

E. Niechwiej-Szwedo · W. E. McIlroy · R. Green ·
M. C. Verrier

The effect of directional compatibility on the response latencies of ocular and manual movements

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Abstract Visuomotor coordination is essential for the successful performance of everyday activities, and it could be affected by the directional compatibility between ocular and manual movements. Many tasks, such as driving or operating devices in the workplace, require a variety of coordination patterns with different levels of compatibility between the eyes and the hand. For example, the movement of the eyes and the arm can be coupled when both effectors point towards the same direction whereas in other tasks the movement of the eyes and the arm can be dissociated, for instance when a peripheral object is foveated while a button press response is executed concurrently. The objective of this study was to examine the latency of ocular and manual movements in tasks characterized by variations in directional compatibility. Four tasks were used to manipulate compatibility:

1. point and look at a peripheral stimulus (POINT AND LOOK)—high directional compatibility;
2. point to a peripheral stimulus while fixating in the center (POINT AND FIXATE)—low directional compatibility;
3. press a button while looking at a peripheral stimulus (PRESS AND LOOK)—low directional compatibility; and
4. press a button while fixating in the center (PRESS AND FIXATE)—no directional motor requirement.

We hypothesized that the latency of (1) manual and (2) ocular responses would be faster in the task with high directional compatibility compared with the tasks with low

compatibility or the task with no directional motor component. Ten healthy participants executed pointing and pressing movements with and without concurrent eye movement to randomly presented visual stimuli. In agreement with the first hypothesis, results showed that in a task with high directional compatibility, manual responses were initiated significantly faster when compared with the tasks with low compatibility or a task with no directional motor component:

1. pointing while looking was initiated 22 ms faster on average than pointing while fixating;
2. pointing while looking was initiated 91 ms faster than pressing accompanied by an eye movement; and
3. pointing while looking was initiated 102 ms faster than pressing while fixating.

The second hypothesis was partially supported by data which showed that eye movements directed toward peripheral stimuli were initiated significantly more slowly (30 ms on average) when accompanied by pressing in comparison with the latency of eye movements in the high-compatibility task. In contrast with the hypothesis, eye movements that were accompanied by pointing were not initiated faster than those in a task which required looking without pointing. In summary, these data suggest that directional compatibility is an important aspect of motor control. The effects of directional compatibility are discussed in a conceptual framework that considers the neurophysiological substrates that might be involved in mediating these effects.

Keywords Saccadic eye movements · Manual responses · Directional compatibility · Visuomotor coordination

E. Niechwiej-Szwedo · W. E. McIlroy · R. Green ·
M. C. Verrier (✉)
Restorative Motor Control Laboratory, Graduate Department of
Rehabilitation Science, University of Toronto,
500 University Avenue Toronto, Ontario, M5G 1V7, Canada
e-mail: m.verrier@utoronto.ca
Tel.: +1-416-978-5935
Fax: +1-416-946-8762

W. E. McIlroy · R. Green · M. C. Verrier
Toronto Rehabilitation Institute,
Toronto, Ontario, Canada

Introduction

Visuomotor coordination is essential for the performance of most daily tasks. For instance, to perform an accurate

reaching movement to an object with the arm, the retinal signal must be ultimately transformed into the execution pattern of muscle activity which has the appropriate force and direction to move the limb to the object. Everyday activities require a variety of continuous coordination patterns between the eyes and the arms with different levels of compatibility between the effectors.

Although compatibility between a sensory stimulus and a motor responses, stimulus-response compatibility (SRC), has been studied extensively (for a review see Kornblum et al. 1990), the compatibility between different types of motor responses has not received as much attention. SRC refers to the degree of conceptual or physical correspondence between stimulus and response whereby high compatibility enhances speed of responding and low compatibility slows speed of responding (Simon 1969; Kornblum et al. 1990). Analogously, we propose that compatibility between different motor responses can be defined as the degree of correspondence between the movements whereby greater compatibility gives rise to faster reaction times. We will focus in particular here on the “directional compatibility” of eye and arm movements. For example, directional compatibility would be highest when effectors move towards a common object (e.g. eyes and arm point towards the same direction). Directional compatibility is lower when the directionality of effector movement is dissociated, for example, fixating the eyes on one object while the arm moves towards another. Directional compatibility can be lower still, when two movements are executed in the opposite direction, which could be considered as a type of an incompatible task. For the purpose of this study, we focus on tasks that involve high and low levels of compatibility, and not the incompatible task.

It is important to understand the effect of directional compatibility on behavioral performance because tasks that are characterized by high and low compatibility are frequently performed during everyday activities, such as driving a car or operating devices in the workplace. Often, eye movements towards peripheral visual stimuli must be suppressed during goal-directed behavior that involves different manual manipulations, such as pressing a button or moving the arm towards a peripheral stimulus. The cortical mechanisms involved in the suppression of reflexive eye movements have been studied extensively (Everling et al. 1998; Bell et al. 2000; Munoz and Everling 2004); however, the effect of saccadic inhibition on the latency of different manual responses has not been examined previously. We attempted to address this issue using the framework of directional compatibility by employing tasks which require the execution of eye movements towards a peripheral visual stimulus or the suppression of reflexive eye movements, concurrently with manual pressing or pointing movements.

Recent studies with non-human primates suggest that ocular and manual movements that are directionally compatible might be planned and executed on the basis of a common frame of reference. Until recently, it had been believed that eye and arm movements are planned in

coordinate frames specific to each effector, for example, arm reaches would be programmed in a shoulder-centered coordinate frame (Desmurget et al. 1998), and eye movements in a gaze-centered coordinate frame (Snyder 2000). However, other studies have suggested that arm movements towards visual or even auditory targets can be planned in a common, eye-centered frame of reference (Batista et al. 1999; Cohen and Andersen 2000). The interaction between the programming of ocular and manual responses was also reported by Snyder et al. (2000). They recorded neural activity of reach-related cells in the parietal reach region while manipulating the type of movement executed (reach, saccade, or both), and initial position of the eyes and the arm. Results from their study showed that the activity of most cells was modified by the initial eye position in cases when the animal performed both eye and arm movements concurrently or just arm reaches. In summary, results from studies that employed electrophysiology suggest that directionally compatible eye and arm movements may share a common co-ordinate frame for movement planning, which could have a shortening effect on their latencies.

Previous behavioral studies that have attempted to examine the effect of motor compatibility between ocular and manual movements in different types of tasks have yielded inconsistent results. For example, some studies found that eye movements were initiated faster and reached higher peak velocities when they were accompanied by an arm movement aimed in the same direction (Epelboim et al. 1997; Lunenburger et al. 2000; Snyder et al. 2002). In contrast, Bekkering et al. (1994) reported that saccades were initiated more slowly when accompanied by pointing, and that the latency of pointing was not affected by the presence of an eye movement. One limitation of the previous studies is that they only examined the effect of arm movement on saccadic latencies (Epelboim et al. 1997; Lunenburger et al. 2000; Snyder et al. 2002). A second limitation is that they did not examine whether unconstrained pointing and pressing responses are affected differently by the presence of an eye movement (Bekkering et al. 1994; Zelinsky and Sheinberg 1997; Verleger et al. 2002).

Because of the limited research, the inconsistent findings, and the limitations described above, we undertook to shed further light on the question of response compatibility. Therefore, the objective of the present study was to examine the effect of directional compatibility on the latency of both ocular and manual movements for both pressing and unconstrained pointing responses. We hypothesized that (1) manual and (2) ocular latencies will be faster when directional compatibility is high in comparison with tasks with low compatibility or a task with no directional motor component. In order to test the hypothesis, we employed a series of tasks that required detection of a salient, visual stimulus in which the degree of directional compatibility between the ocular and manual responses was manipulated. In the POINT AND LOOK task, manual and ocular movements were in the same direction and therefore compatibility was considered to be

highest. Compatibility was estimated to be low in a POINT AND FIXATE task, where participants were asked to point towards a stimulus while maintaining fixation, and in a PRESS AND LOOK task, where participants pressed a button but looked towards a peripheral stimulus. We also employed a task which had no motor directional component, PRESS AND FIXATE, where participants had to press a button and maintain fixation when a peripheral stimulus was detected. In order to selectively examine the effect of directional compatibility, we did not place any requirement on the end-point accuracy of the manual responses. In other words, participants were asked to initiate these responses as fast as possible and they were not required to touch the stimulus.

Materials and methods

Participants

Ten healthy adults (four males and six females) ranging in age from 17 to 36 years (mean age 27.2 ± 5.6) volunteered to participate in the study. Participants were all right-handed, had normal or corrected to normal vision (20/20), and no history of neurological disorders. The protocol for the study received ethical approval from the ethics committee at University of Toronto, and informed consent was obtained from each participant at the beginning of the experimental sessions.

Apparatus

The visual stimulus (black square subtending 1° of visual angle) was projected on to a back-projection screen using a MultiSync MT1030 projector (NEC Technologies, Melville, New York, USA) with the resolution of 1024×768 and 85 Hz synchronization rate. A custom software program was written using the LabView programming language (version 5.1, National Instruments, Austin, Texas, USA) to control the stimulus presentation. The projector and the software program introduced a constant delay which was estimated, by means of a photocell, to be 30 ms.

Saccadic eye movements were recorded using electro-oculography (EOG). Grass silver–silver–chloride surface recording electrodes (diameter=6 mm) (West Warwick, RI, USA) were placed at the outer canthi of both eyes. The ground electrode was placed on the middle, upper part of the forehead. To minimize signal drift, the electrodes were placed on the skin at least 10 min before the start of the experiment, and participants were adapted to the light level in the room. It was ensured that impedance was below 10 kOhms during the collection. EOG signal was amplified using a Neuroscan Model 5083 SynAmps amplifier (Neuroscan, El Paso, Texas, USA), and acquired using the SCAN program (Neuroscan). EOG data were collected in a DC continuous mode (bandwidth 0–100 Hz)

at a sampling frequency of 1000 Hz. Baseline correction was applied during data acquisition to reduce signal drift.

Pressing and pointing responses of the hand were recorded at 360 Hz using a force-sensitive resistor (FSR) and stored for further analysis. The FSR offers a sensitive method of detecting forces applied to the surface by the fingers and reduces the electromechanical delay which would have been longer if traditional mechanical switches were used. Previous studies have found that electromechanical delay between onset of muscle activity and an overt movement can range between 50 and 200 ms, depending on the type of recording device and the complexity of the movement executed (Cavanagh and Komi 1979). It is likely that in the current study the delay was short, because of the method of recording (FSR) and the type of response used (simple press and release movements).

Experimental design

The experimental paradigm employed a within-subject design and involved a simple detection task. The independent variable was the type and combination of motor responses executed: manual (press, point) and ocular (saccade, fixation). The dependent variables were saccadic and manual reaction times (RTs).

Six motor tasks were used in the study: four experimental tasks with different levels of directional compatibility between the ocular and manual movements, and two control tasks, which provided baseline measures of saccadic and manual response latencies when these responses were executed separately. The order in which the experimental tasks were performed was randomized between participants. The following tasks were used with their corresponding levels of compatibility:

1. POINT AND LOOK—high directional compatibility
2. PRESS AND LOOK—low directional compatibility
3. POINT AND FIXATE—low directional compatibility
4. PRESS AND FIXATE—no directional motor requirement.

There were 100 trials collected for each participant in each of the experimental tasks with 80% probability of target appearance at each of the ten target locations: 4° , 11° , 19° , 26° , and 33° in the left and right hemifields. During trials when the target was not presented (20% of all trials) participants were asked to hold fixation and keep their finger on the FSR. Ten target locations were used to decrease the likelihood of anticipatory responses.

In the MANUAL CONTROL task, participants were instructed to press the FSR as soon as the target, which was presented at midline, was detected. This task provided a measure of how fast participants were able to execute the manual response without any directional requirement or concurrent eye movement. In the OCULAR CONTROL task, eye movements were executed without concurrent manual responses towards targets presented at the following eccentricities: 4° , 11° , 19° , 26° , and 33° in the

left and right hemifields. Previous studies (Lunenburger et al. 2000; Snyder et al. 2002) have shown that saccadic eye movements were initiated faster when accompanied by pointing. Therefore, we used the OCULAR CONTROL task to examine this effect in the present study.

Procedure

Participants were seated in a dark room in front of a large screen (1.55 m wide×0.90 m high) at a distance of 1.14 m. The right hand was positioned on a table in front of the participant, slightly to the right of the body midline. Before data collection, participants were trained how to perform the task. Throughout the experimental session participants' performance was carefully monitored by the experimenter to ensure that a pointing response was executed and not just a simple finger lift. At the beginning of each trial, participants were instructed to fixate in the center of the display on a red fixation star (visual angle 1°) which was followed by the target presented for 1500 ms at one of the ten randomized locations along the horizontal meridian: 4°, 11°, 19°, 26°, and 33° in the left and right hemifields. Participants responded with their right index finger which rested on the FSR at the beginning of each trial. In tasks that required pressing (PRESS AND LOOK, PRESS AND FIXATE, MANUAL CONTROL), participants responded by exerting increased force on the FSR. For the pointing tasks (POINT AND LOOK, POINT AND FIXATE), participants applied force to the FSR at the beginning of the trial, and released the FSR when pointing in the direction of the stimulus by executing an abduction or an adduction movement with the index finger. Since pointing and pressing responses are movements that engage different muscle groups, the effect of movement type on response latency was first examined when the stimulus was presented at fixation. Pilot data indicated no significant differences between the response latencies of pointing and pressing movements in a simple detection task with the stimulus presented in the centre. Participants were not required to touch the stimulus in any of the tasks.

In order to minimize the occurrence of anticipatory responses, the inter-trial interval was varied between 1000 and 2500 ms. Participants were instructed to make the appropriate motor responses as fast as possible while keeping their head stationary.

Data analysis

Manual and ocular RTs were defined as the time between target onset and the initiation of a response¹. The following procedure was implemented in a custom software program to determine the manual RT. First, the mean force applied to the FSR at the time of target onset

¹ Due to a delay imposed by the software and the projector the mean latencies are overestimated by approximately 30 ms. Because the delay was a constant, it did not affect the variance or our statistical analysis which was focused on comparisons between the conditions.

was found. Because the amount of force applied to the FSR varied between participants and trials, response initiation was identified when the applied force exceeded five standard deviations of the mean force applied in the first 50 ms of a trial. Five standard deviations were used to ensure that a random increase in the force level would not be identified as a true reaction time (RT) by the program. EOG data were filtered using a 4th-order Butterworth filter (cut-off frequency 0.5 Hz–35 Hz). The eye displacement data were then transformed to velocity by taking the first-order derivative. The following procedure was used to determine saccade initiation:

1. locate the first saccade with velocity $>150^\circ \text{ s}^{-1}$ that occurred after target presentation; and
2. step-back through the data to find the time when saccade velocity was within $\pm 10^\circ \text{ s}^{-1}$.

Before applying statistical procedures, ocular and manual RTs which were below the 1st or above the 99th percentile of the mean for a given participant and task were excluded from further analysis (1.2% of the data). Subsequently, all latency data were transformed using a logarithmic transformation, which resulted in a lognormal distribution of latency data (Zar 1984), and parametric analysis of variance (ANOVA) was performed on the transformed data. Logarithmic transformation was performed because the latency data were not normally distributed.

Results

The objective of the study was to examine the hypothesis that high directional compatibility between ocular and manual movements would lead to faster response latencies for both movements in comparison with tasks that are characterized by low directional compatibility or a task with no directional requirement. Figure 1 shows a typical pattern of these responses recorded by the FSR (manual) and EOG (ocular) in two types of tasks: PRESS AND LOOK and POINT AND LOOK. In all trials participants pointed in the direction of the target, and no overt head movement was observed.

Because the target was presented at ten eccentricities in the left and right hemifields, it was first examined whether the latencies of manual and ocular responses were influenced by the side of target presentation (left or right). Analysis showed that manual and saccadic RTs were not significantly different for a given eccentricity when targets were presented in the left and right hemifields ($P>0.05$). Thus, the following analysis was performed on the data which combined latencies to left and right targets.

First, the effect of directional compatibility on the latency of manual responses was examined by submitting the manual RT data to a three-way ANOVA with the following factors: manual task at two levels (point, press), ocular task at two levels (saccade, fixation), and

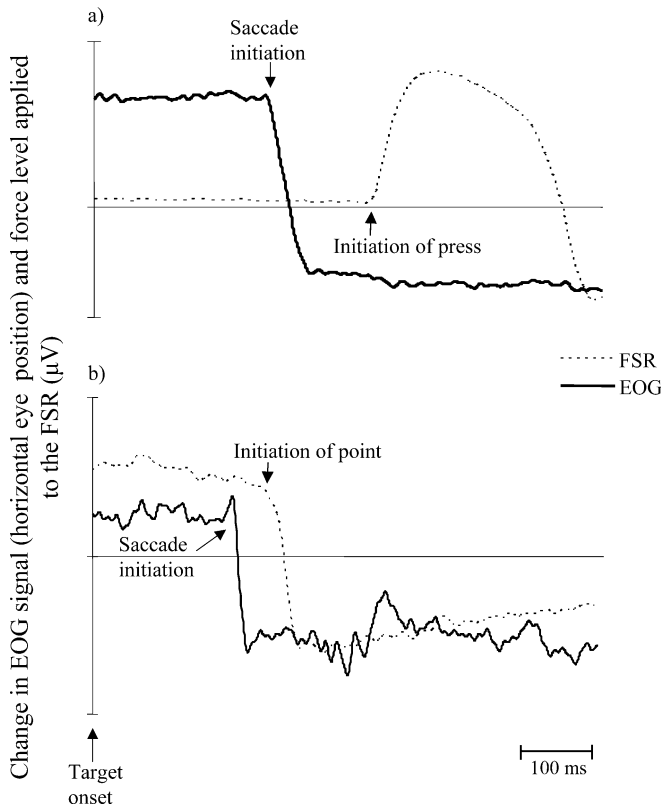


Fig. 1a,b Typical recording from the FSR showing the change in force level in a trial which required (a) pressing, and (b) pointing. Both figures show the corresponding displacement profile for a saccadic eye movement recorded by EOG

eccentricity (i.e. target position) at five levels (4°, 11°, 19°, 26°, 33°).

In support of the first hypothesis, a significant interaction effect between the type of manual task and ocular response was found for the manual RT ($F_{(1,9)}=7.42$, $P<0.05$). As illustrated in Fig. 2 and confirmed with a Tukey's HSD post-hoc test, pointing was initiated significantly more quickly (mean 289 ± 89 ms, $P<0.05$) in a task characterized by high compatibility (POINT AND LOOK) in comparison to the tasks characterized by low compatibility or a task with no directional motor component. The mean latency of pointing while fixating in the center (POINT AND FIXATE) was 311 ± 95 ms. Pressing was initiated significantly more slowly than pointing regardless whether the eye movement was present—the mean latency of pressing while looking toward a peripheral target (PRESS AND LOOK) was 379 ± 103 ms; the mean latency of pressing while fixating (PRESS AND FIXATE) was 390 ± 117 ms. Tukey's test revealed no significant differences in the manual RT between the tasks which required pressing ($P>0.05$). All effects were independent of target location in the visual field as indicated by a lack of a three-way interaction between manual task, ocular response, and eccentricity ($F_{(4,36)}=0.87$, $P>0.05$).

To test the second hypothesis, the saccadic RT data were submitted to a two-way ANOVA with the following

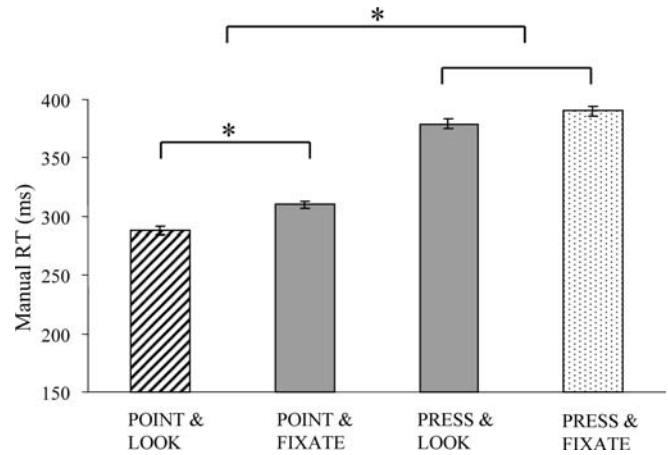


Fig. 2 Effect of directional compatibility on latency of manual responses. Mean manual RT was significantly faster when directional compatibility was high (POINT AND LOOK—hatched bar) compared with tasks with low compatibility (POINT AND FIXATE and PRESS AND LOOK—gray bars), and when the task had no directional motor component (PRESS AND FIXATE—dotted bar). Effects are significant ($*P<0.05$) except for the mean manual RT between the PRESS AND FIXATE and PRESS AND LOOK tasks (error bars show standard errors)

factors: manual task at three levels (point, press, absent), and eccentricity at five levels (4°, 11°, 19°, 26° and 33°).

There was a main effect of eccentricity ($F_{(4,36)}=25.01$, $P<0.0001$). Post-hoc analysis revealed that the latencies of saccades executed to targets presented at 26° and 33° were significantly slower. In addition, in partial support of the second hypothesis, analysis revealed a significant interaction effect between manual task and eccentricity on the latency of eye movements ($F_{(8,72)}=2.16$, $P<0.05$). As illustrated in Fig. 3, saccades that were accompanied by a press (low compatibility) were initiated on average 30 ms more slowly when targets were presented in the periphery of the visual field compared with the other tasks (POINT AND LOOK—high compatibility, OCULAR CONTROL). There were no significant differences between the latency of saccadic eye movements executed in the OCULAR CONTROL and POINT AND LOOK tasks across the eccentricities tested, thus, the hypothesis that eye movements would be initiated faster when accompanied by pointing was not supported.

To further quantify the relationship between the saccadic and manual latencies in the POINT AND LOOK and PRESS AND LOOK tasks, Pearson correlation coefficients were calculated for each participant. It was expected that the correlation between ocular and manual response latencies would be higher when the directional compatibility between the two movements was high. The correlation coefficients were transformed to Z -scores, and submitted to a two-sample Student's t -test.

Pearson correlation coefficients for each participant and task are shown in Table 1. Student's t -test on the Z -transformed correlation coefficients showed a trend only in the degree of correlation between saccadic and manual RTs for the two types of task ($P=0.0989$). The correlation coefficients were significant ($P<0.001$) in the POINT

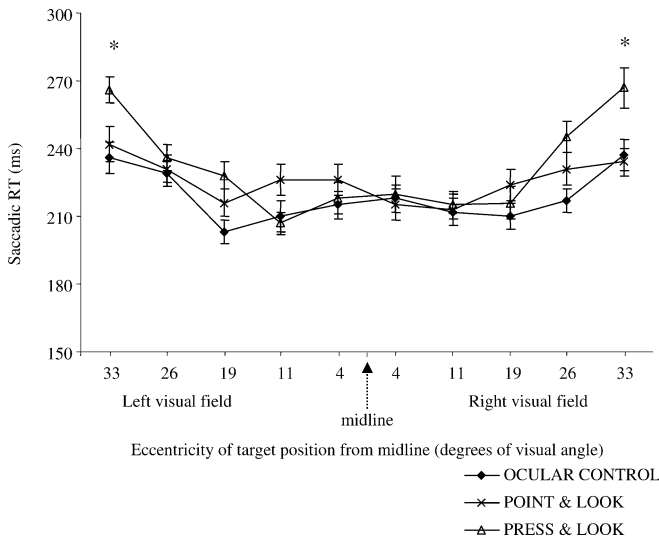


Fig. 3 Effect of directional compatibility on latency of eye movements across all eccentricities tested. Post-hoc analysis revealed that in the low compatibility task (PRESS AND LOOK), saccades accompanied by the press response were initiated significantly slower when targets were presented at the most peripheral locations, * $P < 0.05$ (error bars show standard errors)

AND LOOK task for eight out of ten participants, whereas significant correlation was only present for four participants in the PRESS AND LOOK task. Figure 4 illustrates the relationship between saccadic and manual RTs for individual participants for the two tasks. Despite individual differences, the figure clearly shows that the distribution of manual RT data in the POINT AND LOOK task is shifted to the left (i.e. toward faster response latencies).

To further understand the temporal relationship between saccadic and manual movements, the latency differences between saccadic and manual RTs (latency difference = manual RT - saccadic RT) in the POINT AND LOOK and PRESS AND LOOK tasks were calculated and submitted to a one-way ANOVA with manual task as the independent variable. It was expected that the two movements might be initiated in a closer temporal sequence if they are more compatible.

Table 1 Pearson correlation coefficients for individual participants obtained in the POINT AND LOOK and PRESS AND LOOK tasks

Participant	POINT AND LOOK	PRESS AND LOOK
1	0.32**	0.59**
2	0.45**	-0.07
3	0.58**	0.34**
4	0.44**	0.02
5	0.46**	0.64**
6	0.48**	-0.03
7	0.51**	0.17
8	0.22	0.16
9	0.40**	0.56**
10	0.24	0.24

**Signifies correlations that are significant at $P < 0.001$

The analysis revealed a significant difference between the POINT AND LOOK and PRESS AND LOOK tasks ($F_{(1,9)} = 24.17, P < 0.001$). As shown in Fig. 5, pointing was initiated on average within 60 ms after the initiation of a saccade, whereas pressing was initiated 149 ms after the eye movement started. We further analyzed the temporal proximity of saccadic and manual RTs by examining the latency difference in the pressing and pointing tasks for trials that had a similar latency of eye movements. The mean latency difference was calculated for the following intervals of saccadic RTs: 100–150 ms, 151–200 ms, 201–250 ms, 251–300 ms, 300+ ms. Confirming our previous analysis, pointing was initiated faster than pressing in each of the intervals: 99 ms vs. 277 ms (interval 100–150 ms), 87 ms vs. 192 ms (interval 151–200 ms), 62 ms vs. 176 ms (interval 201–250 ms), 25 ms vs. 99 ms (interval 251–300 ms), 22 ms vs. 38 ms (interval 300+ ms).

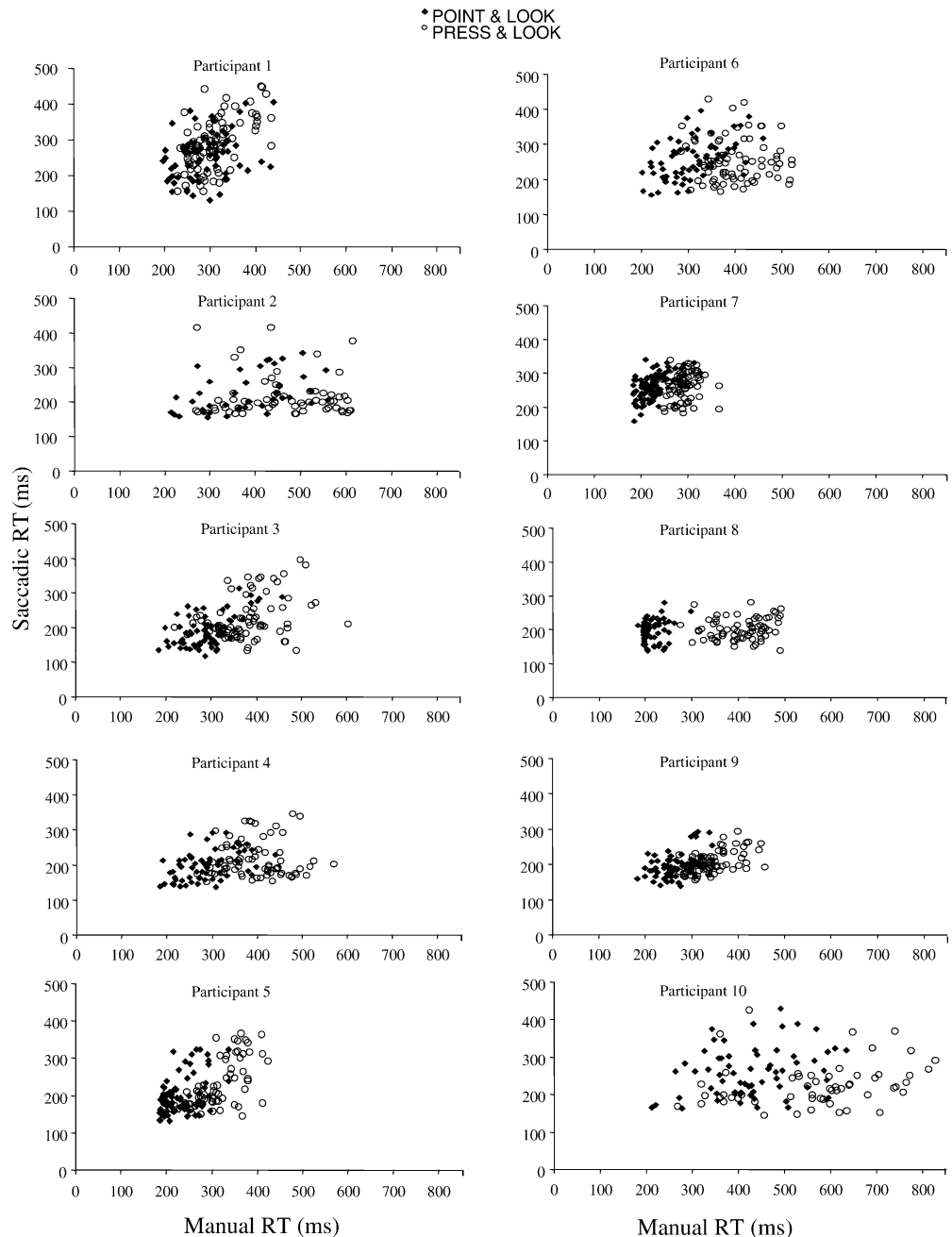
Results from the study also demonstrate the presence of a strong effect of SRC, which is evident in Fig. 2. Data show that pointing was initiated significantly more quickly than pressing, regardless of whether the eye movement was present or absent. The mean latency of responses for tasks which involved pointing and pressing is also plotted in Fig. 6, along with the mean manual RT obtained in the control task. Additional analysis between these tasks (CONTROL, POINT, PRESS) showed a significant difference, $F_{(2,18)} = 23.12, P < 0.0001$. Post-hoc analysis revealed that the latency of manual responses was significantly slower in the PRESS task than in the CONTROL and POINT tasks. These results provide support for the well known effect of SRC and they will not be discussed further in this paper.

Discussion

Results from the present study provide support for the hypothesis that directional compatibility influences the latency of ocular and manual movements. Specifically, our results demonstrate that manual responses were initiated significantly faster in the task characterized by high directional compatibility (POINT AND LOOK) in comparison with tasks with low compatibility in which the direction of eye and hand movement was dissociated (POINT AND FIXATE and PRESS AND LOOK) or in comparison with a task with no directional motor requirement (PRESS AND FIXATE). Analogous effects for the latency of saccadic eye movements in the highly compatible task were not found. In other words, saccades were not initiated faster when accompanied by pointing in comparison with the OCULAR CONTROL task. However, concurrent execution of the pressing response was associated with an increased latency of saccades directed toward targets located in the periphery of the visual field. These results indicate that the directional compatibility between ocular and manual movements contributes to the planning and execution of these responses.

Data from the present study confirm and extend findings from studies that employed manual and ocular

Fig. 4 Relationship between manual and ocular RTs in the POINT AND LOOK and PRESS AND LOOK tasks illustrating a leftward shift toward shorter latencies in the distribution of the manual RT data in the POINT AND LOOK task when compared with the PRESS AND LOOK task for individual participants



responses. Recent studies with humans and primates reported faster saccadic latencies and higher peak velocities when the eye movement was accompanied by a coordinated arm movement (Lunenburger et al. 2000; Snyder et al. 2002). Other studies reported no significant differences or even slower response latencies when manual and ocular responses were executed concurrently compared with a single task (Mather and Fisk 1985; Bekkering et al. 1994; Zelinsky and Sheinberg 1997; Verleger et al. 2002). The focus of the current work was to extend these findings by considering the effect of directional compatibility on the latency of ocular and manual movements in tasks characterized by high and low compatibility. Because of the experimental paradigm used

in the present study, previous apparently conflicting results can be explained by considering the type of manual movement that was performed. Our results from the highly compatible task are analogous with those from previous studies that reported a facilitation effect for unconstrained pointing movements (Lunenburger et al. 2000; Snyder et al. 2002). The results from the low-compatibility tasks are comparable with those from studies that reported slower latencies for constrained pointing responses or button presses, when these responses were accompanied by an eye movement (Bekkering et al. 1994; Zelinsky and Sheinberg 1997; Verleger et al. 2002).

Results from the present study did not confirm the hypothesis that saccadic latencies would be faster when

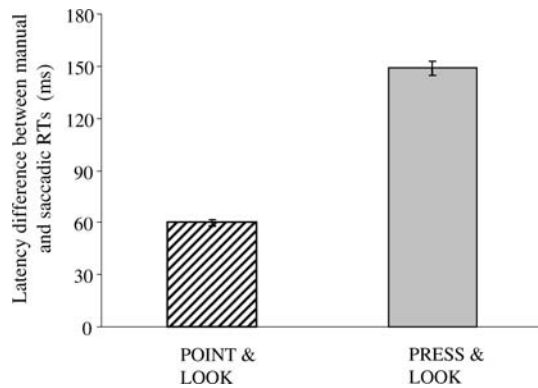


Fig. 5 Manual responses were initiated significantly faster, $P < 0.001$, after the eye movement started when the directional compatibility was high (POINT AND LOOK—*hatched bar*) compared to the low-compatibility task (PRESS AND LOOK—*gray bar*) (error bars show standard errors)

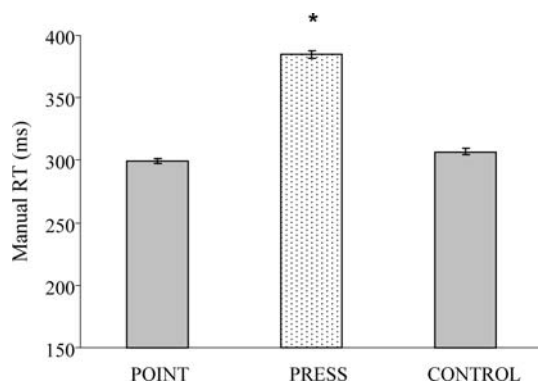


Fig. 6 Effect of SRC on latency of pressing and pointing responses of the upper limb. Pressing was initiated significantly more slowly, $P < 0.0001$, when the target was presented at the periphery because of low SRC (*dotted bar*). Fast response latencies were obtained when SRC was high (*gray bars*). Pointing responses were executed toward peripheral targets and pressing responses were initiated to targets presented at midline (error bars show standard errors)

accompanied by pointing. The mean saccadic latencies ranged from 213 ms for targets presented closer to midline to 242 ms for targets presented at the periphery. Although these latencies are overestimated by approximately 30 ms, they are representative of long-latency regular saccades, and it could have been expected that participants were capable of generating eye movements at shorter latencies. For example, express saccades range in latency from 90 ms to 120 ms, and the latencies of short-regular saccades fall in the range of 135–170 ms (Gezeck et al. 1997). In contrast with results from Lunenburger et al. (2000) and Snyder et al. (2002), our data showed that concurrent pointing did not significantly affect saccadic latencies. There are several possibilities that could account for the differences between these results. First, Lunenburger et al. (2000) used only two spatial locations for target presentation, whereas in the present study the target was displayed randomly at ten locations in the left and right hemifields. Thus, it is possible that the facilitatory effect of a coordinated arm movement on saccadic latency is dependent, to some extent, on the spatial uncertainty of the

target. In the study by Snyder et al. (2002), subjects were primates and the uncertainty of target location was also high (their target was presented at eight locations). However, the subjects were highly trained, whereas the participants in our study were naïve young adults. In addition, the above mentioned studies examined only the effect of a coordinated arm movement on the latency of ocular response but did not examine the effect of an eye movement on the speed of the manual response. It is possible that the latency of either the ocular or the manual response is facilitated, which could depend on the strategy used by the subject. Alternatively, it is also possible that the facilitatory effect of an arm movement on saccadic latency could also depend on the spatial uncertainty of the target and the extent of subject training or a combination of factors.

Eye movements toward the two most peripheral targets were initiated more slowly in all the tasks, which is in agreement with previous studies that examined the effect of eccentricity on saccadic latencies (Kalesnykas and Hallett 1994; Fuller 1996). It is unlikely that slower saccadic latencies to the peripheral targets were due to head movement. First, participants were instructed to keep the head stationary which was monitored throughout the experiment. Second, previous studies that examined saccadic latencies in tasks when the head was immobilized and when the head was free to move reported no significant differences between these conditions or even faster saccadic latencies when the head was free to move (Guitton et al. 1984; Laurutis and Robinson 1986; Pelisson et al. 1988).

Although saccadic latencies were not faster when accompanied by pointing, saccades executed to the most peripheral targets were slower when accompanied by pressing. This partly supports the hypothesis that the latency of response initiation would be slower when the directional compatibility between motor responses is low. These results suggest that low directional compatibility between the ocular and manual movements might create an interference effect and increase the processing requirement of the task. In the present study the interference effect of pressing on the latency of eye movement was evident only for targets presented at 33° to the left or right from the midline. However, the effect might become more evident, even at smaller eccentricities, if the direction of the ocular and manual movements is incompatible, for example, when both movements are executed in the opposite directions (Snyder et al. 2002).

In order to explain the results from the present study we propose a conceptual framework that considers the possible underlying neurophysiological substrates that could be involved in mediating the effects of motor compatibility. We propose that motor compatibility can be conceptualized by considering the following stages of sensorimotor processing:

1. target acquisition;
2. sensorimotor transformation; and
3. movement execution.

The main assumption of the framework, which we believe is reasonable, is that movements that are highly compatible could share processing stages which would lead to faster response latencies and higher correlations between the latencies of these movements. At the target acquisition level, high compatibility occurs when both eye and arm movements are initiated by a common stimulus, and low compatibility occurs when different stimuli guide the initiation of the two motor responses. Sensorimotor transformation involves transforming the sensory input into a frame of reference appropriate for the effector movement. For example, eye and hand movements can be planned and executed in gaze-centered, head-centered, or shoulder-centered coordinate frames (Desmurget et al. 1998; Snyder 2000). Accordingly, movements executed in the same direction might be highly compatible because they would share a common frame of reference. The third stage of sensorimotor processing is movement execution. The degree of compatibility at this stage might depend on the interaction between descending motor pathways for ocular and manual movements. For instance, the motor pathways of highly compatible movements would require reciprocal neural connections to reinforce the descending motor commands.

When a single target guides ocular and manual movements, the acquisition stage would be shared and should remain the same for the two responses. This would mean that target detection would be performed by the same neurons in primary and secondary visual areas, such as V1 and V2. Our tasks involved the same acquisition process. The fact that concurrent eye movement significantly affected the latency of pointing but not pressing suggests that ocular and manual pointing movements are more closely related, and might share further processing stages.

In order to execute a visually guided pointing movement with the eyes or the arm, the sensory input must be transformed into the appropriate reference frame. These coordinate transformations are reported to be performed by the neural networks in the posterior parietal cortex (Colby 1998; Andersen and Buneo 2002; Cohen and Anderson 2002). The visually acquired target is initially represented in a retinocentric frame of reference, which is closely related to the reference frame used by the ocular system. However, in order to execute a reaching movement with the arm, the target must be coded with respect to the limb, or at least the position of the limb must be taken into account and combined with the retinal position of the target and the eye-in-head signal (Snyder 2000; Snyder et al. 2000). Recent studies suggest that the earliest stage of sensorimotor transformation for reaching could be performed by neurons in area V6A (Shipp et al. 1998; Battaglia-Mayer et al. 2000). The responses of cells in area V6A are modulated by eye and hand position as well as the direction of eye and hand movement, and they project to the parietal areas, such as the lateral and medial intraparietal areas (LIP, MIP), which are involved in the planning of these responses. It is possible that faster latency of pointing when accompanied by a concurrent eye movement in the compatible condition could have

occurred due to neural activity in area V6A where the target was coded in an eye-centered coordinate frame, which was used to plan both movements.

Descending motor pathways that project to motor neurons controlling eye and hand movements could be influenced by activity in the dorsal pre-motor area (PM_d) area and the superior colliculus (SC), which both receive direct projections from area V6A (Shipp et al. 1998). The activity of cells in PM_d is not only dependent on the spatial location of the target and the direction of the planned movement, but is also modulated by the oculomotor context, which includes whether eye and arm movements are executed separately or together (Jouffrais and Boussaoud 1999). In addition, PM_d projects to cortical areas directly involved in the programming of arm movements (primary motor cortex) and eye movements—frontal eye fields (FEF) and SC. The SC has been traditionally classified as an oculomotor structure involved in eye movement control because of its input (LIP, V6A, and FEF), and output (brainstem oculomotor nuclei) projections (Fisher 1987; Gaymard et al. 1998). The traditional view of the SC as a strictly oculomotor control center was modified recently when cells with reach-related activity were identified in the deeper layers (Werner et al. 1997a; Stuphorn et al. 2000). The reach-related cells in the SC could not directly influence the alpha motor neurons that control the limb muscles, but they could modulate the excitability of these neurons via the tectospinal and the reticulospinal pathways (Werner et al. 1997b).

In summary, the faster latency of manual pointing when accompanied by a concurrent eye movement could be due to shared processing at several cortical and sub-cortical sites. For example, when movements are compatible, cells in area V6A might transform the sensory input into a common reference frame for ocular and manual movements, and neurons in PM_d or SC could influence the activity in the descending motor pathways to ocular and limb muscles.

Conclusion

The study was conducted to examine the effect of directional compatibility between ocular and manual movements. Data from the study indicate that the latency of these responses depends to some extent on the level of directional compatibility. Specifically, when both movements were executed toward the same direction, pointing was initiated earlier in comparison with tasks in which the direction of eyes and hand movement were dissociated or with a task with no directional, motor component. Eye movements were also initiated later in some cases when the manual response was not directionally compatible. The framework we propose considers the properties of the neuronal networks involved in the sensorimotor transformation and movement planning of eye and hand movements. Specifically, we propose that neural areas, such as V6A, PM_d, and SC could be involved in the programming of both ocular and manual movements when they are

directionally compatible. Our findings should be considered when interpreting other behavioral studies. For instance, the latency of ocular and manual responses is used extensively to indicate the outcome of visual or attentional processes; however, our results indicate that the compatibility between these responses could also influence how visual information is processed. Also, these findings need to be taken into consideration when designing paradigms for assessment of visuomotor coordination in individuals with neuropathologies.

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