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Eye-hand coordination to visual versus remembered targets

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Abstract It has been suggested that the basal ganglia preferentially contribute to movements made to remembered targets, whereas the cerebellum preferentially contributes to movements based on visual cues. Thus, it is possible that eye-hand coordination may differ in these two types of movement. To examine this issue we compared the response characteristics of combined eye and hand movements made towards visual versus remembered targets. In addition, the influence of the eye movement on the hand movement was investigated by comparing the effects of visual fixation in each task. Our results demonstrated that hand movement amplitude was greater when the hand movements were produced in isolation versus in combination with an eye movement. This was true regardless of whether the movement was made to a visual or a remembered target. This suggests that the integration of eye position information into the manual motor response occurs at a common neural site for both tasks. By contrast, the timing between saccade and hand onsets and offsets differed in the two conditions. This is consistent with the idea that the timing inherent in eye-hand coordination is the result of separate processing within either the basal ganglia or cerebellar systems. Taken together, the results from this study demonstrate that certain processes underlying eye-hand coordination during movements to visual versus remembered targets share a common neural substrate whereas others function independently.

Key words Eye-hand coordination · Basal ganglia · Cerebellum

Introduction

The coordination of eye and hand movements to visual targets is fairly well understood. Following the appearance of the peripheral target the saccadic eye movement is typically initiated first and the hand movement second (Biguer et al. 1984). Because of the ballistic nature of saccades the eye fixates on the peripheral target well before the hand movement is completed (Carnahan and Marteniuk 1991). As a result, the retinal and extraretinal information derived from the saccade is thought to contribute to the accurate guidance of the hand to the target. The fact that hand movement accuracy is systematically modulated when eye movements are restricted (Bock 1986) or perturbed in some manner (Binsted and Elliott 1999; de Graaf et al. 1995; van Donkelaar 1997) is consistent with this idea.

In contrast to the abundant literature on eye-hand coordination during responses to visual targets, the characteristics of coordinated eye and hand movements to remembered target locations have rarely been investigated. The purpose of the present study therefore was to compare the nature of coordinated eye and hand movements to visual versus remembered targets. Neurophysiological, clinical, and human imaging studies have demonstrated that separate neural systems contribute to these two types of tasks. In particular, the cerebello-thalamo-cortical system appears to be preferentially involved in movements based upon external sensory cues such as those arising from the appearance of a visual target (Inoue et al. 1998; Jueptner et al. 1996; Mushiake and Strick 1993; van Donkelaar and Lee 1994; van Donkelaar et al. 1999, 2000). By contrast, the basal ganglio-thalamo-cortical system appears to be preferentially involved in movements based upon internal cues such as those required to direct the eye and hand to a remembered target location (Crawford et al. 1989; Hikosaka and Wurtz 1985; Mushiake and Strick 1995; van Donkelaar et al. 1999, 2000). It is important to emphasize that this dissociation is relative rather than absolute: numerous studies have demonstrated that each system is involved in both types of movement. However, it is clear

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that *specific subcircuits* within each system preferentially contribute to the control of visually triggered vs internally generated movements (Mushiake and Strick 1993, 1995; van Donkelaar et al. 1999, 2000). Based upon this evidence we predicted that the characteristics of eye-hand coordination in each case would be quite different. Our results showed that the timing between the eye and hand movements was indeed different for each type of movement, whereas the influence of eye position information was not. These findings have been published previously in abstract form (Staub and van Donkelaar 1999).

Materials and methods

Subjects

Seven subjects (three females, four males; mean age 26.8 years) served as subjects in this experiment after giving informed consent. All were self-reported right-handers with normal or corrected-to-normal vision, and were free from any neurological deficits that could affect vision or eye or hand movements.

Apparatus and procedure

The subject sat in a dimly illuminated room looking down at a horizontal mirror onto which target images were projected. Pointing movements were performed on a table underneath the mirror in an open-loop fashion. A Watsmart system tracked the position of an infrared-emitting diode on the tip of the right index finger. An infrared corneal reflection device (IRIS Skalar) monitored the position of the right eye. A bite bar stabilized the head for this purpose. Both devices sampled at a rate of 200 Hz.

At the start of each trial a central fixation target appeared in the midsagittal plane approximately 35 cm in front of the subject. The subject was required to look and point at this target. A small disk on the table aligned with the target allowed the subject to accurately localize the start position with their hand. In the first experiment the subject performed under the following conditions:

Visual: after a variable delay (500–1500 ms) the central fixation target was extinguished and a peripheral target appeared 5, 10, or 20 cm to the right; the subject redirected their eye and hand to the peripheral target.

Remembered: after a variable delay (500–1500 ms) a visual target appeared for 200 ms 5, 10, or 20 cm to the right; after a further variable delay (1–4 s) the central fixation target was extinguished and a tone sounded to cue the subject to initiate eye and hand movement to the location of the previously flashed target.

Each condition was completed in separate blocks with the eye and hand moving together or while the subject visually fixated at the starting position and pointed at the peripheral location of the visual or remembered target.

In addition, to control for the effects of the spatial precue a second experiment was completed in which the *Remembered* condition was redone and the *Visual* condition was replaced with the following:

Visual-cued: after a variable delay (500–1500 ms) a visual target appeared for 200 ms 5, 10, or 20 cm to the right; after a further variable delay (1–4 s) the central fixation target was extinguished, the previously flashed peripheral target reappeared, and a tone sounded to cue the subject to redirect their eye and hand to the target.

After a series of warm-up trials each subject completed 30 trials for each condition (3 target amplitudes \times 10 trials in a pseudorandom order). The order of conditions was counterbalanced across subjects.

Data analysis

The amplitude of the hand movement in all the conditions as well as the timing of saccade and hand movement onset and offset in

the *Visual*, *Remembered*, and *Visual-cued* conditions were the main dependent variables measured. The beginning and ending of each type of movement were determined using velocity/time criteria. Comparison of each of these dependent variables across the different conditions was accomplished using repeated-measures analyses of variance (RM ANOVAs) with target amplitude (5, 10, and 20 cm), target type (visual vs remembered), and when appropriate eye movement (hand alone vs eye and hand) as independent variables. Amplitude was chosen as the main kinematic measure because we were interested in the effects of visual fixation on the movement. Previous research has demonstrated that this variable is sensitive to this manipulation (Bock 1986). It would have been just as informative to use accuracy as our measure and discuss the effects of visual fixation in terms of undershoot versus overshoot. Although reaction time and the spatial variability of the responses were also measured, they will not be discussed here because our results reconfirm what has been demonstrated previously – namely, that reaction time and variable error are increased during movements to remembered targets (e.g., Berkinblit et al. 1995; White et al. 1994).

Results

Figure 1 displays the group means for hand movement amplitude for the three different target amplitudes and each of the conditions from the first experiment. Requir-

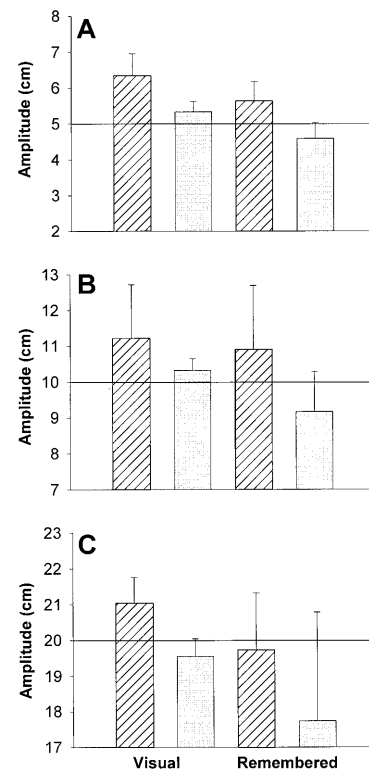
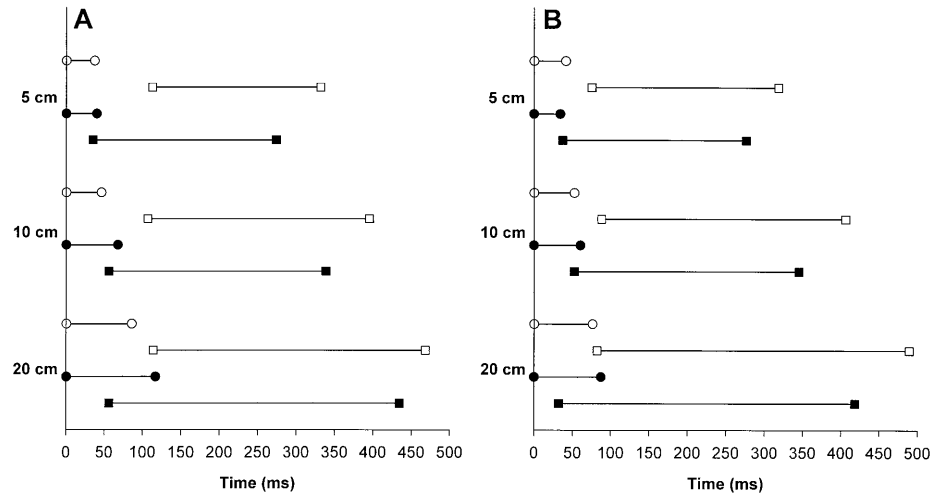


Fig. 1 Group means for hand movement amplitude for responses directed 5 (A), 10 (B), or 20 (C) cm to the right of the central starting position. *Hatched bars* represent hand movements generated while visually fixating; *gray bars* represent hand movements generated in conjunction with a saccadic eye movement. Responses in the *Visual* condition are on the left of each graph and responses in the *Remembered* condition are on the right. *Horizontal lines* in each graph represent target amplitude (error bars 1 inter-subject SD)

Fig. 2 Group means for saccade (*circles*) and hand (*squares*) movement onsets and offsets in the *Visual* (*open symbols*) and *Remembered* (*solid symbols*) conditions in the first (**A**) and second (**B**) experiments. All responses are aligned on saccade onset. *The leftmost point of each horizontal line represents movement onset and the rightmost point movement offset.* The responses to the 5-, 10-, and 20-cm target amplitudes are plotted at the top, middle, and bottom respectively of each graph



ing subjects to visually fixate and point to the peripheral target location led to a significant increase in hand movement amplitude compared to when a saccade accompanied the pointing response [$F_{(1,72)}=28.4998$, $P<0.001$]. This was true regardless of whether the hand movement was made to a visual or a remembered target. Thus, the influence that the generation of a saccade had on the simultaneously produced limb movement was similar for both types of tasks.

Figure 2A shows the timing of saccade and hand movement onsets and offsets in *Visual* and *Remembered* conditions in the first experiment. Clearly, the hand movement temporally overlapped with the saccade to a much greater degree in the *Remembered* condition than in the *Visual* condition. An RM ANOVA demonstrated that the difference between saccade offset and hand movement onset was significantly shorter (i.e., negative) in the *Remembered* condition than in the *Visual* condition [$F_{(1,24)}=11.35$, $P<0.0025$]. Thus, the type of task that the subject performed influenced the timing of the eye and hand movements.

It is possible that the spatial precue provided by the flashed peripheral target in the *Remembered* condition led to the timing differences. To test this possibility we completed the second experiment using the *Remembered* and *Visual-cued* conditions. Figure 2B shows the timing of the saccade and hand movements from this experiment. Although the temporal overlap between the saccade offset and hand movement onset was reduced in the *Visual-cued* condition, it was still significantly longer than in the *Remembered* condition [$F_{(1,24)}=4.92$, $P<0.036$]. This implies that the timing differences observed were the result of differences in the processing underlying the responses in each type of task rather than the simple presence of a spatial precue.

It has previously been shown that aiming accuracy starts to decrease for remembered targets only after they have been extinguished for at least 2 s (Elliott and Madelena 1987). We did not note any significant changes in either the amplitude or timing variables when com-

paring responses made to remembered targets following 1- to 2-s delays versus 3- to 4-s delays. However, because we were not explicitly testing this notion we did not run enough trials to examine it properly. It would be interesting to do so in future experiments.

Discussion

In the present investigation we examined the characteristics of coordinated eye and hand movements to visual versus remembered targets. Based on previous neurophysiological evidence we have assumed that the cerebellum preferentially contributes to the former task and the basal ganglia the latter. In this way we hoped to gain insight into how the brain organizes these two types of responses. Our results demonstrated that the influence of eye movement on the hand movement was similar for both types of tasks, whereas the timing of hand movement onset relative to saccadic offset was markedly different in each task.

The first result implies that eye movement information (or the lack thereof in the case of visual fixation) contributes to the processing required to perform both types of tasks in a similar manner. This could occur in one of two possible ways. First, saccadic signals may be integrated into the planning of the pointing response at a common neural substrate interconnected with both the cerebellum and basal ganglia. There are several candidate sites at which this could occur. The dorsal (Boussaoud et al. 1998; Joffrais and Boussaoud 1999) and ventral (Fujii et al. 1998; Mushiake et al. 1997) premotor cortices (PMd and PMv) each possess limb movement related cells that are modulated by changes in the direction of gaze – a fact that has recently been confirmed in humans using functional imaging techniques (Baker et al. 1999). In addition, the supplementary eye field (SEF) contains saccade-related cells that change their firing patterns when a limb movement is generated (Mushiake et al. 1996). Finally, the superior colliculus

(SC), a structure traditionally thought to contribute only to the control of gaze, has more recently been shown to possess limb movement related cells (Werner et al. 1997). Neuroanatomical studies have shown that each of these areas receives either direct projections from the cerebellum and basal ganglia (SC: Huerta and Harting 1984; May et al. 1990) or indirect projections via the thalamus (PMd and SEF: Matelli and Luppino 1996; PMv: Hoover and Strick 1993; Matelli et al. 1989).

Unfortunately, the data demonstrating eye-hand interactions at each of these sites are based on responses made to visually present targets. Analogous experiments have not been completed in which neurophysiological recordings are obtained from these areas during combined eye and hand movements to remembered targets. However, the fact that cells in the supplementary eye field differentiate between pro- and antisaccades (Schlag-Rey et al. 1997) and that cells in the superior colliculus are active prior to remembered saccades (Stanford and Sparks 1994) suggests that at least these two structures may also be involved in eye-hand coordination during responses to remembered targets.

The second possible interpretation regarding the similar effects of visual fixation in each task is that saccadic signals are integrated into the planning of the pointing response in the same way *within* both the cerebellum and basal ganglia. Each of these structures contains cells that possess either saccade or limb movement related activity (e.g., Hikosaka et al. 1989; Marple-Horvat and Stein 1987, 1990; Mushiaki and Strick 1995). However, the extent to which these different cell groups interact during coordinated eye-hand tasks has not yet been examined. Thus, the available evidence is more conducive to the possibility that saccadic and limb movement related information is integrated at cortical and/or collicular levels. Conceptually, this implies that information relating to the cues used to trigger and guide movement (i.e., visual vs remembered) arises from the cerebellum or basal ganglia and subsequently is modulated by saccadic signals at the sites discussed above.

The second main finding from the present study was that the temporal coordination between the eye and hand was markedly different in the two types of tasks. This implies that the different types of cues used in each task have a different impact on the processing of information related to the timing of the responses. The fact that differences were observed suggests that this aspect of the coordination may be controlled independently within the cerebellum and basal ganglia, rather than at a common site. Although direct neurophysiological support for this notion is currently unavailable, the cerebellum (Hore et al. 1991; Ivry et al. 1988) and basal ganglia (Boecker et al. 1998; Kermadi and Joseph 1995) are both involved with motor timing and sequencing. These functions could very likely contribute to the temporal aspects of coordinated eye and hand movements. Future research in which the ability of patients with cerebellar damage or Parkinson's disease to perform these tasks is examined would shed light on this issue.

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