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RESEARCH ARTICLE

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Ocular perturbations and retinal/extraretinal information: the coordination of saccadic and manual movements

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Abstract Two experiments were conducted to examine the interactions between the ocular and manual systems during rapid goal-directed movements. A point-light array was used to generate Müller-Lyer configuration target endpoints (in-Müller, out-Müller, 'X') for 30 cm aiming movements. Vision (of the limb and target), eye position, and the concurrence of eye movement were varied to manipulate the availability of retinal and extraretinal information. In addition, the Müller-Lyer endpoints were used to generate predictable biases in accuracy of these information channels. Although saccadic amplitude was consistently biased, manual bias in response to illusory targets only occurred in trials with concurrent eye movement and elimination of retinal target information on limb movement initiation; covariation of eye and hand displacement was also most prevalent in these trials. Contrary to previous findings, there was no temporal relation between eye and hand movements. In addition to any role in coordinated eye-hand action, the availability of vision of both the limb and target again had strong performance benefits for rapid manual aiming.

Key words Ocular perturbations · Retinal/extraretinal information · Saccadic movements · Manual movements

Introduction

On a day to day basis, people are required to extract precise information from their environment and act/react to external stimuli to perform even the simplest of tasks. Historically, researchers (e.g., Woodworth 1899) have examined the influence of movement information on behavioural adaptation to the external environment. In Woodworth's now famous monograph, he described the importance of visual information during goal-directed movements. In particular, he described the role of vision in the preparation of an initial impulse and for the current control of ongoing movements. The initial impulse was proposed to cover the bulk of the movement amplitude under the control of a visually generated movement plan. During the final portion of movement visually detected inaccuracies in the initial impulse are corrected through a process of 'current control'.

Although behavioural researchers have demonstrated the importance of vision in the control of goal-directed movement (e.g., Carlton 1981; Carson et al. 1993; Chua and Elliott 1993), less attention has been paid to the identification of the visual information involved in the planning and corrective processes. There have, however, been some attempts to explicitly define the *nature* of the information that facilitates observed performance benefits (see Abrams et al. 1990 for a review). Specifically, there are two classes of ocular information: retinal, which most closely reflects the behavioural descriptions of vision mentioned above, and extraretinal, which represents a compilation of internally generated information. Retinal information includes stimuli position (and movement) on the retina, thus providing the basis for object identification and, in aiming, the relative positions of the target and the hand. While spatial accuracy is maximized in foveal vision, peripheral vision is important for detection of stimulus movement. Extraretinal information is acquired from the integration of two sources. The first source is output based and may include a copy of the motor commands (efference copy) that enable the eyes to achieve the desired end location. This efferent information may also calibrate the rest of the visual, and possibly manual, systems for the processing of new retinal information[1]

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[1] The terms 'efference' and 'efferent information' are used throughout this manuscript and are intended to include efferent copy, corollary discharge, and movement intention/programing information.

(e.g., corollary discharge, Jeannerod et al. 1979; Teuber 1964). The second source is a composite of oculoproprioception (i.e., the position of the eye within the socket), muscle feedback (e.g., muscle spindle activation), and head/neck orientation feedback sources (e.g., vestibular feedback). The combined signal from these sources gives integrated position information (Abrams et al. 1990; Vercher et al. 1994).

Oculomanual coordination

Gauthier et al. (1988) have developed a functional model that allows the reciprocal exchange of sensory and motor information in the visuo-oculo-manual system (see also Gauthier and Mussa Ivaldi 1988; Vercher and Gauthier 1988). This framework describes the interactions between the manual and ocular smooth pursuit systems based on both neurophysiological and behavioural data. The benefits of inflow from the arms to the ocular system are described with regards to target tracking. When a target is tracked simultaneously with both arm and hand, the ability of the ocular system to foveate the object by smooth pursuit improves (smooth pursuit threshold increases to 100°/s; Gauthier et al. 1988). Also, the smooth pursuit reaction time decreases to as little as 30 ms if the hand is ‘attached’ to the object.

The afferent inputs to the ocular system are highlighted in humans by the oculo-brachial illusion. If the arm of a participant is held stationary while a vibration is applied to the biceps or triceps, a target attached to the finger of the affected arm is perceived to move (Gauthier et al. 1988). This information exchange, although perceptually inconsistent with the external environment, can be viewed as a phenomenological demonstration of the interplay between ocular and manual systems. Gauthier et al.’s (1988) interconnection model places the control of coordinated systems during goal-directed tasks in specialized modules within the central nervous system, using timing and mutual coupling as common control variables. Although the dentate nucleus of the cerebellum was directly investigated as a component structure in baboons (Vercher and Gauthier 1988), no specific structure(s) were suggested by the authors for coordinative roles in humans. Van Donkelaar and colleagues (1994), however, have investigated oculomanual coordination using patients with cerebellar damage. The findings of these researchers implicate areas within the cerebellum and the superior colliculus.

An organizational explanation for these interconnections is that both the manual and ocular systems share a common motor command (Bizzi et al. 1971; Bock 1986). This hypothesis holds that a single order is issued to both eye and hand systems for an aiming movement. Initial data in support of this idea came from Biguer et al. (1982, 1984) when the initial EMG signals from both the manual and ocular systems began within a 20-ms window. More recently, however, Carnahan and Marteniuk (1991, 1994) reported that eye-hand movement order in pointing is dependent on speed-accuracy instructions. While their results are damaging to a common code theory, their findings indicated completion order as potential control variable for the eye-hand connection. Functionally, this invariance of completion order may facilitate feedback and feedforward processes by ensuring a static eye-hand spatial relation during the corrective stages of the hand movement, thus aiding the monitoring of ongoing movements (Abbs et al. 1984). Although these results indicate a separation in motor program delivery order, they also necessitate communication between the eye and hand motor systems early in the control process.

Coordination between eye and hand has also been shown to affect the terminal accuracy of the aiming movement. Restriction of eye motion, by requiring a subject to fixate an alternate stationary target, results in a tendency to underestimate movement amplitude and increased aiming errors (Abrams et al. 1990). The reduction of movement precision by static manipulation of eye position seems consistent with a disruption in extraretinal information, but fails to allow for the differentiation between source components. Similar interactions have been demonstrated using active manipulation of eye position via saccadic adaptation (Abrams et al. 1992; Bekkering et al 1995) to bias saccadic movements, thus allowing examination of the changes in the manual system that result from variations in ocular output. Interestingly a predictable biasing of the manual aiming system was observed in response to ocular adaptations even in the absence of visual feedback of the hand. The concurrent changes suggest that a common signal was used by both systems to specify eye and hand endpoint localization. A proposition was also made that target locus is defined within the motor system, not the perceptual system (Coren 1986), and that mapping inconsistencies between the perceptual and motor system are rectified by sharing of a common gain parameter for output (Bekkering et al. 1995). With this viewpoint, the final displacement of an intended limb movement would be some constant proportion of the saccadic extent.

A recent attempt to identify connections between the ocular and manual systems used eye location and concurrence of eye movement as global variables during ‘natural’ eye-hand pointing (Vercher et al. 1994). Three sets of events were suggested as critical to the sensorimotor process involved in precise aiming (Vercher et al. 1994): (1) the target must be located in relation to the body by location on the fovea, by the eye’s orientation within the orbit/head, and by the head’s relation with the body, (2) the arm’s position must be defined by proprioception and/or visual afference, and (3) there must be synergetic action of active segments (i.e., eye, head, and arm). Based on these assumptions, the research strategy used by Vercher and colleagues was to control the amount of synergy (i.e., eye and hand movements occurred either simultaneously or sequentially) and to observe any temporal or spatial disturbances. Surprisingly, no accuracy differences were found between sequential and synergetic eye-hand movement conditions. Subsequently, Vercher et al. (1994) concluded that eye-hand coupling is not based solely on mechanical limitations, but instead on neurally mediated variables. Although the researchers did not speculate on any specific mechanisms, evidence can be found in human neurophysiological research suggesting preexisting structures for eye-hand coordination within the posterior parietal cortex (e.g., Sakata et al. 1995; Taira et al. 1990), while behavioural data indicate such structures exist within the cerebellum (e.g., van Donkelaar and Lee 1994).

Experiment 1

The purpose of this study was to examine the level of dependence of the manual system on selected channels of ocular/visual information. The Müller-Lyer illusion represents a unique tool for examining this type of oculomotor coordination. By systematically biasing eye movement in response to the illusion (Binsted and Elliott 1999; Festinger et al. 1968; Yarbus 1967), any hardwired (omnipresent) or highly information dependent mechanisms for oculomanual coordination should be evidenced by predictable errors in the manual aiming system. Specifically, subjects made rapid aiming movements toward endpoints consisting of Müller-Lyer figures. The information available for limb control was manipulated by altering vision and the accuracy of oculoproprioceptive afference, and ocular efference. The impact of manipulating these information sources was expected to manifest itself in an information-dependent illusory bias in participants' arm movements.

Materials and methods

Participants

Eleven students (three female, eight male) from the McMaster University community (mean age 24.7 years) gave informed consent prior to their participation in this study. This investigation was carried out with the approval of the McMaster University President's Committee for Ethical Considerations in Human Experimentation.

Task

In all conditions, subjects were asked to move as quickly and accurately as possible from the home position to the centre point of the presented figure. This middle point was defined for participants as the light-emitting diode (LED) that occupied the middle of the neutral 'X' configuration, regardless of the presented shape. Participants were also informed that their reaction time in response to the start tone was being recorded for each trial. No knowledge of results was given regarding reaction time, movement time, or movement accuracy for any trials. Room illumination was reduced for all conditions. This was necessary for maintenance of consistent and accurate eye movement recordings. Adequate light was still available for vision of the limb.

Apparatus

A common home position and endpoint figure were positioned 30 cm apart. The home position consisted of a 2-cm-diameter button. The endpoint was a 37 LED (Dialight-558, 10 mcd) 'X', generated by the intersection of perpendicular lines. Each arm of the figure consisted of 9 LEDs spanning a distance of 9.5 cm; the resulting total figure area was 49 cm^2. The cross was oriented such that illumination of ipsilateral arms generated the 'in' and 'out' Müller-Lyer figures, while the illumination of all points resulted in a neutral, 'X', configuration. The three endpoint formations (in-Müller, out-Müller, and X) shared a common central point (Fig. 1).

Liquid crystal occlusion goggles (Milgram 1987) were employed in trials where vision of the hand was to be removed. Due to the translucency of the goggles and the illumination of the target, the endpoint configuration was still available to participants throughout these trials. During occluded trials, the goggles changed state from transparent to translucent (2 ms switching time) concurrent with the start tone. While removing vision of the participant's hand, the state change of the goggles did not significantly alter the amount of light reaching the eyes (e.g., Elliott et al. 1994).

Hand movements: Optotrak-3020. An IRED (infrared-emitting diode) was attached to the participant's right index finger using a guitar pick 'pointer', thus allowing a wall-mounted Optotrak three-dimensional movements recording system to measure manual movements. The three Optotrak cameras record IRED position with a spatial accuracy of 0.3 mm.

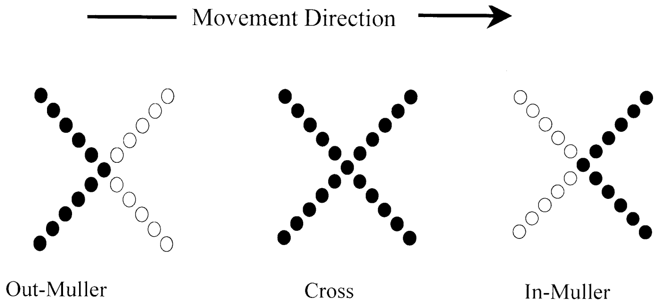

Fig. 1 Müller-Lyer and cross endpoint configurations for experiment 1 and 2

Table 1 Eye action and available information sources for eye conditions in experiment 1

Condition	Saccadic timing	Information		
		Efference	Proprioception	Vision of hand
FULL (saccade to illusion)	Simultaneous with hand	Bias	Bias	Yes
NOEFF (saccade to X)	Prior to hand	No	Unbias	Yes
NOVIS (saccade to X)	Prior to hand	No	Unbias	No

Point of gaze: ASL-4100/Ascension–Flock of Birds. Eye movements were measured by an Applied Sciences Laboratories, series 4000-SU HMO, head-mounted eye-tracking system. The eye-monitoring system was integrated with an Ascension, Flock of Birds, magnetic head tracker (MHT); this integration allowed participants free head motion during the experiment. The ASL-4000 series eye tracker is a based video system (120 Hz), which utilizes a pupil centre/corneal reflection method of determining point of gaze (POG, Young and Sheena 1975). The associated MHT recordings are accomplished by tracking a 'flock' receiver attached to the ASL helmet within a pulsed DC magnetic field. Head position and orientation is thus determined with a spatial accuracy of 0.6 mm within a 1-m^3 detection radius.

Eye-hand coordination. In order to attain temporal matching between kinematic traces, several common markers were used. Eye movement recording began several seconds prior to each trial. The start tone, to which subjects reacted, began Optotrak recording as well as placed a temporal marker on the already started eye/head recording. Release of the home button placed a second marker on the eye trace. Optotrak sampling rate was set at twice the eye tracker frequency (i.e., 240 Hz) to minimize sampling asynchronies while maintaining the spatial and temporal accuracy in the hand recordings.

Procedure

The aiming apparatus was placed on a table in front of the subject such that the participant's midline was aligned with the centre point between the start and end positions. Chair height and distance from the table were adjusted to maximize free movement of the subject's arm. Prior to all trials, the participants placed their index finger on the home position, depressing the button. Subjects then assumed the appropriate fixation point for the upcoming trial and signalled their readiness.

In full information conditions (FULL), subjects made concurrent eye and hand movements, presumably making available all forms of information normally present for eye-hand coordination. Subjects began each trial by placing both their finger and their gaze on the home position. Upon their confirmation of finger and gaze position, the experimenter gave a "ready?" command; at this time the endpoint figure changed to the appropriate formation for the trial. Following a variable foreperiod (1, 2, or 3 s), the start tone sounded and the trial began. Participants were instructed to move both eye and hand as they normally would, with the restriction that both eye and hand remained in the start position until the "go" signal.

In the NOEFF conditions, the eye attained an accurate (non-illusion biased) position prior to each trial. No concurrent eye efference was available for modulating hand movements in this situation. Also, eye position (proprioception) was unbiased. Participants started each trial by placing their finger on the start button while fixating the centre of the 'X' formation of the endpoint. Once again, subjects indicated attainment of gaze position. The experimenter gave a "ready?" command, at which time the end point changed (if the condition demanded), and the start tone followed after a variable foreperiod.

The no-vision conditions (NOVIS) allowed neither concurrent eye movement nor vision of the hand in motion. These conditions were similar in all aspects to NOEFF conditions with the exception that vision of the hand was removed concurrently with the start tone. Vision was returned following the completion of each trial.[2]

Participants completed a total of 135 aiming trials in three 45-trial blocks. Presentation of information conditions was blocked, with condition order randomized across subjects. Endpoint configuration condition was randomized across trials for each subject, but with the same order within a subject across information condition blocks. Thus subjects performed 15 trials in each of the 3 endpoint configuration × 3 information conditions.

Data reduction and analysis

Point of gaze: ASL-4000/Ascension–Flock of Birds. A previously defined saccade and fixation algorithm (Helsen et al. 1997) was applied to the raw eye displacement data. Initial fixation start was identified as the first of 12 consecutive point of gaze (POG) samples having a standard deviation of less than 1°, with a temporary value for the location of the fixation being the average horizontal and vertical components of these 12 samples. A saccade was determined to have started, and therefore the fixation to have ended, when three consecutive POG samples occurred beyond 1.25° from the temporary fixation location. Once a fixation was complete, a final value for its location was calculated across all fixation samples.

Several descriptors of POG and saccade were analysed. These variables included: reaction time, movement time, mean primary saccade amplitude, location of POG after corrective saccades, and the mean magnitude of corrective saccades.

Hand movements: Optotrak-3020. Raw hand movement data were filtered using a second-order dual-pass Butterworth filter (low-pass cutoff frequency of 6.0 Hz). Both instantaneous velocity and acceleration were obtained by differentiation of the filtered displacement and velocity data using a two-point central finite-difference algorithm. All data were reduced and analysed in only the plane of the primary movement (i.e., y-axis).

An interactive program was used to identify critical kinematic landmarks for each trial (Elliott et al. 1995). Movement initiation was defined as the first sample where the instantaneous velocity exceeded 50 mm/s (Chua and Elliott 1993), with the reaction time being the elapsed time from collection start to movement start. The end of the movement was defined as the first point below the absolute value of 30 mm/s, where the following five points remained below this cutoff value.

In addition to kinematic variables typically examined, the velocity and acceleration traces yielded both the location (in time and space) of the beginning of the first correction and the total number of corrections that occurred prior to movement completion. A correction could be attained in one of two manners, a significant deviation or a movement reversal. A significant deviation in the acceleration trace was defined as a departure from the sinusoidal trend of the curve with the opposing amplitude being greater than one-tenth of the maximum acceleration magnitude and having a duration of greater than 50 ms. Movement reversals were defined as sign changes in the velocity trace that did not satisfy the requirements for movement completion (e.g., Chua and Elliott 1993).

Many dependent measures relating to the hand were examined. These included several performance variables: movement time, total movement displacement, and variability of location at movement completion. Also examined were landmarks pertaining to the programming of the initial movement (i.e., reaction time) and the execution of this impulse (i.e., peak acceleration, peak velocity, and location temporally and spatially for peak velocity). In combination with the features of the initial impulse, primary movement displacement, peak deceleration, and the time to peak deceleration were used as descriptors of the primary submovement. The total number of discrete corrections and the proportional time after peak velocity were taken to reflect the degree of current control.

Eye-hand coordination. The degree of coordination between ocular and manual systems was assessed by examining the correlations of several kinematic and temporal variables between eye and hand on a trial to trial basis. All correlations were transformed to z-scores prior to statistical evaluation to allow the use of parametric tools. Pearson product moment correlations were calculated between: (1) location of the eye and hand at the end of their respec-

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[2] For trials when the liquid crystal goggles were employed, no eye movements were recorded as the goggles precluded use of the E4000 system.

tive primary movements, (2) location of the eye at the end of the primary saccade and final hand position, (3) eye reaction time and hand reaction time, (4) total time of the eye to reach the end of the primary saccade with total time of hand to peak velocity (Helsen et al. 1997, 1998), and (5) time to complete the primary saccade with hand time to peak velocity (reaction times removed). This final correlation was performed to examine the relation between movements without the contribution of any relations between reaction times.

All hand-dependent measures were examined with separate, 3 endpoint configuration (in-Müller, out-Müller, and cross) × 3 information availability (FULL, NOVIS, NOEFF) repeated measures analysis of variance, with each subject mean based on 15 trials. Each eye measure was examined with an independent one-way 3 end-point configuration repeated measures analysis of variance, with each subject mean composed of 15 trials. The mean eye-hand correlation/*z*-scores, calculated across the three endpoint configurations, were compared with zero using single-sample *t*-tests. Each subject's correlation was based upon 45 trials. Tukey's (HSD) post hoc procedures were further applied to significant effects where appropriate. Alpha was set at $P<0.05$ for all statistical analyses.

Results

Eye movements

General saccadic movement descriptors determined a mean primary saccade duration of 84 ms and a reaction time of 292 ms. A significant effect of endpoint configuration was found for the primary saccade, $F_{(2,20)}=49.9$, $P<0.001$, and the final location of the eye after corrective saccades, $F_{(2,20)}=5.2$, $P<0.05$. All levels of endpoint configuration were different from each other for the primary saccade. This again demonstrates the efficacy of the Müller-Lyer formations at biasing eye movements (Fig. 2). Even when corrective eye movements were considered, the illusory figures still showed a substantial biasing effect. However, the differences were only significant between the outward pointing illusion and the inward/neutral figures (see Table 2).

Although the analysis of the amplitude of corrective saccades failed to produce any significant effects of endpoint figure, $F_{(2,20)}<1$, it did reaffirm a trend for eye movement corrections to gravitate toward an amplitude of 2° visual angle (see Binsted and Elliott 1999).

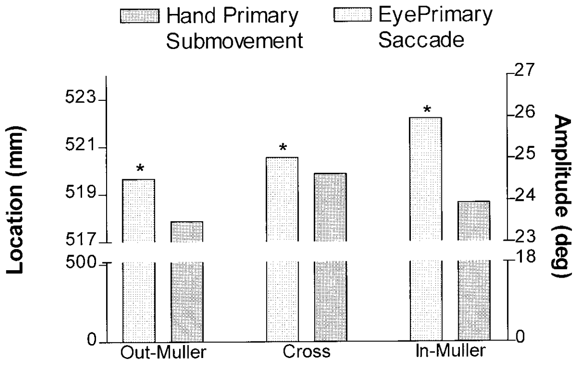

Fig. 2 Primary submovement displacement (axis-Y^1) and primary saccade amplitude (axis-Y^2) as a function of endpoint configuration (* indicates points differing reliably from all others, $P<0.05$)

Table 2 Summary of mean values for saccadic eye variables in experiment 1

	Out-Müller ⟶>	X	In-Müller ⟶<
Reaction time (ms)	287	290	301
Movement time (ms)	84	81	89
Primary amplitude (°)	24.5	25.0	25.9
Final location (°)	12.2	12.9	14.2
Corrective amplitude (°)	2.4	2.3	2.3

Hand movements

The general hand movement descriptors found a mean reaction time for this task to be 228 ms with a movement time of 375 ms. Contrary to the findings for the eye movements, no displacement-biasing effects of endpoint configuration were apparent (Fig. 1). Analysis of the total movement displacement revealed a main effect for vision, $F_{(2,20)}=8.6$, $P<0.01$. Further examinations of this effect revealed participants moved significantly less distance in the NOVIS trials than in either FULL or NOEFF situations. An interaction between endpoint and information was also apparent, $F_{(4,40)}=2.6$, $P<0.05$. However, this effect accounted for less than 5% of the total variance and was primarily due to the out-Müller figure causing significantly longer movements than the other two endpoints in the NOVIS and NOEFF conditions, a trend that was in the reverse direction of any predicted illusory effects. As has been extensively demonstrated previously (see Carlton 1981 for a review; Chua and Elliott 1993; Elliott et al. 1998b), hand movement variability increased significantly, $F_{(2,20)}=6.5$, $P<0.01$, in conditions where vision of the hand was removed (NOVIS). Movement time also decreased when vision of the hand was eliminated, $F_{(2,20)}=5.4$, $P<0.05$, as did time to peak deceleration, $F_{(2,20)}=4.6$, $P<0.05$, and time to peak velocity, $F_{(2,20)}=3.7$, $P<0.05$. Contrary to vision/no-vision expectations, there was no difference in the number of corrections between vision (FULL, NOEFF) and NOVIS conditions. Although a significant interaction between endpoint configuration and available information was apparent for both the displacement at peak velocity, $F_{(4,40)}=3.5$, $P<0.05$, and peak deceleration, $F_{(4,40)}=4.3$, $P<0.01$, these effects were due primarily to the resistance of the outward pointing illusory condition to display the traditional effects with the removal of vision. One final effect of vision was for reaction time, $F_{(2,20)}=15.5$, $P<0.001$. Participants reacted more quickly in conditions where vision was removed (NOVIS). Such decreases in reaction time may result from the increased salience of a visual cue, or from a strategic attempt by subjects to begin moving more quickly in order to retain and utilize any spatial representation of the

Table 3 Summary of mean values for hand variables in experiment 1

	Out-Müller ——>			X			In-Müller ——<		
	FULL	NOVIS	NOEFF	FULL	NOVIS	NOEFF	FULL	NOVIS	NOEFF
Temporal (ms)									
Reaction time	240	206	233	241	214	236	244	207	237
Movement time	390	350	369	396	355	388	397	351	387
Time to peak velocity	168	152	158	171	151	161	168	150	157
Spatial location (mm)									
Location of primary movement	319	317	317	320	318	322	320	316	319
Location at end of movement	322	319	323	322	318	323	323	316	322
Variability at end of movement	6.65	8.13	6.59	5.65	7.65	5.88	6.45	8.07	5.87
Location of peak velocity	170	169	171	174	168	173	175	166	169
Other variables									
Peak velocity (mm/s)	1756	1927	1835	1750	1902	1831	1800	1887	1810
Peak acceleration (mm/s/s)	18982	22394	19513	18456	22031	19695	19105	21720	19561
Peak deceleration (mm/s/s)	–18849	–22667	–19505	–18949	–21977	–19497	–19620	–21143	–19084
Proportional time after peak velocity	0.56	0.57	0.56	0.57	0.57	0.56	0.54	0.56	0.55
Number of corrections	0.77	0.73	0.88	0.81	0.74	0.85	0.86	0.77	0.82

Table 4 Summary of *Z*-transformed Pearson product moment correlations for eye-hand data in experiment 1

	Z-scores
Eye reaction time with hand reaction time	0.73
Time to primary saccade end with time to peak velocity (incl. HRT)	0.61
Duration of primary saccade with time to peak velocity (minus HRT)	0.07
Location of primary saccade with location of primary movement	0.09
Location of primary saccade with final location	0.07

target before it had an opportunity to decay (Elliott and Madalena 1987). The remaining dependent measures for hand movement failed to show any significant condition effects (see Table 3).

Eye-hand coordination

Analysis of the transformed *z*-scores for eye-hand coordination revealed a significant relation between eye and hand reaction time, $t_{(10)}=5.8$, $P<0.01$ ($M=0.73$). This relation, although statistically significant, is theoretically inconclusive by itself, as it was impossible in the present investigation to determine whether these variables were related due to purely attentional factors or whether the planning phases of the movements were related. The correlations may only represent the normal fluctuations in attention/motivation over time (e.g., momentary inattention during a given trial would result in both long eye and hand reaction times). However, establishing this reaction time relation is necessary for discussion of the correlations for total time.

As reported previously (Helsen et al. 1997, 1998), a significant relation was found between saccadic response time and hand time to peak velocity, $t_{(10)}=5.9$, $P<0.01$ ($M=0.43$). However, when reaction time was removed, the correlation approached zero, $t_{(10)}=0.5$, $P>0.15$ ($M=-0.05$). Neither the correlation between the displacements of the primary movements of the eye and hand nor those for the final displacements reached conventional levels of significance (see Table 4).

Discussion

As previously demonstrated (Binsted and Elliott 1999; Festinger et al. 1968; Yarbus 1967), the Müller-Lyer illusion effectively biased saccadic eye movements in this experiment. Due to the primarily ballistic nature of saccadic movements, the conclusion can be drawn that sufficient illusory information is available to participants in FULL trials during movement preparation, even when the target is presented in the periphery. The biasing information is also powerful enough to prevent corrective eye movements from overcoming the induced bias (*M* number of saccadic corrections=1.2). The inability of the ocular system to correct these errors immediately produces a corollary expectation based on coordination theories of eye-hand action; because the eye is biased in its primary movement, the hand should be biased as well. The findings of this study do not support this hypothesis; the hand was not affected by the illusion, with or without concurrent eye movements (cf. Daprati and Gentilucci 1997, for grasping; Elliott and Lee 1995; and Gentilucci et al. 1996, 1997, for pointing).

Although the methodologies of Elliott and Lee (1995) and others (Daprati and Gentilucci 1997; Elliott and Lee 1995; Gentilucci et al. 1996, 1997) are essentially the same as those of the present investigation, some subtle differences exist. Specifically, ‘complete’ illusions were presented in these studies while only the endpoint was displayed in the present investigation, possibly decreasing illusory influence. Also, each participant's movements were performed over much smaller displacements than the present amplitude of 30 cm, thereby allowing much less time for feedback-based error correction.

This second difference, one of opportunity for correction, increases in potency when we consider the equivocal findings for visual presentation shown by Mack et al. (1985). Of the three experiments Mack and colleagues performed, two experiments found illusory carryover to manual movements, whereas one did not. Specifically, these experiments found illusory effects when participants were shown the illusion only prior to movement (during programming), not during aiming. Conversely, the experiment Mack et al. (1985) performed that displayed no carryover allowed continual viewing of the figure throughout aiming. Regardless, the present study's result still weakens any theory that requires either the hand and eye to share common information or for the manual system to base its planning and control upon efference from the initial saccade. If these connections had been based on 'hard-wired' phenomenon, the illusory bias induced in manual movements should have been far more robust.

Although the illusion manipulation in this experiment failed to create manual biases, the lack of significant correlation between manual and ocular systems, both spatially and temporally, raises some interesting questions. Helsen et al. (1997) proposed a temporal relation between peak velocity of the hand and the completion of the primary saccade. In addition, they suggest a spatial relation between the final position of both, reflecting a commonality of visual and/or proprioceptive information. Given the induced variation of eye movement via Müller-Lyer figures in this experiment, and the directionality of that variation (i.e., illusory bias), the strength of any spatial eye-hand relation should have been accentuated while leaving temporal coupling unaffected.

When the spatial relations were examined, bias for both the eye and hand should have become apparent if both systems share a common information source. No such relation developed, but the predicted temporal relation between eye and hand described by Helsen et al. (1997, 1998) was replicated. Once the covariation between eye and hand reaction time was removed from the relation, all trace of a temporal connection disappeared. This effect should not be unexpected. Given the ballistic properties of eye movements, their temporal invariance (saccadic velocity is directly related to amplitude), and the huge variation within a subject for reaction time, the difference between the correlations can be explained by the strong relation between manual and ocular reaction times. Even if only random noise variation was to occur between the ocular and manual systems following reaction time, a remnant relation may remain. This is not to say that the reaction time relation does not reflect some higher centre connection; it may be indicative of anything from common programming to intertrial fluctuations in attention. The nature of any connection, however, cannot be determined solely from a correlation and must be left to future investigations.

Although there appears to be considerable independence in the information used for preparation of manual and ocular movements, the relative timing of some critical events does continue. Similar to the findings of previous investigations (e.g., Carnahan and Marteniuk 1991, 1994; Helsen et al. 1997, 1998; Vercher et al. 1994), the eyes arrived at the target prior to the hand in FULL movement trials (mean eye total time=377 ms; mean hand total time=605 ms). This time differential allows the hand control system access to vision of the hand from a target-centred frame of reference. Given the biased final position of the eye, either the manual system is ignoring this positional information source or it is unable to use it. A probable explanation is based on the temporal delay associated with extraretinal feedback. The complex integration of extraretinal sources to provide eye reference position likely takes considerable time. Perhaps, the arrival difference between hand and eye is inadequate to allow this integration. This temporal explanation has validity in two main respects. Traditionally in rapid aiming movements, participants begin with their eyes fixated on the target and thus the manual system has adequate time to maximize position information. Even in movements where the eye is not already fixated (dynamic situations) and time is inadequate for this efferent form of extraretinal information, any increase in error is likely accommodated by retinal information which can be used quite quickly (e.g., Carlton 1981; Elliott and Allard 1985). Alternately, visual information is simply more salient, and thus the preferred information source.

Vision manipulations (retinal and peripheral inclusive) yielded results that are reflective of many previous investigations (e.g., Carlton 1981; Chua and Elliott 1993; Woodworth 1899). Movements became less accurate, faster, and displayed fewer features indicative of closed-loop control when subjects completed the aiming movements without vision of the limb. The replication of traditional findings provides reassurance that the reduced lighting environment needed to utilize the eye movement equipment did not generate any discernible effects. Contrary to expectations (e.g., Chua and Elliott 1993), reaction time decreased when vision was removed. In retrospect, this perhaps was simply a function of the time of vision removal. When vision is eliminated at movement initiation, the participant likely uses a strategy of overplanning as they know they will need to perform in a top-down manner, thus increasing reaction time. However, when vision is removed at the start tone, a subject may adopt a strategy of minimizing reaction time in order to reduce the degradation of their representation of the movement space over time (Elliott and Madalena 1987).

Table 5 Eye action and available information sources for eye conditions in experiment 2

Condition	Saccade timing	Information		
		Efference	Proprioception	Vision of target
FULL (saccade to illusion)	Simultaneous to hand	Bias	Bias	TAR/NOTAR
BIAS (saccade to illusion)	Prior to hand	No	Bias	TAR/NOTAR
UNBIAS (saccade to X)	Prior to hand	No	Unbias	TAR/NOTAR

Experiment 2

Unlike previous investigations, the results from experiment 1 failed to reveal any effect of the Müller-Lyer illusion on discrete hand movements (cf., Elliott and Lee 1995; Gentilucci et al. 1996). To completely examine the illusory implications for efferent theory and eye-hand coordination, the biasing effects on manual movements must be recreated.

To reproduce the earlier findings, an explicit attempt was made to replicate specific procedural practices used by those researchers within our framework. Both the procedures employed by Elliott and Lee (1995) and Gentilucci et al. (1996) enabled subjects free viewing of the illusion endpoint prior to movement initiation. This presumably biases eye position prior to and during the planning phases of a response. Both investigations also demonstrated an increased impact of the illusion on limb movement when vision of the figure was removed upon or before movement initiation, thus making the performer more dependent on memory for limb control.

Materials and methods

Subjects

Ten students (three female, seven male) from the McMaster University community (mean age 28.3 years) gave informed consent prior to participation in this study. The investigation was carried out with the approval of the McMaster University President's Committee for Ethical Considerations in Human Experimentation.

Task

The task in experiment 2 was nearly identical to that of experiment 1. In contrast to experiment 1, however, participants were explicitly asked to place the end of the pointer over the centre point of the LED. This instructional adaptation decreased the goal tolerance to successfully reach the target.

Apparatus

The aiming apparatus was identical to that in experiment 1 with some additions. An additional switch was attached to the home position such that on selected trials the LED display went off on hand initiation. A tinted plate was placed over the LED display, so that, when the display was turned off, the LEDs became essentially invisible. Movements of the eyes and the finger were recorded in the same manner as in experiment 1 and pertinent hand kinematics and eye-hand correlations were once again analysed.

Procedure

Participants were seated in relation to the apparatus in the same manner as in experiment 1. Specifically, the subject's midline was aligned with the centre point of the aiming movement.

In the full information condition (FULL), all forms of extraretinal feedback and feedforward normally available during concurrent eye and hand movements were available. When the illusory endpoints were present, however, all of these information sources were biased.

In biased proprioception conditions (BIAS), concurrent efference was removed; eye position was incorrect on selected trials due to the illusory endpoint. Similar to the FULL condition, each trial began by the participant placing their finger and gaze on the start button. Once again a "look at your finger" instruction was given followed by "ready". On the ready prompt, the endpoint changed to its alternate formation (either in-Müller, out-Müller, or X). Following the ready command, participants made their primary saccade to the Müller-Lyer endpoint. After a variable foreperiod of 1, 2, or 3 s following the „ready" command, the start tone sounded, and the participant initiated their movement.

In non-biased proprioception conditions (NBIAS), concurrent efference was removed and the eye attained a veridical (non-illusion biased) position prior to each trial. Participants started each trial by placing their finger as well as their POG on the start button. On the "look at the X" instruction, subjects moved their gaze to the 'X' (neutral) formation of the endpoint. Subjects indicated successful attainment of final gaze position; the experimenter then gave a final "ready?" command. Concurrent with the ready command the endpoint changed to its alternate configuration (either in-Müller, out-Müller, or remained 'X'). Following a variable foreperiod of 1, 2, or 3 s, the start tone sounded, and the subject began to move.

Subjects performed one block of each of the eye position conditions in each of two target vision conditions. During the TAR block, the endpoint configuration remained illuminated throughout the trial. In the NOTAR block, the endpoint was extinguished upon hand initiation.

Participants completed a total of 90 aiming trials. All presentations of information condition (FULL, BIAS, and UNBIAS) and target vision were blocked, with order of presentation randomized across subjects. Endpoint configuration condition was randomized across trials for each subject, but with the same order within a subject across information and target vision condition blocks. Thus subjects performed 5 trials in each of the 3 endpoint configuration × 3 information limitation × 2 target vision conditions.

All hand-dependent measures were examined with separate 3 endpoint configuration (in-Müller, out-Müller, and X) × 3 information availability (FULL, BIAS, UNBIAS) × 2 target vision (TAR, NOTAR) repeated measures analysis of variance, with each score based on the mean of 5 trials. Eye amplitude measures were examined with separate 3 end-point configuration × 2 target vision repeated measures analyses of variance. Mean eye-hand correlations were again compared with zero with single sample *t*-tests. Tukey's (HSD) post hoc procedures were applied to significant effects involving more than two means. Alpha was set at $P<0.05$ for all statistical analyses.

Data analysis and reduction

Methods for evaluating both POG and hand performance were carried out in the same manner as in experiment 1.

Results

Eye movements

The mean primary saccade duration was found to be 94 ms with a reaction time of 315 ms. As in experiment 1, a significant effect of endpoint configuration was found for the amplitude of the primary saccade, $F_{(2,18)}=22.1$, $P<0.001$. Again, all levels of endpoint configuration were significantly different from each other, consistent with predicted illusory biases, following the primary saccade (see Table 6). When the position of the eye at hand completion was examined, the main effect of endpoint, $F_{(2,18)}=22.1$, $P<0.001$, was again present; this replicates the inability of the eye to correct its initial illusory bias demonstrated in experiment 1. A main effect of eye position, $F_{(2,18)}=19.7$, $P<0.001$, and an interaction between eye position and vision of the target, $F_{(3,36)}=8.9$, $P<0.001$, were also significant. These latter results reflect two trends. First, although hand movements were far slower than eye movements, the eye failed to overcome its predictable undershooting tendency prior to hand movement completion. Second, the previously mentioned undershooting was increased in conditions where the eye was to maintain a fixation without a visible target. Finally, an interaction between endpoint and eye position occurred for eye position at hand completion, $F_{(4,36)}=8.9$, $P<0.001$. This interaction resulted largely from the illusory bias in the FULL conditions as compared to the UNBIAS trials. Inconsistent with predictions, however, the BIAS condition *failed* to produce a biased position. This suggests that although the saccadic system seemed unable to correct perceptual bias immediately following the primary saccade, the eye did overcome the error over the course of several seconds (i.e., the foreperiod).

Table 6 Summary of mean values for saccadic eye variables in experiment 2

	Out-Müller —>	X	In-Müller —<
Reaction time (ms)	296	300	348
Movement time (ms)	92	94	95
Primary amplitude (°)	25.9	26.5	27.1
Final location (°)	17.2	18.2	19.3
Corrective amplitude (°)	2.1	1.8	2.4

Hand movements

Similar to the eye descriptors, both movement time and reaction time for aiming movements were somewhat slower in this second experiment (movement time=360 ms, reaction time=320 ms) than in experiment 1 (see Table 7). Analysis of reaction time elicited both a main effect for vision of target, $F(1,9)=7.0$, $P<0.05$, and eye position, $F_{(2,18)}=7.8$, $P<0.01$, with reaction time increasing as a result of simultaneous eye-hand movement and removal of target vision. In movement time, a main effect was found for eye position, $F_{(2,18)}=6.6$, $P<0.01$. When this effect was submitted to post hoc analysis, larger time values were once again found for the eye-hand condition (FULL). This 'coordination' effect may reflect the time taken by the manual system to access available extraretinal output (corollary discharge, motor efference, or movement preparation).

Analysis of final hand displacement yielded several key findings. Endpoint configuration generated both a main effect, $F_{(2,18)}=4.0$, $P<0.05$, and interacted with both vision of target, $F_{(2,18)}=4.7$, $P<0.05$ (see Fig. 3a), and eye position, $F_{(4,36)}=4.6$, $P<0.01$ (see Fig. 3b). Not only do these findings indicate illusory effects on manual aiming

Table 7 Summary of mean values for hand variables in experiment 2

	Out-Müller —>			X			In-Müller —<		
	FULL	BIAS	UNBIAS	FULL	BIAS	UNBIAS	FULL	BIAS	UNBIAS
Temporal (ms)									
Reaction time	323	292	279	329	296	301	312	293	287
Movement time	374	347	358	399	362	359	389	340	357
Time to peak velocity	170	161	165	168	161	164	166	162	166
Spatial location (mm)									
Location of primary movement	304	305	306	309	309	306	313	306	305
Location at end of movement	303	304	305	307	306	308	311	305	307
Variability at end of movement	7.96	6.44	7.42	7.82	7.77	6.97	9.26	7.18	7.72
Location of peak velocity	149	152	152	151	151	152	154	153	153
Other variables									
Peak velocity (mm/s)	1790	1918	1849	1828	1905	1875	1877	1902	1869
Peak acceleration (mm/s/s)	17253	18840	18316	17887	19055	18287	18543	18745	18213
Peak deceleration (mm/s/s)	–18255	–21400	–20163	–20286	–20797	–19228	–20753	–21191	–21593
Proportional time after peak velocity	0.51	0.56	0.56	0.55	0.53	0.56	0.55	0.50	0.54
Number of corrections	0.62	0.56	0.57	0.54	0.62	0.65	0.61	0.57	0.63

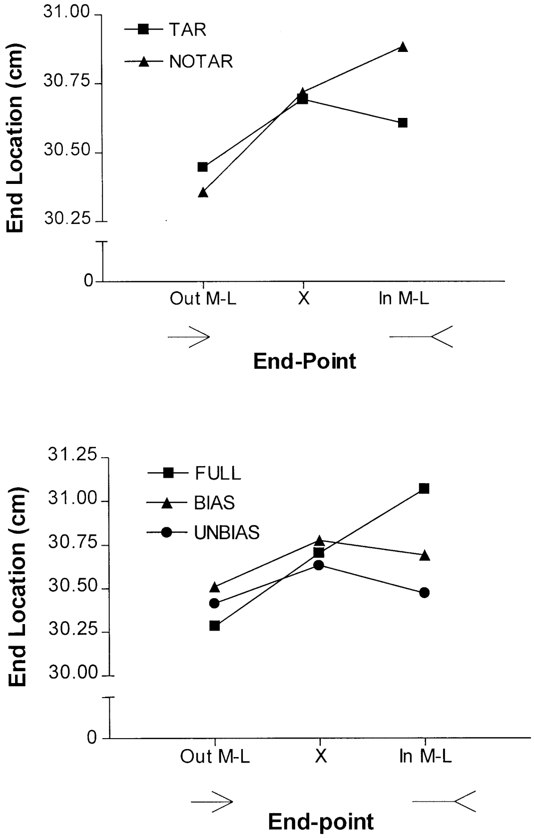

Fig. 3 Hand locations at the completion of movement

movements, they also indicate that such transfer from eye to hand only takes place in the presence of biased efferent information. These results also appear to explain the lack of illusory effects in our first experiment. No illusion bias was present when the figure remained illuminated. However, the illusory bias reappeared when the endpoint figure disappeared on hand initiation. The variability in final movement displacement revealed an effect only for vision of the target, $F_{(1,9)}=5.9$, $P<0.05$, replicating the traditional finding of decreased movement consistency in the absence of vision of the target (e.g., Chua and Elliott 1993; Woodworth 1899).

Analyses performed on displacement values at the end of the primary submovement showed similar trends to those of the final displacement. There was again an interaction between vision of target and endpoint configuration, $F_{(2,18)}=6.0$, $P<0.05$; however, the other effects found for final displacement failed to reach conventional levels of significance. No effects were discernible when variability of the movement at the end of the primary movement was examined.

Analyses of kinematic variables associated with hand movement produced few remarkable findings. As would be expected, peak velocity of the aiming movements increased with the removal of vision of the target, $F_{(1,9)}=13.9$, $P<0.01$, likely reflecting participants' desire to reach the remembered location of the target prior to degradation of their short-term spatial memory for its position. Likewise, peak hand deceleration increased in the absence of vision of the target, $F_{(1,9)}=8.7$, $P<0.05$. Peak deceleration was also affected by endpoint configuration, $F_{(2,18)}=4.8$, $P<0.05$. Specifically, deceleration was greatest when participants were aiming at the in-Müller configuration. This may reflect participants realizing their tendency to 'overshoot', and applying extra effort to minimize and reverse this induced error.

Eye-hand coordination

None of the correlations involving the location of the eye and that of the hand were significantly different from each other (Fig. 4). However, when these values were compared with zero, the correlations for both position at movement completion, $t(9)=3.8$, $P<0.01$, and at the end of the primary movement, $t_{(9)}=2.3$, $P<0.05$, were significant in NOTAR–FULL trials ($z=0.29$ and 0.46 respectively). These relations seem to reflect considerable flexibility in the interconnections of visual and manual systems. When there is increased ambiguity of the specific target location information (Daprati and Gentilucci 1997), the hand appears to covary with the eye to a greater extent. This is distinct from the effects discussed above for means summed across conditions as those effects merely reflect similar tendencies. Inconsistent with these no-vision effects and correlations, however, there was a small, although significant, eye-hand relation in BIAS-TAR trials, $t_{(9)}=2.3$, $P<0.05$ ($z=0.14$).

Discussion

The purpose of this second investigation was to recreate manual biases by manipulation of target endpoint (e.g., Elliott and Lee 1995). In order to accomplish this, several alterations to the conditions from experiment 1 were used. These changes included the removal of the target at movement initiation in some blocks of trials, and the addition of a biased stationary eye condition. In this manner, the availability of information was manipulated so that the source information for any induced bias could be identified (i.e., efference or proprioception).

Eye movement findings in experiment 2 were the same as in our first investigation (see also Binsted and Elliott 1999); the Müller-Lyer illusion successfully biased the planning and execution of saccades. However, unlike experiment 1, the Müller-Lyer figures *did* generate biases in manual movements, but only when the target lights were extinguished at movement initiation.

The removal of visual target information in some blocks of trials had the potential to influence performance in at least two ways. Knowing in advance that the target lights would be extinguished at movement start, participants may have prepared their hand movements differently. For example, there are several studies which indicate that performers will adopt a more 'prepro-

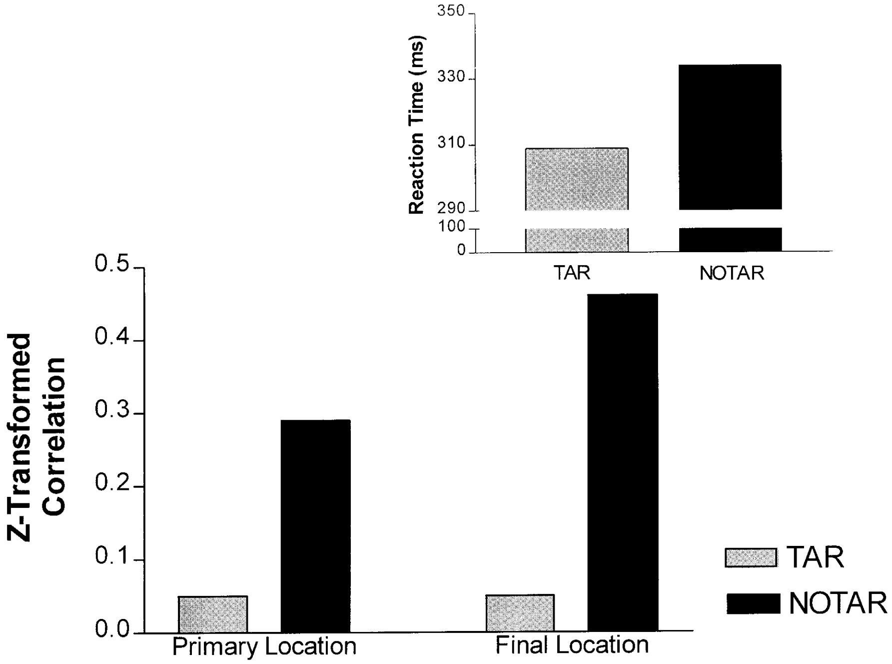

Fig. 4 Correlations between the location of the hand at the end of the primary submovement and at movement completion with the primary saccade. Inlay: hand reaction times

grammed' strategy when they know that vision will be eliminated upon movement initiation (Elliott and Allard 1985; Zelaznik et al. 1983). Alternatively, when visual information from the target lights was available throughout the entire movement, participants may have had a greater opportunity to amend their movement trajectories en route to the target, thus reducing their aiming bias. These two explanations are not mutually exclusive. Specifically, changes in programming and current control may both occur.

In a similar manner to Mack et al. (1985), this study's findings for target visibility indicate that the hand may only depend on extraretinal ocular information when retinal information about the position of the target is not available to the hand during movement. If the hand is more dependent on extraretinal information when the target is extinguished, the degree of oculo-manual coordination should increase. A higher degree of coordination would presumably require a more complex representation of the movement (i.e., motor program). The complexity of the program should be reflected in movement latencies (Henry and Rogers 1960). Evidence for this programming explanation was apparent in the eye-hand correlations. When the participant expected target information to be removed, the level of covariation between the eye and hand movements increased. In agreement with the programming hypothesis, the conditions with increased correlations (no vision of target) also showed increased reaction times (Fig. 4). However, other studies in which vision was eliminated at movement initiation have also found increases in reaction time with 'eye-fixed' aiming paradigms (Elliott and Calvert 1990; Elliott and Madalena 1987). The inflated programming times in these studies preclude attributing all the reaction time increases in the present investigation to coordination processes.

An alternate explanation for the influence of continuous target vision on eye-hand coordination is based on 'current control'. Given this view, the eye and hand movements are prepared and executed in a similar manner regardless of target condition. Once movements are underway, the performer has the opportunity to correct the hand movement based upon vision, comparing the present location of the hand with the desired endpoint. While making no specific predictions for reaction time, this 'control' hypothesis makes similar predictions to the programming position about the influence of vision on the covariation of eye and hand movement. Support for this explanation is provided by the overall tendency for positive correlations across all conditions. In addition, the hand was observed to slow in the presence of simultaneous eye movement, compared to situations in which the eye was focused on the target position prior to the limb movement. The increased movement duration of the hand may reflect the time taken by the eye to achieve the target and to provide retinal information about the target's position. Both the correlational trend and the manual movement times reflect common preparation of eye and hand movements for all vision conditions. However, the 'control' hypothesis would predict vision condition differences to exist for kinematic characteristics of the corrective processes (e.g., discrete corrections). While no such differences were present in this study, we have shown elsewhere (Elliott et al. 1998a) that performance benefits can be demonstrated for vision, presumably due to active modulation of the trajectory, in the absence of discrete discontinuities in acceleration/deceleration.

Although the changes in methodologies from experiment 1 to experiment 2 did allow the demonstration of coordinated action between the ocular system and manual system, the reasons remain unclear. Previous manipulations of vision in relation to an illusion (Elliott and Lee 1995) suggest that improved endpoint illusion potency with a no-vision delay is primarily due to an increase in the strength of the perceptual illusions when drawn from memory. Participants in experiment 2, however, only lost vision on movement initiation and showed illusion biases in the primary movement. Thus, movement programming was affected by the target context, but these performance biases were relatively weak. The influence of the illusion appeared to increase after the primary movement was completed. The larger bias is possibly due to misperceptions held in memory, which bias the error correction phase of the movement. To evaluate the influence of memory and its role in current control and preparation explanations of movement bias, experiments involving multilevelled temporal manipulations of vision are required (Elliott and Calvert 1990).

As demonstrated in experiment 1, and in previous investigations (Carnahan and Marteniuk 1991, 1994), the timing of limb and eye events remains relatively constant. The eye reached the target well before the hand in all conditions while the hand usually preceded the eye at movement initiation (cf. Biguer et al. 1982, 1984). The constancy in the order of the eye and hand appears complementary to the use of both ocular proprioception and other sources of information for manual control. Kinematic characteristics reflective of such use did not differ across information availability conditions. However, this lack of differences in current control features likely reflects the inadequacy of current criteria for identification of discrete corrections and/or more continuous feedback-based control (Elliott et al. 1998a).

General discussion

Experiments 1 and 2 reaffirmed the importance of vision for accurate goal-directed movement. While demonstrating normal effects for many manual variables, the availability of current visual information about the target also determined the degree of illusory covariation between the eye and the hand. The similar behaviour of the two effectors may be related to the availability of oculomotor efference for movement planning and execution, but only when the opportunity of visually based current control is limited. The dependency of this system interaction on the task environment was at odds with the ease with which the oculomotor system was biased by illusory endpoints in both experiments.

The central issue in these two studies was the identification of the type of information that mediates any eye-hand coordination. The availability of retinal information and concurrent efference as well as the accuracy of oculo-proprioception and efference was manipulated by altering eye action and position. The influences of both retinal and extraretinal channels of information were evident in the generation and active control of aiming behaviour. Coordination between these two systems appears mediated by both channels, with the level of coordination varying within a single aiming action dependent on the relative importance of movement preparation and current control.

Recently, Daprati and Gentilucci (1997) evaluated the type and quality of information provided by a target to a participant. In all cases, the amount and type of information was reflected in the subject's performance. The conclusion was made that subjects performed ‘global analyses’ on the visual representation of the object. Moreover, not only was information regarding the axis of the figure evaluated, but also the context within which those axes existed. This context information had a reduced, but still significant, impact on performance. The asymmetrical compilation of these egocentric (“where?” information) and allocentric (“what?” information) cues for stimulus evaluation was interpreted as an indication of visuomotor integration.

In light of Daprati and Gentilucci's (1997) suggestions, the implications of the present investigations become more apparent. The effects of current target vision on the magnitude of illusory bias may represent process interactions between allocentric and egocentric cues. From a physiological standpoint, these cue distinctions are divisible into previously described neural tracts. Work by Goodale and Milner (1992; see also Milner and Goodale 1993 for a review) suggests independent pathways for visual information exiting the striate cortex; the ‘dorsal stream’ projects to regions in the posterior parietal lobe bearing information pertaining to object location (i.e., egocentric) while the ‘ventral stream’ reaches areas within the inferotemporal cortex and relates to object identification (i.e., allocentric). The cognitive procedures for cue utilization proposed by Daprati and Gentilucci (1997) implicate cross-talk between these pathways as a mechnanism for perceptually based oculo-manual covariation. If interactions are occurring between these pathways with the regularity that the results of Gentilucci et al. (1996) and the present investigations suggest, it is unlikely that our visual system would have developed the two streams as physically or functionally separate. These interactions also happen with surprising rapidity (less than 120 ms for visual feedback utilization, see Carlton 1992 for a review); how would a ‘choice’ regarding integration based upon the relative precision of each pathway take place so quickly if the pathways were discrete? Instead, perhaps viewing these visuo-perceptual systems as a single distributed network is more appropriate (e.g., Goodman and Anderson 1989). During target finding, the relative clarity and importance of stimuli regarding object location and properties would be coded to common ‘integrating’ nodes. The existence of these focal points allows rapid compilation of physical, perceptual, and cognitive factors. The framework would also allow for the intermittent action of independent mediating networks (e.g., common coordination, Gauthier et al. 1988; common timing, Ivry and Keele 1989; Ivry and Corcos 1993).

A common integrated pathway for all allocentric and egocentric target information appears consistent with the current control hypothesis for explaining visually induced manual bias. Such a perceptually influenced network would not only explain erroneous corrections in the absence of continuous vision, but would also allow for the representation of the network to be updated in the presence of concurrent vision, thus allowing corrections to overcome initial perceptual errors. A common perceptuomotor pathway also allows coordinated eye-hand preparation, dependent on the availability and strength of other inputs (i.e., continuous vision, concurrent efference) – consistent with a pre-programming hypothesis.

The illusory effects of the Müller-Lyer configuration have already been discussed with regard to how they reflect what target information the aiming system uses and within which 'pathway' this information flows. Also at issue is when and whether the manual and ocular systems use the same information for movement preparation. This problem is exhibited most clearly by the inconsistency with which the manual system reacts to biases in target properties as compared to the regularity with which saccades are affected by the same input. If both systems are programmed synchronously, regardless of the level of planned coordination, features of both movements should reflect the common information upon which movement preparation was based. Moreover, the movements should covary more during the early stages of movements and then depart. The rate and amount of deviation would depend on the level of current control used to amend the arm trajectory during the correction phase. The kinematic data in this study do not support this conjecture; instead, the similarities between eye and limb movements increased (i.e., the arm became more biased) as the movement progressed. Thus, the movement adaptations are likely incorrect, inappropriately based upon (mis)representations of the endpoint held within memory.

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