectory of the hand closely matched that of the target and the eyes. In contrast, in the interception task the hand movement bore no close relation to the

oculomotor output.

Eye movement accuracy may have also been influenced by vision of the hand. In particular, the increased saccadic frequency in the smooth pursuit response of the cerebellar subjects during the tracking task may have been partly a consequence of the subjects' attempts to make visually-based corrections for the error between the target and the hand. The example shown in Figure 3.21B certainly supports such a notion: the subject made a series of catch-up saccades that resulted in alternate foveation of the target and hand. When the hand was restricted from vision or not used to track the target there was no need to make such visual comparisons and the eye movements were improved accordingly. In contrast, in the interception task the hand was not in close proximity to the target until the terminal phase of the response. As such, making saccades back and forth from the target to the hand would have been an inappropriate strategy and, in fact, was never used. Indeed, when vision of the hand was restricted in this task the occurrence of saccadic interruptions remained unchanged.

Taken together, this evidence suggests that information associated with the movement of the eyes and hand interacts at one or more levels in the CNS. There are several potential locations where this may occur. As mentioned above, the influence that each of these systems has on the other may be partly mediated by the changes in retinal stimulation that are a consequence of their outputs. This notion is supported at a neurophysiological level by studies which have shown that the activity of some visually-sensitive neurons in the extrastriate cortical areas comprising the dorsal visual processing stream is modulated by movements of the eyes (Anderson et al. 1985; Duhamel et al. 1992), the eyes and head (Their and Erickson 1992), or the hand (Taira et al. 1990). Indeed, on the basis of this and other evidence Goodale and Milner (1992;

Milner and Goodale 1993) have suggested that the processing that takes place in the dorsal stream is used for the on-line visual control of goal-directed motor output. This control is likely mediated by corticocortical connections with the premotor cortex (Cavada and Goldman-Rakic 1993), an area that has recently been shown to contain cells whose limb movement related activity is modulated by gaze direction (Boussaoud 1993); and/or corticopontine projections from the parietal cortex to the pons and subsequently to the cerebellum (Glickstein et al. 1985). In the context of the present findings, these visual responses would presumably be degraded by the deficient oculomotor output of the cerebellar subjects. As a result, any other output that relies on the stable visual information normally supplied by these neurons would also suffer.

Another site at which interactions between eye and hand motor output may occur is in the superior colliculus. Traditionally, this structure is thought to be involved in the sensorimotor transformation required to generate saccadic eye movements (Sparks and Mays 1990). More generally, it has been shown to play a role in orienting responses produced by coordinated movements of the eyes and head (Guitton 1992). The contribution of the superior colliculus to hand movements is less well understood. A recent report demonstrated that there are cells in this structure whose activity is related to hand movements in primates (Werner et al. 1993). These cells could modulate the output of the manual motor system via tectospinal projections to the C3-C4 propriospinal system which has been shown to play a vital role in reaching movements of the forepaw in the cat (Alstermark et al. 1981; Illert et al. 1978). Furthermore, if these cells are located in the same layer of the superior colliculus as those involved in oculomotor control then the potential exists for the occurrence of interactions. Indeed, multisensory integration is known to occur in single cells located in the deep layers of the superior colliculus (Peck et al. 1993; Stein et al. 1993). Therefore, it would not be surprising to find similar integration at the level of motor output.

A final site at which interactions between eye and hand movement signals may occur is in the cerebellum itself. This structure receives proprioceptive information arising from limb movements via the dorsal spinocerebellar tract, as well as a signal likely carrying efference copy information from descending corticospinal tract collaterals (Bloedel and Courville 1981). In addition, visual information from cortical areas involved in motion processing reaches the cerebellum via corticopontine pathways (Glickstein et al. 1985). The cerebellum subsequently has projections to brainstem and cortical areas that are either directly or indirectly involved in the efferent control of manual and oculomotor output. This combination of inputs and outputs makes the cerebellum ideally suited for influencing ongoing eye and hand movements in a potentially interactive manner. For interactions to occur, however, the separate inputs must converge onto specific cells or groups of cells. This restriction makes it unlikely that the cerebellar cortex itself is the site of interaction because activity related to oculomotor output is generally confined to the flocculus, paraflocculus, and vermis; whereas that related to manual output occurs mainly in the lateral and intermediate hemispheres. There is some overlap in the intermediate cerebellum where the activity of individual cells is related to either eye or hand movements, but not both (Marple-Horvat and Stein 1987; 1990). The converging projections from the cerebellar cortical areas onto the deep nuclei, however, make these latter structures more suitable candidates for sites of interaction. The dentate nucleus in particular has been shown to contain cells that respond to both eye and hand movements (MacKay 1988).

Furthermore, lesions to the dentate result in temporal uncoupling between manual and oculomotor output (Vercher and Gauthier 1988). Taken together, these results suggest that the dentate may be involved in the "coordination control" between eye and hand movements as postulated by Vercher and Gauthier (1988).

The fact that the eye and hand movements of the cerebellar subjects used in this study still influenced each other suggests that this structure in general and the dentate nucleus in particular can not be the sole site at which interactions occur. Rather, it is likely that each of the areas cited above contributes in a significant way to the types of responses observed. In particular, the interactions occurring at a visual-motor level appear to be taking place in the extrastriate cortical areas that compose the dorsal stream of visual processing. In contrast, the more direct influences between the outputs of each system may be occurring in the premotor cortex or subcortical structures such as the superior colliculus and cerebellum - that is, structures that are involved either directly or indirectly in generating and/or modulating movements of the eyes and hands. Further neurophysiological studies are required before this question can be answered more clearly. The fact remains, however, that because of these interactions subjects with cerebellar dysfunction display a significantly larger degree of discoordination during combined eye-hand tasks than when each of these motor systems are used in isolation.

4.3. Conclusions

The results of these experiments suggest that motor planning progresses through a series of stages when initiating a response to a moving target. First, target motion is detected after a threshold distance is crossed. Subsequent to this there is a delay required to prepare and produce the response. If target velocity is determined prior to the end of this stage the response is appropriate from the outset. This occurs when target velocity is predictable, or when target motion can be viewed for an extended period of time as occurred in the auditory cuing experiments and when the cerebellar subjects used their affected hand. If, in contrast, target velocity remains undetermined there is an initial "default" response which is subsequently corrected following computation of target velocity. Such responses were observed under normal conditions when target velocity was randomized from trial to trial.

Throughout the initiation of the response and during the subsequent "steadystate" portion signals arising from a variety of sources have an impact on the success of the movement. Extraretinal signals associated with the smooth pursuit eye movements generated to keep the target foveated appear to provide information related to the velocity of the target. These signals allow accurate target velocity matching in the tracking task and normal constant terminal errors in the interception task when vision of the hand is restricted. In addition, perturbations to this signal cause alterations in the output of the manual motor system. This was exemplified by the dependence of hand latency and initial acceleration on eye target velocity in the incongruent pursuit condition and the negative influences of the inaccurate or poorly coordinated eye movements of the cerebellar subjects on their ability to produce consistent manual motor output. In contrast, information derived from vision of the hand contributed to those aspects of the responses of the hand related to target position. In particular, the extent to which positional error was present in the tracking task was dependent upon the duration for which the hand was initially visible. Furthermore, in the interception task, vision of the hand appeared to allow on-line corrections to the trajectory resulting

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in significant reductions in the variability of the endpoint error.

Finally, the processing required to produce the appropriate oculomotor and manual motor output in these tasks as well as the information arising from this output appeared to interact. For example, by moving the eyes to follow the motion of the target, information was generated that influenced the response with the hand and vice-versa. In particular, in the tracking task signals derived from limb proprioceptive sources influenced the accuracy of the eye movements. Under normal conditions, these interactions contribute to the accurate responses that are observed. However, when either or both of these motor systems are disrupted then they tend to adversely affect the other. This negative interaction appears to be at the root of a significant proportion of the problems cerebellar subjects have during tasks that require combined movements of the eyes and hand. As such, it may be helpful for such subjects, as well as others with motor deficits of this nature, to segregate their eye-hand responses such that one effector moves then the other. In this way, they would avoid these negative influences and potentially produce more accurate responses.

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