

ATTENTION AND THE VISUOMOTOR SYSTEM: CAN THE DORSAL STREAM
PROCESS TWO ACTION TARGETS SIMULTANEOUSLY?

by

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Abstract

The processing of visual information for the purpose of executing goal-directed actions is, according to dual-stream theory, carried out by the 'dorsal stream', an occipito-parietal route of visual processing in the primate brain. The current study investigated the attentional capacity of the dorsal stream: Can it attend to more than one action target at a time? Two experiments were carried out to address this question. In the first experiment, 11 healthy participants executed fast sequential aiming movements in which they tapped two horizontally aligned targets. On a given trial, either, or both, of the targets could jump to a new location. This perturbation was tied to the participant's saccade so that the target movement would not be consciously perceived, and the targets were extinguished 20ms after the perturbation. The targets were, therefore, no longer visible when the eyes landed. The results of Experiment 1 revealed that participants consistently adjusted their aiming movements in accordance with the perturbations, regardless of which target jumped. Experiment 2 employed a similar protocol, but added a 3sec delay between the saccadically-triggered double-step and the onset of the participant's movement. This manipulation was intended to eliminate dorsal-stream involvement in the guidance of the movement, as the dorsal-stream is thought to retain visual information for, at most, 2sec. After this 2sec period, movement guidance should rely on a ventrally-stored conscious visual representation. We hypothesized, therefore, that the delay would eliminate the effect observed in Experiment 1. Nine healthy participants took part in Experiment 2, and, contrary to our hypothesis, produced aiming movements very similar to those of Experiment 1. The results of Experiments 1 and 2 demonstrate that location information about both targets in a sequential aiming movement is processed simultaneously and that

this information can be used to update the movement. However, the results do not allow us to confidently conclude that the *dorsal* stream can process two targets simultaneously. Potential problems with the saccadically-triggered double-step design as a means of investigating dorsal stream processing are discussed.

Table of Contents

Abstract.....	ii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
Acknowledgements.....	viii
Chapter 1	
Introduction.....	1
The Dual-Stream Theory of Visual Processing.....	2
The Double-Step Paradigm and Saccadic Blindness.....	4
Movement Complexity and Sequential Aiming.....	7
Attention and Action.....	9
Attention, Action, and Sequential Aiming Movements.....	13
Chapter 2	
Experiment 1: Introduction.....	14
Methods.....	14
Participants.....	14
Apparatus.....	15
Procedure.....	16
Analysis.....	20
Results.....	21
Discussion.....	34

Chapter 3

Experiment 2: Introduction.....	37
Methods.....	38
Participants.....	38
Apparatus and Procedure.....	38
Analysis.....	39
Results.....	40
Discussion.....	43

Chapter 4

General Discussion.....	49
Attention and Action.....	50
Other Issues.....	51
Limitations of the Current Study.....	53
Future Directions.....	54
References.....	57

List of Tables

Table 1.	Perceptual report from Part 2 of Experiment 1.....	33
Table 2.	T-test analysis of the perturbation effect in the NO-DELAY and DELAY conditions.....	43
Table 3.	Perceptual report results for Experiment 2.....	43

List of Figures

Figure 1.	The apparatus.....	16
Figure 2.	The 16 possible target configurations in Part 1 of Experiment 1.....	19
Figure 3.	The 4 configurations added to Part 2 of Experiment 1.....	19
Figure 4.	The influence of target perturbations on CE for trials in which one of two targets jumped.....	22
Figure 5.	The influence of target perturbations on CE for trials in which both targets jumped.....	24
Figure 6.	The influence of target perturbations on CE for single-target trials.....	24
Figure 7.	The influence of target perturbations on PV in Experiment 1.....	28
Figure 8.	The influence of target perturbations on TtPV in Experiment 1.....	30
Figure 9.	The influence of left and right target jumps on CE in the NO-DELAY condition of Experiment 2.....	41
Figure 10.	The influence of left and right target jumps on CE in the DELAY condition of Experiment 2.....	42

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Chapter 1

Introduction

How does attention operate in the visuomotor system? Does the system select only one target at a time, or is it capable of attending to two or more targets simultaneously? When I pick up a sugar cube and subsequently drop it into a cup of tea, the visuomotor areas of my brain that guide this sequence of actions might select only the sugar cube as an action target until it has been grasped, after which they might select the cup. Alternatively, both the cube and the cup might be selected simultaneously, so that even as I initiate my reach for the sugar cube, action-relevant features of the cup are being processed. While considerable research has examined attention-for-perception, relatively little has investigated attention-for-action, and those studies that have done so have typically focused on responses to a single target. The purpose of the current study was to further our understanding of attention-for-action, specifically in terms of the visuomotor system's ability to monitor changes in more than one target at a time. I hypothesized that the visuomotor system **can** attend to multiple targets simultaneously. This hypothesis was based on the results of previous research on sequential aiming movements and on the logic that a more effective visual system is one that attends to both current and subsequent targets. The following introduction reviews relevant research on visual processing for action, the programming of sequential aiming movements, and attentional selection-for-action. Chapters 2 and 3 outline each of the study's two experiments and provide analyses and discussions of their results. Finally, Chapter 4 is a general discussion of the study's findings.

The Dual-Stream Theory of Visual Processing

An intuitive understanding of vision suggests that we first perceive the world and then act upon it: a serial progression of visual information from perceptual processing to action planning. While it is certainly likely that we use our conscious perception of the world to plan our actions in a global, prospective sense (indeed, as Ward (2002) points out, perception would be of little use and our actions potentially chaotic if this were not the case), considerable evidence suggests that vision for perception and vision for the real-time control of action are processed in parallel (Milner & Goodale, 1995).

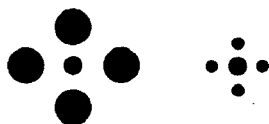
Mishkin, Ungerleider, and Macko (1983) were the first to suggest parallel cortical routes of visual processing in the primate brain. They proposed, on the basis of research in monkeys, that a *dorsal* route of visual processing proceeding from primary visual cortex into posterior parietal cortex processes spatial information (“where”) and that a *ventral* route proceeding from primary visual cortex into inferior temporal cortex processes object information (“what”). Several years later, however, Milner and Goodale (1995) suggested a different role for the dorsal stream. They agreed with Mishkin, Ungerleider, and Macko about the function of the ventral stream, but they argued that the dorsal stream was specialized for action processing (“how”), rather than for spatial processing per se. The basis for their claim was primarily neuropsychological evidence. A series of experiments with DF, a patient with lesions to her ventral stream, revealed that while DF’s ability to consciously perceive and identify objects in the world was dramatically impaired, her ability to effectively interact with objects was largely preserved (see Milner & Goodale, 1995, and Goodale & Milner, 2004 for overviews of this evidence). Further support for their theory is that lesions to the dorsal stream produce optic ataxia, a syndrome characterized by an impaired ability to interact with objects but

a preserved ability to identify them (see Milner & Goodale, 1995), in many ways the reciprocal of DF's condition. Furthermore, individuals with dorsal stream lesions are unable to make the fast, automatic corrective movements to displaced targets that non-patients produce (Pisella et al., 2000). The dorsal stream, therefore, appears to play a pivotal role in the on-line control of our actions.

Support for Milner and Goodale's version of dual-stream processing can also be found in experiments with healthy participants. Some of the most interesting (and most controversial) support comes from experiments in which participants interact with visual illusions. Aglioti, DeSouza, and Goodale (1995), for instance, had participants reach to and grasp the central circle in an Ebbinghaus (or Titchener) illusion¹. While participants' perceptual reports were influenced by the illusion, the scaling of their grip apertures was not. The researchers argued that this demonstrated dissociation between vision for perception and vision for action. Subsequent studies with illusions have been divided in their support for this position. The details of the debate will not be outlined here, but the reader can refer to Carey (2001) for a review of the illusion literature.

Less controversial support for Milner and Goodale's theory is provided by experiments that examine participants' adaptations to target perturbations when they are making fast aiming movements. (The 'double-step' paradigm that is employed in these experiments will be described in detail in the following section. It is a useful tool for

¹ The typical display for this illusion includes two identically sized circles, one of which is surrounded by large circles and one of which is surrounded by small circles. Most people report that the circle surrounded by small elements appears larger than the circle surrounded by large elements.



investigating on-line movement control and is a key component of the proposed experiments.) Some of the most compelling support is provided by an experiment by Desmurget et al. (1999). These researchers examined participants' aiming responses to a perturbed target under normal conditions and under transcranial magnetic stimulation (TMS) of the posterior parietal cortex, the suggested location of the visuomotor modules of the dorsal stream (Milner & Goodale, 1995). Desmurget et al. hypothesized that the de-activating effect of TMS on dorsal stream processing would hinder the stream's on-line error correcting functions. Consistent with this hypothesis, participants were unable to correct their movements to the perturbed target when TMS was applied.

While the perception/action version of dual-stream processing is not without controversy, considerable evidence has accumulated in its favour, only a fraction of which has been presented here. The design of my proposed experiments has been informed by perception/action thinking, and the results will, in part, be interpreted within this theoretical framework.

The Double-Step Paradigm and Saccadic Blindness

The double-step paradigm is a design in which a movement target jumps twice: the target starts at the same location as the participant's finger and/or eye fixation, jumps to a new location at the start of the trial, and then jumps again. (The trigger for the target's second jump will vary between studies, but it might be tied, for example, to the onset of the participant's hand movement or saccade.) The second jump is of primary

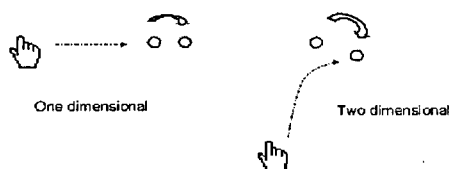
interest, as it is the one that enables the investigator to examine how the visuomotor system adapts to changes in a target's location².

Goodale, Pelisson, and Prablanc (1986) used a double-step design to show that the correction of a movement to a perturbed target could occur in the absence of any awareness of the perturbation. Participants made rapid aiming movements to a target that underwent either a single or a double step. In the double-step trials, the second step was tied to the participant's initial saccade: the target jumped when the saccade reached peak velocity. As a result of this pairing of the saccade and the jump, participants were unaware of the target perturbation. Despite this lack of awareness, participants consistently adjusted their aiming movements to the target's new location. Prablanc and Martin (1992) found similar results for a two-dimensional double-step design, i.e., a design in which the target jump was in a direction tangential to the axis of the initial movement³. Again, participants non-consciously adjusted their movements to the target jump.

The pairing of the target jump with the saccade is an important feature of the double-step experiments described above. It takes advantage of people's lack of conscious awareness of motion during their saccadic eye movements (the absence of

² The target's first jump as described above (from proximal to distal location) is not, in practice, necessary for a double-step trial; the key feature is that the distal location of the target changes at some point during the trial. In other words, a double-step trial could begin with the target already at, or simply appearing at, a distal location.

³



motion ‘blur’ as we move our eyes from location to location is an example of this phenomenon). The mechanism behind this ‘blindness’ is not entirely clear, although it appears that a reduction in neuronal sensitivity to motion, perhaps operating at the level of the magnocellular pathway, is at least in part responsible (see Ross et al., 2001 for a review). Central mechanisms, such as the perceptual system’s assumption of space constancy (i.e., the assumption that motion during a saccade is due to the saccade itself and not displacement of the world) may also play a role (Deubel, Schneider, and Bridgeman, 2002). For the purposes of the current study, however, it is sufficient that saccadic suppression exists as a robust phenomenon; it allows us to examine motor behaviour in the absence of conscious awareness, hopefully providing a window into uniquely dorsal stream processes⁴.

It is worth noting that all double-step experiments to date have involved a single target. The goal of the participants in such studies is to make a single movement to a single target. The target may change location, but it remains the same target. We do not know how the visuomotor system would respond if the goal was to aim at two (or more) targets sequentially under conditions in which one, or both, of the targets could change location. The current study pertains to precisely this issue.

⁴ There is a potential problem here, however. If saccadic suppression is operating at the level of the magnocellular pathway, which is the primary source of visual input to the dorsal stream, one might expect *dorsal* operations to be impaired during a saccade. The ventral stream, which receives input from both magnocellular and parvocellular pathways, should at least retain its parvocellular-mediated signals (although there is evidence that the high spatial frequency information processed by the parvocellular pathway is also impaired during a saccade due simply to the high speed of the saccade (see Ross et al., 2001)). The extrageniculate input to the dorsal stream (i.e. input from the superior colliculus) may provide a way around this problem.

Movement Complexity and Sequential Aiming

In 1960, Henry and Rogers investigated the influence of response complexity on reaction time. They found that as a movement task's complexity was increased, the reaction time (RT) to initiate the task was also increased. (Their study involved 3 levels of complexity: 1) lifting a finger, 2) reaching out and grasping a ball, 3) reaching out and hitting a ball, reaching down and pressing a button, and then reaching out and hitting a second ball.) The same influence of task complexity on RT has also been demonstrated with aiming tasks in which participants make pointing movements to two circular targets in sequence (Lajoie & Franks, 1997). These studies provide evidence that more complex movements require increased programming time. More importantly, these studies provide evidence that more than just the initial portion of a movement is programmed prior to movement release: if a task involves multiple targets, at least some of these are considered during the initial programming.

Further support for the idea that the second target in a sequence is considered during initial response programming comes from a study by Ricker et al. (1999). In their study, Ricker et al. had participants make fast sequential aiming movements to two targets. In one experiment, they varied the size of the second target. They found that the size of the second target influenced the peak velocity of the movement to the first target (the larger the second target, the higher the peak velocity of the movement to the first target), suggesting that the planning of the movement to the second target was occurring well before the end of the first portion of the movement. In a second experiment, they manipulated the visibility of the targets. Trials were blocked by condition, of which there were three: 1) vision of the targets was removed at movement onset and then returned at

touchdown on the first target, 2) vision of the targets was available throughout the trial, 3) only the first target was present (and was always visible). There were two important findings. First, reaction time was longer when there were two targets than when there was only one. Second, reaction time was longer in the vision-temporarily-removed condition than in the full-vision condition. Both of these findings suggest that movement planning to the second target can occur prior to the initiation of the first movement. The second finding also suggests that the amount of initial programming depends on the availability of vision during the movement to the first target. On the basis of these findings, Ricker et al. suggested that, during a normal sequential aiming movement, planning to the second target occurs both prior to and during the movement to the first target. They suggested that a 'rough' plan of the entire movement was prepared prior to movement initiation and that this plan was then refined during the first phase of the movement. This potential for on-line 'refinement' bears on the current investigation, which will examine dorsal stream (on-line) processing immediately after an initial movement plan has been formulated.

Henry and Rogers' (1960), Lajoie and Franks' (1997), and Ricker et al.'s (1999) studies all provide evidence that more than one target is attended to during initial motor programming. What they do not tell us is how attention will be distributed after the motor program has been loaded. Will the visuomotor system still monitor more than one target simultaneously?

Attention⁵ and Action

Allport (1987) was one of the first to emphasize the interaction between attention and action. He pointed out that, prior to the execution of any action, the visual system must select an action target from an array of potential targets. If one wishes to pick an apple from a tree, a single apple must be selected, and all others (potentially vying for motor representation) must be inhibited (Allport, 1987). If such a selection process did not occur, we would presumably be incapable of coherent action – or even any action at all – as every object would activate a response. Allport argued for a coupling between perception and action; indeed, he suggested that one could not understand attention-for-perception without understanding selection-for-action.

Empirical evidence for the link between attention and action can be found in studies that examine the influence of action intentions on attentional selection. For example, Craighero et al. (1999) showed that the preparation to grasp a bar of a particular orientation enhanced perceptual selectivity of bars of the same orientation. Bekkering and Neggers (2002) showed that the type of action intended (e.g. pointing vs. grasping) influences selective processing during visual search. Participants in their experiment were instructed either to point to or to grasp the target object, which was located amongst an array of distractor objects. Participants' initial eye movements (used as an indicator of attention's spatial allocation) were equally likely, in the two conditions, to be captured by distractor objects of the incorrect *colour*. However, eye movements were less likely to be captured by distractors of the incorrect *orientation* when participants made a grasp than

⁵ I will not attempt, here, to provide a comprehensive definition of attention. My use of the term will be restricted to the visual domain and I will use it to refer to the process according to which a given region of space, an object, or a feature is selected for increased processing relative to other regions, objects, or features.

when they pointed. This stronger selectivity for orientation during a grasp, as compared to during a pointing movement, is consistent with the fact that orientation is relevant to the execution of a grasp but not to a pointing movement. Colour, on the other hand, is irrelevant to the execution of both types of action. Participants' action plans, therefore, had a non-conscious influence on the selectivity of their visual processing.

How does this selection-for-action processing map onto the regions of the visual brain? Milner and Goodale (1995) suggest that the ventral and dorsal streams each possess their own attentional mechanisms, the ventral stream having selective mechanisms that lead to conscious awareness of attended items, the dorsal stream having selective mechanisms that enhance the spatial features of an action target. Thus, according to Milner and Goodale, selection-for-action would be largely under the purview of the dorsal stream. As evidence for these non-conscious selection processes in the dorsal stream, Milner and Goodale point to experiments by Ingle (1975) showing that frogs' prey-catching responses to primed locations are faster than those to unprimed locations, presumably due to selective processing at the primed location. Because frogs have, effectively, only a 'dorsal stream' for visual processing (which, as the sole visual pathway, must be responsible for the observed priming effect), it can be argued that the dorsal stream in primates should also be capable of selection-for-action (Milner and Goodale, 1995).

Deubel, Schneider and Paprotta (1998) have investigated selection-for-perception and selection-for-action from a dual-stream perspective, specifically in terms of whether the two types of selection can operate independently. Their Visual Attention Model (VAM) posits that perception and action processing are obligatorily coupled to the same

target: if an object is selected for action (if a saccade or a grasp, for example, is planned toward an object), perceptual selection becomes bound to the same object. According to VAM, selection first operates at the level of primary visual cortex (V1), prior to the division of the cortical visual streams, and the representation of the object selected at this level then feeds into both streams. Initial support for VAM came from an experiment by Deubel and Schneider (1996) in which participants were instructed to saccade to a location specified by a cue. A discrimination target (a forward or reverse 'E') was briefly presented at the cued location or at a different location, and the participant's task was to report the target's identity⁶. Even when participants knew in advance precisely where the discrimination target would appear, they were unable to effectively discriminate it if its location did not coincide with the saccade target's location. Identification was always preferentially enhanced at the saccade target location. Deubel and Schneider took this as evidence that attention for perception could not be decoupled from attention for action. Schiegg, Deubel, and Schneider (2003) made a similar finding when the task was to grasp an object: discrimination performance (using the same type of discrimination targets as Deubel and Schneider (1996)) was enhanced at the to-be-grasped locations of an object relative to the non-grasped locations of the object.

Conflicting, to some extent, with the VAM of Deubel and Schneider, evidence has been found by Liu, Healey, and Enns (2003) that the dorsal and ventral streams may operate with separate attentional resources. Liu et al. used a visual search task in which participants either made a pointing response to the target (a direct response thought to tap into the dorsal stream) or made a spatially-coded key press (an indirect response thought

⁶ Note: the discrimination target always disappeared prior to saccade termination, so that discrimination performance could be attributed to attentional allocation alone (and not to increased acuity from foveation).

to tap into the ventral stream) to indicate target location. When participants had to make a detection response prior to the localization response, the localization accuracy decreased for the indirect response alone (the ‘key press’ response). This interference from the detection task on only the indirect response may suggest that the two streams have independent attentional resources, as the dual-task interference would be expected for both response types if the two streams shared a common attentional resource (Liu et al, 2003). The current study will address neither the issue of separate resources nor the issue of coupling between selection-for-action and selection-for-perception. It will, however, rely on the idea that the dorsal stream has attentional mechanisms that can operate in the absence of perceptual selection⁷.

So far, this discussion of attention-for-action has centered on selection-for-action, a process largely concerned with the exclusion of non-relevant stimuli. While this process is certainly relevant to the current study’s experiments, the question driving the study (Can the dorsal stream attend to more than one target simultaneously?) deals perhaps more directly with *dividing* attention-for-action, a process concerned with the inclusion of multiple relevant stimuli⁸. Because research on attention and action has typically focused on responses to a single target at a time, there is little background literature that explicitly deals with divided attention and action. Sequential aiming movement studies (see previous section and below) provide perhaps the best insight into this process.

⁷ Note that this does not imply that selection-for-perception and selection-for-action can be decoupled at the level of object selection. It only implies that, under certain circumstances, processing of a selected object in the dorsal stream can proceed to the level of response modification, while processing in the ventral stream does not reach the level of activating a conscious representation. (Both systems can still be processing the same object.)

⁸ There is not a clear separation here between selective and divided attention; my reference to ‘relevant’ stimuli in describing divided-attention-for-action implies a certain degree of selection. The key point here is that because my experiment’s design will involve only 2 stimuli, both of which are relevant action targets (i.e., there are no distractors beyond those already present in the lab environment), the selection demands will be low.

Attention, Action, and Sequential Aiming Movements

A recent study by Deubel and Schneider (2004) directly examined the allocation of perceptual attention during a two-target sequential aiming movement. The display for the experiment was a circular array of 12 potential targets (masked letter stimuli). At the start of a trial a central arrow cue indicated which of the targets was the initial aiming target. Participants were to point to this target as well as the target located two positions further in the clockwise direction. After the movement signal, a discrimination target (a forward or reverse 'E') would very briefly appear at one of the twelve locations⁹. Discrimination performance was then used as an indicator of attention allocation. The researchers found that perceptual performance was enhanced at both the first and second movement targets, suggesting that both were attended during movement programming.

Like Ricker et al.'s (1999) sequential aiming movement study, Deubel and Schneider's (2004) study suggests that both targets in a sequential aiming movement are processed during initial movement programming. The current study investigates whether both targets are still attended during early on-line processing. Ideally, it will tell us specifically about dorsal stream attending during a sequential aiming movement, complementing Deubel and Schneider's (2004) study, which measured ventral stream processing during a sequential aiming movement.

⁹ The discrimination target disappeared before the onset of the movement.

Chapter 2

Experiment 1

Experiment 1 examines the ability of displaced targets to influence on-line control when there is more than one aiming target. If the dorsal stream is able to process more than one target at a time, location perturbations in either or both of two aiming targets should impact the movement. Specifically, these perturbations should influence the movement even if the perturbed targets only persist at their new locations very briefly before disappearing (e.g. 20ms) and even if the perturbations are not consciously detected. The short (20ms) post-perturbation presentation time that is used in Experiment 1 should ensure that any observed adaptations to perturbations are a result of the simultaneous processing of the two targets, as serial processing would result in a failure to respond to any changes in the target that is processed second (since it would no longer be visible). And, to strengthen the case that adaptations to any perturbations are a result of dorsal processing, Experiment 1 pairs the onset of the perturbations to the participant's saccade. This pairing exploits the reduction in awareness of object displacement that occurs during a ballistic eye movement. If motor modifications occur in the absence of awareness of a change in target position, we can infer that the modifications are (probably) dorsally mediated.

Methods

Participants

Eleven students (6 female, 5 male) from the University of British Columbia participated in the experiment. The average age was 22 (range: 18-34). All participants were right-

handed and had normal or corrected-to-normal vision. Participants were paid \$20 for approximately two hours of participation.

Apparatus

The targets to which participants made aiming movements were red dots of light (5mm diameter) produced by light emitting diodes (LEDs). The LEDs were set beneath an inclined Plexiglas surface (figure 1). The 'home' position LED was located to the left of the participant's midline, and the 'target' LEDs were horizontally aligned to the right of the 'home' position. The target LEDs were located at the following distances from the home position: 150mm, 175mm, 200mm, 225mm, and 250mm (these will also be referred to as positions 3, 4, 5, 6, and 7, respectively). Participants sat with their head in a chinrest, their eyes positioned approximately 60cm from the display surface. They held a stylus in their right hand. An infrared emitting diode was fixed to the front surface of the stylus, and this allowed us to track the movement with Optotrak (Northern Digital), an optical motion tracking system sampling at a frequency of 500 Hz. The stylus's pressure-sensitive tip allowed us to record movement lift-off and touch-down. Electrooculography (EOG) was used to record the occurrence of saccades. Details regarding the collection and processing of the EOG signal have been outlined elsewhere (please see Chua & Enns, 2005).

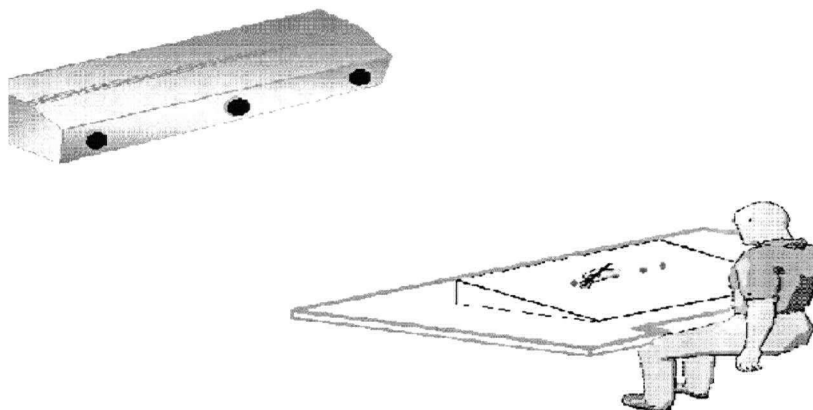


Figure 1. The apparatus. The Optotrak is depicted in the upper left corner. The participant (with disembodied hand) is in the bottom right corner, seated facing the display surface.

Procedure

The experiment was divided into two parts. Part 1 was a manual aiming task used to measure the influence of target perturbations on the motor response. Part 2 was a perceptual report task designed to assess conscious awareness of the same types of perturbations that had been used in the first part of the experiment.

In Part 1 of the experiment participants began each trial with the stylus placed just below the home position LED and their eyes fixated on the home position LED. On a given trial, one or two targets could appear to the right of fixation. Participants were told that if a single target appeared they should look and point to the target as soon as it appeared. Participants were told that if two targets appeared they should look and point to both targets as soon as the targets appeared, tapping the nearer target first and the farther target second. Participants were told to always execute their pointing movements as fast and as accurately as possible. Participants completed a total of 360 trials (preceded by 20 practice trials), divided into three blocks of 120 trials. Half of the trials were perturbed trials (trials in which one or both of the targets jumped to a new location), and half were

unperturbed trials. Perturbed and unperturbed trials were randomly interspersed. On perturbed trials, the target jump was triggered by the saccade: using the EOG signal, we triggered the target jump at approximately the midpoint of the saccade. On single-target trials, only one type of jump was possible: a rightward jump of 25mm. There were three possible locations for the target's initial position: 150mm, 175mm, and 200mm to the right of the home position (i.e., positions 3, 4, and 5). On two-target trials, three types of target jump were possible: 1) the nearer target (T1) jumped right while the farther target (T2) remained stationary, 2) the farther target jumped right while the nearer target remained stationary, 3) both targets jumped right. Each of these conditions could occur at two locations, producing 6 different types of perturbed trial. In the two-target trials there were 4 types of unperturbed trial. (Figure 2 shows the 16 possible target configurations for Experiment 1.)

On every trial the targets disappeared 20ms after the saccade midpoint was reached (i.e. on perturbed trials, the targets disappeared 20ms after the target jump; on unperturbed trials, the targets disappeared 20ms after the target jump would have occurred had the trial been a perturbed trial). Consequently, the targets were gone by the time the saccade was completed¹⁰. After completion of the first part of the experiment, participants were asked if they noticed the targets change locations during any of the trials. This question provided a rough measure of participants' awareness of target perturbations. The second part of Experiment 1 served as a more rigorous test of awareness.

¹⁰ In Experiment 1, average saccade MT was 72.9ms (SD: 8.16ms). Average time of the perturbation was 35.4ms (SD: 7.25ms) after the start of the saccade. Therefore, on average, the target disappeared 55.4ms into the saccade, or 17.5ms prior to the completion of the saccade.

In Part 2 of Experiment 1 the same 16 target configurations were used as in the first part plus 4 configurations that included leftward target jumps (see Figure 3). The additional configurations were added to control for a potential strategy in which the participant reasons that an increasing gap size¹¹ between the nearer target and the farther target indicates a farther target jump and that a decreasing gap size indicates a nearer target jump. If only rightward jumps are possible, such reasoning would enable accurate perceptual report in the absence of actual perception of a specific target jump.

No pointing movements were executed in Part 2. Participants began each trial by fixating their eyes on the home position LED, and were instructed to look at the targets as soon as they appeared. As in Part 1, target perturbations were triggered by the EOG signal passing a threshold voltage that corresponded to approximately the midpoint of the saccade. Targets disappeared 20ms after the saccade midpoint. Participants provided a verbal response at the end of each trial. On single-target trials they responded with either “no jump” or “jump”. On two-target trials, they responded with “no jump”, “nearer target jumped”, “farther target jumped”, or “both targets jumped”. The experimenter recorded the participant’s response after each trial. Participants completed 108 trials (except for participant 1, who completed 88 trials).

¹¹ A changing gap size is perceptually easier to detect than a change in a target’s egocentric position

Distance from home position →	150	175	200	225	250mm		Aiming
	o	o				2-target, no jump	x 30 trials
		o	o			2-target, no jump	x 30 trials
	o		o			2-target, no jump	x 30 trials
		o		o		2-target, no jump	x 30 trials
	8	o	o			2-target, T2 jumps right	x 20 trials
		8	o	o		2-target, T2 jumps right	x 20 trials
	o	o	8			2-target, T1 jumps right	x 20 trials
		o	o	8		2-target, T1 jumps right	x 20 trials
	o	o	o	o		2-target, both jump right	x 20 trials
		o	o	o	o	2-target, both jump right	x 20 trials
	o					Single target, no jump	x 20 trials
		o				Single target, no jump	x 20 trials
			o			Single target, no jump	x 20 trials
	o	o				Single target, jumps right	x 20 trials
		o	o			Single target, jumps right	x 20 trials
			o	o		Single target, jumps right	x 20 trials
			o	o		Single target, jumps right	x 20 trials
							360 trials

Figure 2. The 16 possible target configurations in Experiment 1 with their corresponding number of trials. Perturbation trials are depicted with two rows of dots: the upper row represents target configuration prior to the perturbation, while the bottom row represents target configuration post-perturbation. (The actual perturbation did not involve any vertical displacement.)

Distance from home position → 150 175 200 225 250mm					
	8	o	o		2-target, T2 jumps left
		8	o	o	2-target, T2 jumps left
	o	o	8		2-target, T1 jumps left
		o	o	8	2-target, T1 jumps left

Figure 3. The 4 configurations added to Part 2 (the perceptual report) of Experiment 1.

Analysis

The analysis of Experiment 1 focused on 3 features of the participant's response: 1) the constant error of the aiming movements, 2) kinematic features of the movements (peak velocity and time to peak velocity were analyzed), and 3) accuracy of the verbal report regarding target perturbations.

Constant Error (CE) Analysis: Double-target trials and single-target trials were analyzed separately. For the double-target trials the comparisons of interest – namely, comparisons between CE (with respect to the target's initial location) on perturbed trials and CE on the corresponding control trials – were known in advance. Therefore, the Dunn (Bonferroni) method of planned multiple comparisons was used. Eight separate one-tailed¹² correlated t-tests were carried out. The corrected alpha level for each comparison was $.05/8 = .0063$.

For the single-target trials, a 3 x 2 (3 locations x 2 jump) repeated-measures ANOVA was carried out.

Reaction Time Analysis: We compared the reaction time (RT) on one-target conditions to the RT on two-target conditions to assess whether both targets were being included in initial motor planning. A longer RT in the two-target condition would imply that both targets are included in the initial planning (Henry & Rogers, 1960). RT data were analyzed with a 1-way repeated-measures ANOVA.

Kinematic analysis: We examined two variables: Peak Velocity (PV) and Time to Peak Velocity (TtPV). Both measures provide insight into the programming of the initial impulse of an aiming movement. Movements that are initiated toward targets at the same

¹² The direction of any mean differences was strongly predicted to be in the same direction as the target perturbations.

distance would be expected not to differ in PV and TtPV, whereas movements that are initiated toward targets at different distances would be expected to differ in PV and TtPV (both measures tend to increase with target distance). Therefore, we used these variables to compare movements on no-jump and jump trials and assess whether the movements in each condition were initiated toward the same target location or toward different target locations. If PV and TtPV are not influenced by target jump, we can infer that any endpoint differences in the jump trials are due to modifications during the latter portion of the movement (i.e., subsequent to the initial impulse of the movement).

PV and TtPV were each analyzed with 4 separate repeated-measures ANOVAs. One ANOVA was used to analyze the data from single-target trials, two were used to analyze the data from double-target trials in which one target jumped (one ANOVA for T1 jump trials and one for T2 jump trials), and one was used to analyze the data from double-target trials in which both targets jumped.

Perceptual Report: Hit rates were calculated for both single-target and double-target trials. Sensitivity (d') to target displacement was also calculated in an attempt to control for possible criterion effects.

Results

The constant error results for double-target trials (figures 4 and 5) suggest that the perturbed targets influenced the aiming movement. Figure 4 shows the difference in CE between perturbed and unperturbed trials when only one of the two targets jumped. Clearly, the jumping target tended to pull the hand in the direction of the jump, even though it was only present for 20ms at its new location. Statistical analysis shows that the nearer target (T1) jumping from position 3 to 4 significantly increased the average CE

($t(10)=5.94$, $p<.0001$, one-tailed). When the nearer target jumped from position 4 to 5, the resultant increase in CE did not reach significance ($t(10)=2.02$, $p>.0063$, one-tailed). When the farther target (T2) jumped from position 4 to 5, the CE increased significantly ($t(10)=12.55$, $p<.0001$, one-tailed). When the farther target jumped from position 5 to 6, the CE again increased significantly ($t(10)=5.12$, $p<.001$, one-tailed). Thus, like the nearer target jump, the farther target jump did influence the movement. In fact, a perturbation in the farther target appeared to have an even larger impact on the movement than a perturbation in the nearer target (on average, T2 jumps produced an approximately 7mm larger effect than T1 jumps). These results for trials in which one of the two targets jumped strongly suggest that the visuomotor system is processing both targets simultaneously. If only one target were being processed at a time, we would not expect to see any modifications to the movement when the farther target jumped.

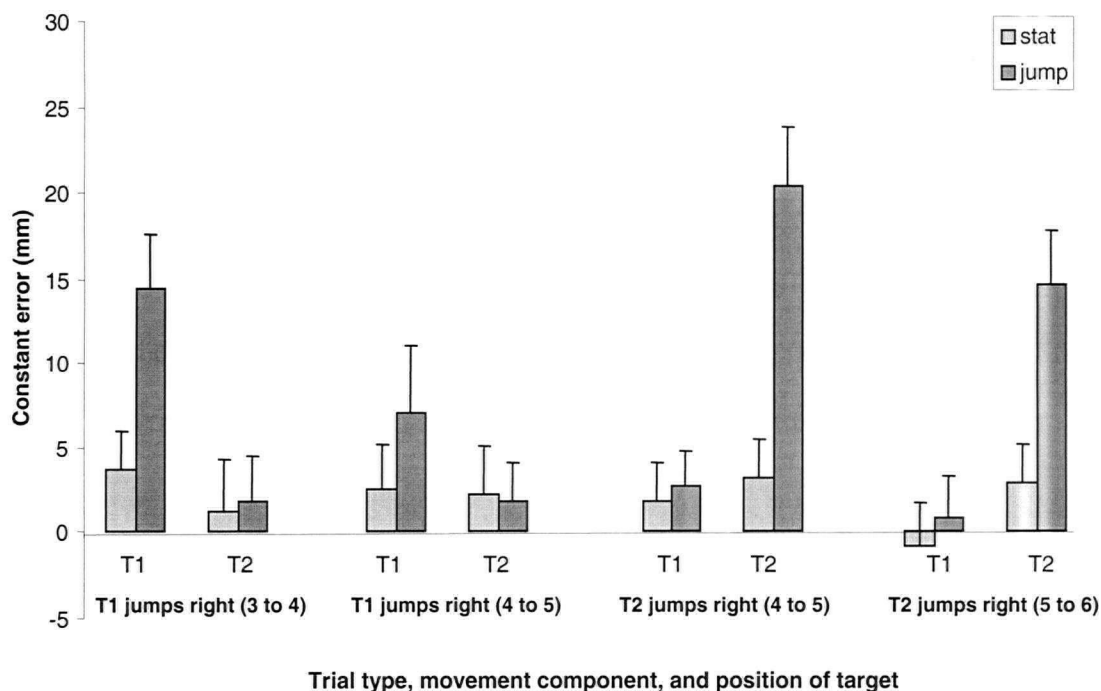


Figure 4. The influence of target perturbations on CE for trials in which one of the two targets jumped. Error bars represent standard error of the mean.

The results for trials in which both targets jumped (fig. 5) provide further support for simultaneous processing. As figure 5 shows, the jumping targets consistently attracted the movement in the direction of the jump. Each target was analyzed separately, with comparisons being made between CE (with respect to initial position) when the target jumped vs. CE when it remained stationary. When the nearer target jumped from position 3 to 4 and the farther target jumped from 5 to 6, the CE for the nearer target increased significantly ($t(10)=6.02$, $p<.0001$, one-tailed) and the CE for the farther target also increased significantly ($t(10)=5.99$, $p<.0001$, one-tailed). When the nearer target jumped from position 4 to 5 and the farther target jumped from position 6 to 7, the CE for the nearer target increased significantly ($t(10)=4.91$, $p<.001$, one-tailed), as did the CE for the farther target ($t(10)=4.57$, $p<.001$, one-tailed).

The CE results for trials on which only a single target was present (fig. 6) do not bear directly on the issue of multiple target processing. However, they do tell us about the influence of target proximity on the perturbation effect. Figure 6 shows that as the distance between a single target and the home position increases, the extent of the perturbation's influence on the movement decreases. Statistically, this is captured by the significant interaction between jump and target position ($F(2,20)=8.16$, $p<.01$). The main effect of target jump ($F(1, 10) = 61.73$, $p<.001$) replicates the finding of previous double-step studies that a target perturbation influences the movement endpoint.¹³

¹³ It is worth noting, however, that unlike most double step studies, the target in this experiment disappears prior to the completion of the saccade. To my knowledge, the only other experiment that has used a disappearing target is that of Cressman, Franks, Martens, and Chua (2004, conference presentation), which also showed that a 20ms perturbation influences on-line control, although to a lesser extent than longer target presentations.

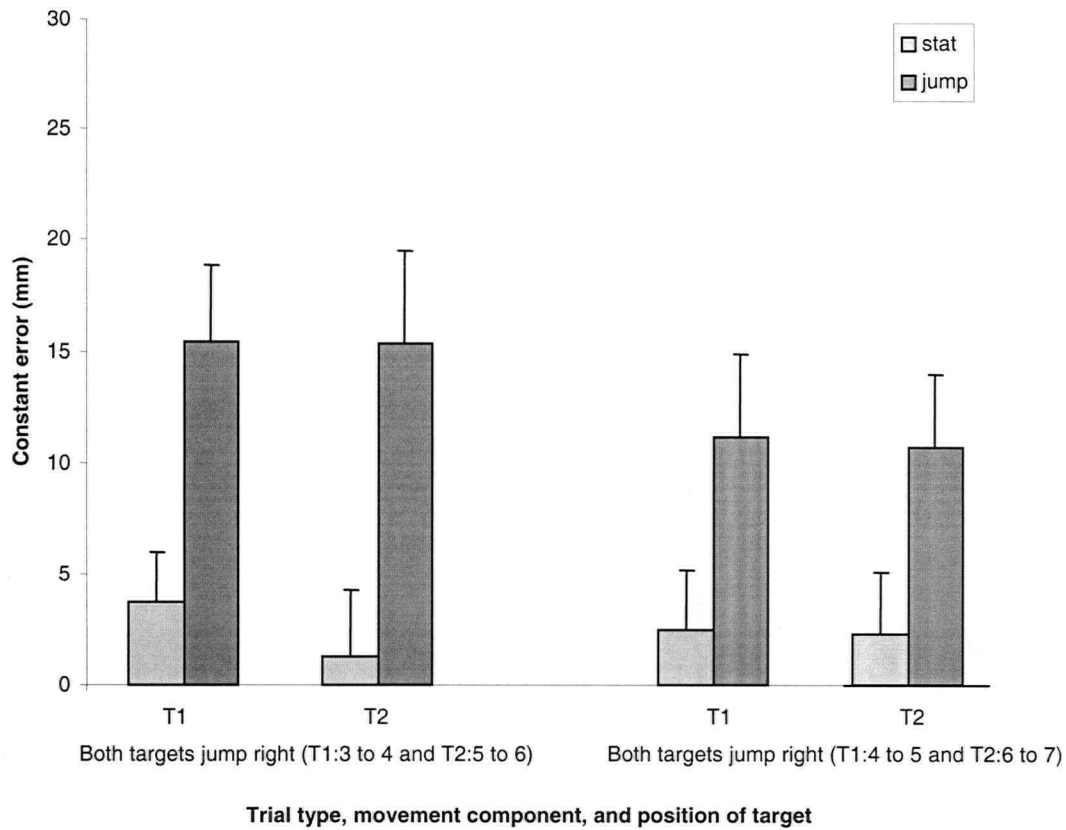


Figure 5. The influence of target perturbations on CE for trials in which both targets jumped. Error bars represent standard error of the mean.

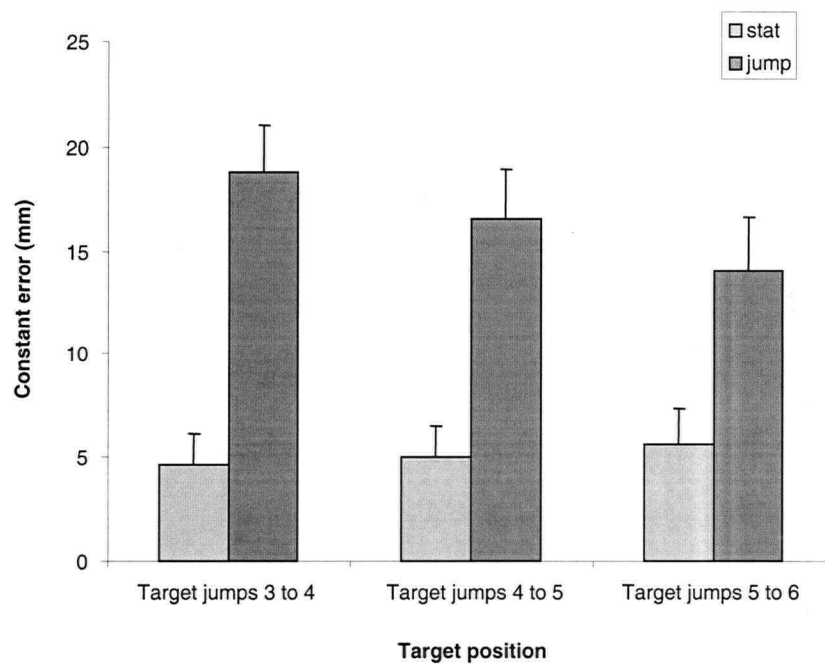


Figure 6. The influence of target perturbations on CE for single-target trials. Error bars represent standard error of the mean.

Accuracy in single-target vs. double-target trials

The inclusion of single-target trials allowed us to compare accuracy on these trials to the accuracy on double-target trials. This comparison was designed to reveal any processing costs associated with two-target trials: a decline in accuracy on double-target trials might suggest that location encoding was impaired when two targets had to be incorporated into movement programming.

Two variables, CE and VE, were used as measures of accuracy. A comparison of CE for T1 on stationary double-target trials (3.7mm) to CE on corresponding stationary single target trials (4.6mm) revealed no significant difference, $F(1,10) < 1$. Similarly, no difference in VE was found between these two trial types (double-target: 7.0mm, single-target: 7.0mm), $F(1,10) < 1$. The same analysis was carried out for T2. A comparison between CE for T2 on stationary double-target trials (3.2mm) to CE on corresponding stationary single-target trials (5.0mm) revealed no significant difference, $F(1,10) = 1.9$, $p = .19$. The analysis of VE also revealed no difference (double-target: 6.1mm, single-target: 6.3mm), $F(1,10) < 1$.

These results appear to suggest that location encoding was as effective for double-component movements as for single-component movements. One potentially confounding factor, however, is the extra stimulus present in the double-target trials. A second target may provide an allocentric cue that enhances location coding, counteracting any potential detriment in performance that might result from programming a two-component movement. To control for this possibility, one would have to include trials in which two stimuli were present while the task required only a single component movement.

Reaction time

Another reason for including single-target trials was so that we could compare the RT on these trials to the RT on double-target trials. Surprisingly, the RT on double-target trials was significantly shorter than the RT on single-target trials (316ms vs. 325ms), $F(1,10)=7.47$, $p=.021$. While such an effect may appear to suggest that both targets in the double-target case were not being included in the initial motor plan (or, nonsensically, may seem to suggest that programming is actually *faster* for two targets than for one), these results likely have nothing to do with motor programming; rather, the decrease in RT for the double-target trials is probably a result of easier discriminability when two targets are present. In retrospect, the single- and double-target trials should have been run in separate blocks so that stimulus discrimination would not have been a factor. As the experiment stands, little can be inferred from the RT results.

Kinematics

The results of the kinematic analysis, on the other hand, can tell us something about motor programming. Figure 7 shows the mean peak velocities (PV) for each of the conditions of Experiment 1. For single-target trials (fig. 7a), a 3 POSITION (near, mid, far) x 2 JUMP (jump, no jump) R-M ANOVA was carried out. There was a small, but significant, increase in PV on jump trials relative to no-jump trials. This is reflected in a main effect of jump, $F(1,10)=30.71$, $p=.0003$. As expected, there was also a main effect of target position, with farther targets producing higher PVs, $F(2,20)=325.29$, $p<.0001$. There was no interaction between jump and position, $F(2,20)<1$.

For double-target trials in which T1 jumped (fig. 7b), a 2 POSITION x 2 JUMP R-M ANOVA was carried out. There was no significant interaction between position and

jump, $F(1,10)<1$. There was also no significant effect of jump on PV, $F(1,10)=2.18$, $p=0.17$, unlike in the single target trials. There was a main effect for position, $F(1,10)=118.55$, $p<.0001$, such that farther targets produced higher PVs.

A similar pattern of PV results was found for double-target trials in which T2 jumped¹⁴ (fig. 7c). Again, a 2 POSITION x 2 JUMP R-M ANOVA was carried out. No significant interaction was found, $F(1,10)<1$, and there was no significant effect of jump, $F(1,10)=1.62$, $p=.23$. As in the other conditions, target distance did influence the PV, producing a main effect of position, $F(1,10)=141.00$, $p<.0001$.

The PV results for double-target trials in which both targets jumped are depicted in figure 7d. A 2 POSITION x 2 JUMP R-M ANOVA revealed no significant interaction, $F(1,10)=2.81$, $p=.12$. There were, however, main effects for jump, $F(1,10)=9.23$, $p=.013$ and position $(1,10)=152.47$, $p<.0001$.

The significant effects of jump on PV in the single-target trials and the double-target trials in which both targets jumped suggest that in these conditions, some modifications to the movement occurred prior to or during the initial impulse of the movement. The implications of these effects will be explored in greater detail in the discussion section.

A similar analysis was carried out for Time to Peak Velocity (TtPV). For the single-target trials (fig. 8a), a 3 POSITION x 2 JUMP R-M ANOVA revealed no interaction between POSITION and JUMP, $F(2,20)=1.77$, $p=.20$. There was also no main effect of JUMP, $F(1,10)=2.38$, $p=.15$. There was, however, a significant effect of

¹⁴ Note that any effect of jump on PV in this condition would reflect an influence of a T2 jump on the initial impulse to T1, as only the kinematics of the first segment of the sequential movement are included in the analysis.

POSITION, $F(2,20)=42.81$, $p<.0001$, indicating that TtPV increased as the distance to the target increased.

For the double-target trials in which T1 jumped (fig. 8b), a 2 POSITION \times 2 JUMP R-M ANOVA revealed a significant interaction, $F(1,10)=6.03$, $p=.03$. Post-hoc

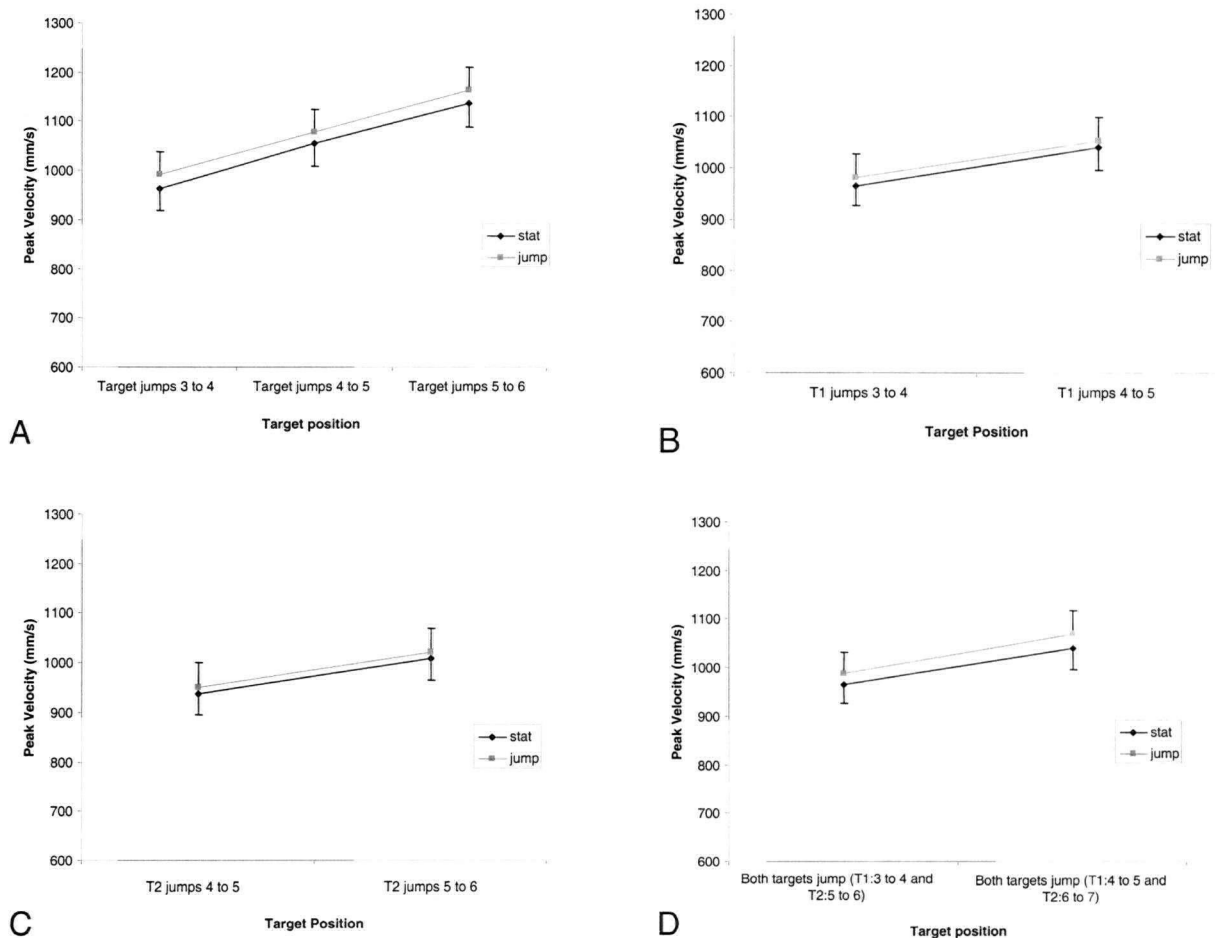


Figure 7. The influence of target perturbations on PV in Experiment 1. (A) shows mean PV values for single target trials. (B) shows mean PV values for T1-jump trials. (C) shows mean PV values for T2-jump trials. (D) shows mean PV values for both-jump trials. Error bars represent standard error of the mean.

(N-K) testing of the interaction showed that a jump at the nearer position significantly increased TtPV, $p=.03$, but that a jump had no effect on TtPV at the farther position,

$p=.41$. There was no main effect of jump, $F(1,10)=2.21$, $p=.17$, but there was a main effect of position, $F(1,10)=28.59$, $p=.0003$.

For the double-target trials in which T2 jumped (fig. 8c), a 2 POSITION x 2 JUMP R-M ANOVA revealed neither a significant interaction, $F(1,10)<1$, nor a significant main effect of jump, $F(1,10)<1$. There was a main effect of position, $F(1,10)=68.51$, $p<.0001$.

For double-target trials in which both targets jumped (fig. 8d), a 2 POSITION x 2 JUMP R-M ANOVA revealed no significant interaction, $F(1,10)<1$, and no significant main effect of jump, $F(1,10)=2.23$, $p=.17$. Position again had an impact on TtPV, with farther targets producing higher TtPV, $F(1,10)=31.12$, $p=.0002$.

The TtPV results, like the PV results, show a consistent effect of position, such that both measures tend to increase as the distance to the targets increases. However, the effect of position was stronger for PV than for TtPV, suggesting that (at least for the current experiment) the former may be more sensitive to target-position effects on the initial movement impulse.

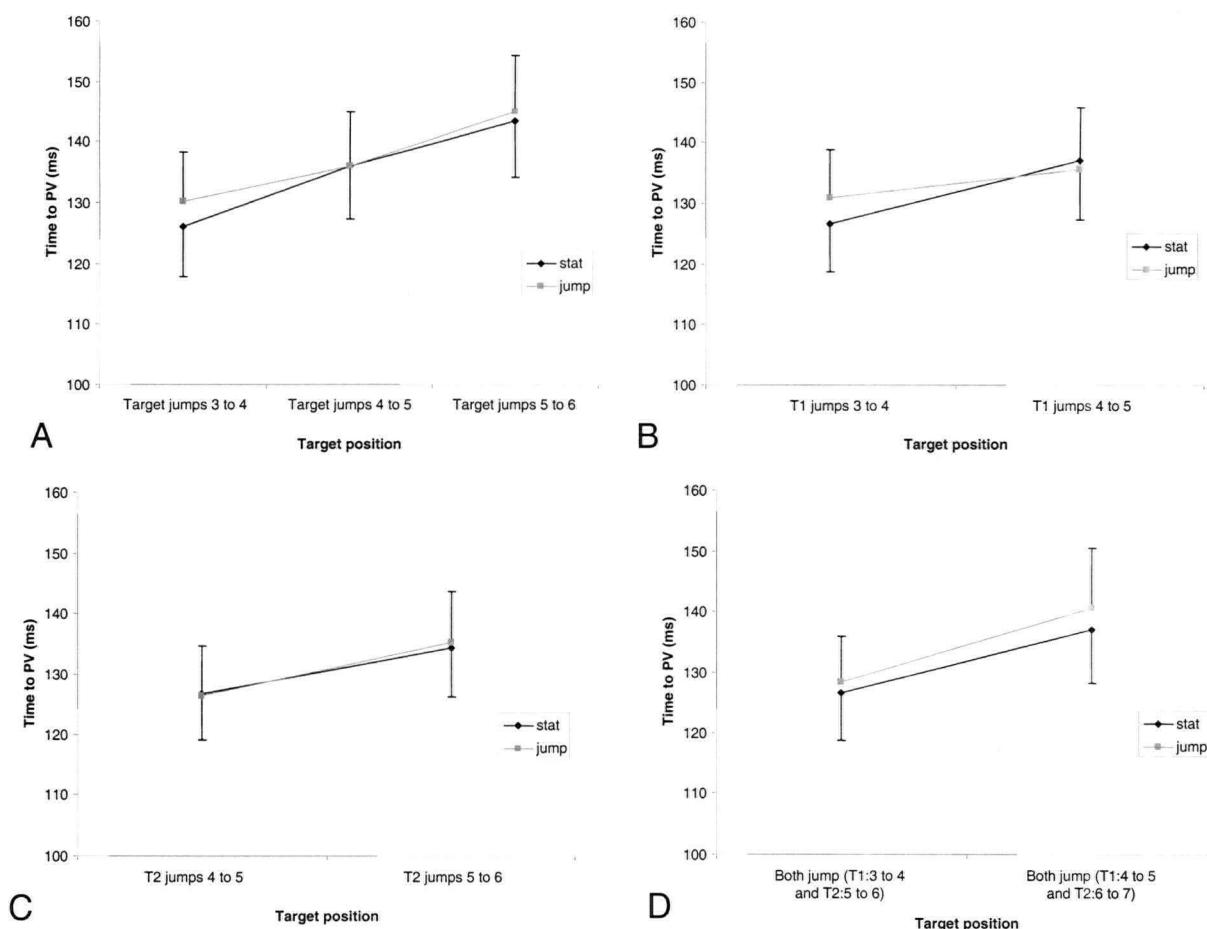


Figure 8. Influence of target perturbations on TtPV in Experiment 1. (A) shows mean TtPV in single-target trials. (B) shows mean TtPV in T1-jump trials. (C) shows mean TtPV in T2-jump trials. (D) shows mean TtPV in both-jump trials. Error bars represent standard error of the mean.

Perceptual report

Subsequent to their completion of Part 1 of Experiment 1, participants were asked if they noticed any of the targets jumping to a new location during the trials. With the exception of Participant 1, who reported noticing some changes in gap size on double-target trials, all participants reported no awareness of any target displacements during the experiment. We have some indication, then, that participants were probably not consciously using displacement information to guide their movements. However, as a

stronger test of participants' awareness of the target displacements during saccades we ran Part 2 of the experiment: a condition in which participants made a perceptual judgment on every trial.¹⁵

The results of the perceptual report for each participant are presented in table 1. Of particular interest are the participants' rates of detection on trials in which a target jumped. For single target trials, the average hit rate was .29. Thus, on average, participants reported a target jump on less than a third of the trials in which the target did jump. Unfortunately, on its own this statistic has little meaning, as it may simply indicate that participants have a high criterion (i.e., are cautious in responding and thus biased towards a 'no jump' response). For these single-target trials, we can calculate a criterion-free sensitivity (d') value. Taking the average of the group's sensitivity values produces a d' of .62, which implies a fairly low perceptual sensitivity to the single target jumps. However, there is considerable variation between participants, with d' values ranging from 0 to 1.96.

The perceptual report results for double-target trials are more complicated. On these trials, participants had 4 response options: 'no jump', 'T1 jumped', 'T2 jumped', and 'both jumped'. If these possibilities are re-coded as 'no jump' and 'any type of jump reported' the average hit rate for double-target trials is .5, and the average d' is .56, which is roughly equal to the average d' in the single-target trials.

¹⁵ There is a subtle, but perhaps meaningful, difference between the awareness measured by the single post-experiment question and the trial-by-trial perceptual report, aside from the greater rigor of the latter test. Whereas the trial-by-trial test probes the *accessibility* of the visual information to consciousness awareness when the participant is pressed to extract it, the single post-experiment question tells us about what was *used* during manual aiming, which may be the more relevant question. (The issue of awareness will be discussed at greater length in the General Discussion.)

Sensitivity to the presence of a jump in the double-target trials does not tell the whole story, however. In trials where one of the two targets jumps, the gap between the targets either increases or decreases after the jump, a change that may produce increased detection of a jump, while perception of *which* target jumped might remain low. In order to perform the aiming task effectively, egocentric position information for each of the targets is required (not simply information about a changing gap size); therefore, the appropriate perceptual measure may be jumping target *specification*, rather than merely jump detection. Accordingly, hit rates were calculated for each of the 3 types of double-target jump trials separately (table 1). The average hit rate for 'T1 jump' trials was .32; it dropped to .12 for 'T2 jump' trials, and to .06 for 'both jump' trials. Because the data reflected discrimination performance rather than simple detection performance, d-prime values were not calculated.

Two noteworthy features of these data are 1) the hit rate dropped to almost 0 when both targets jumped, and 2) the hit rate was much higher in the 'T1 jump' trials than in the 'T2 jump' trials. The low hit rate on 'both jump' trials is interesting because there was a greater 'total' amount of displacement on these trials compared to trials in which only one of the two targets jumped. A potential explanation may be that the higher hit rates in the 'T1 jump' and 'T2 jump' trials are due to the presence of a stationary reference, or landmark (i.e., the non-jumping target) on these trials, which increased participants' ability to discriminate the jumping target – even if this state of jumping target vs. landmark target only persisted for 20ms.

Table 1. Perceptual report from Part 2 of Experiment 1.

Subject	Hit rate (single target)	Correct rejection rate (single target)	Sensitivity (single target)	Hit rate (2 target)	Correct rejection rate (2 target)	Sensitivity (2 target)	Hit rate on T1 jump trials	Hit rate on T2 jump trials	Hit rate on both jump trials
1	0.00	1.00	0.00	0.34	0.96	1.34	0.50	0.10	0.00
2	0.13	1.00	1.96	0.38	0.96	1.45	0.25	0.15	0.10
3	0.13	0.93	0.35	0.48	0.64	0.31	0.60	0.00	0.00
4	0.40	0.80	0.59	0.84	0.35	0.61	0.35	0.37	0.30
5	0.33	0.69	0.06	0.44	0.63	0.18	0.10	0.06	0.10
6	0.08	0.71	0.00	0.62	0.46	0.21	0.40	0.20	0.00
7	0.69	0.50	0.50	0.29	0.56	0.00	0.05	0.00	0.00
8	0.43	0.50	0.00	0.74	0.26	0.00	0.30	0.20	0.20
9	0.07	1.00	1.61	0.42	0.81	0.68	0.05	0.00	0.00
10	0.53	0.67	0.52	0.44	0.71	0.40	0.30	0.05	0.00
11	0.40	0.93	1.22	0.56	0.79	0.96	0.65	0.15	0.00
Mean	0.29	0.79	0.62	0.50	0.65	0.56	0.32	0.12	0.06

The lower hit rate on 'T2 jump' trials (.12) relative to 'T1 jump' trials (.32) is interesting because this is an *opposite* trend to the one observed in the aiming condition of the experiment. Recall that in the aiming condition T2 jumps had a larger impact on the movement than T1 jumps did. This may reflect different attention allocation strategies on aiming trials vs. look-only trials, such that participants are biased toward attending to the second target on aiming trials but are biased toward attending to the first target on look-only trials. Alternatively, it may reflect different attentional distribution for action systems than for perception systems.

Discussion

The purpose of Experiment 1 was to examine target processing in the dorsal stream. We were interested in whether the dorsal stream can attend to multiple targets simultaneously. Previous double-step experiments in which conscious awareness of target perturbation was suppressed (e.g. Goodale, Pelisson, and Prablanc, 1986; Prablanc & Martin, 1992) involved a single movement target on any given trial. These experiments provided behavioural support for the existence of an unconscious 'action' stream, but they did not tell us about its attentional capabilities/limits. Here we employed two movement targets, either of which, or both, could move during a trial, in an attempt to examine these capabilities.

Our CE results suggest that the dorsal stream is able to attend to two movement targets simultaneously. Participants consistently corrected their movements in response to target perturbations of which they were unaware. They had no foreknowledge of which of the two targets would jump, yet they were able to correct their movement regardless of which target jumped, suggesting that both targets were being attended to.

Because the targets in our experiments were only visible for 20ms after the midpoint of the initial saccade was reached, the targets had disappeared long before the initial leg of the manual movement was completed (and usually before it had even started). If the dorsal stream only operates in real-time, and thus is unable to draw on a memory representation of the visual scene to modify the movement, we might expect that the dorsal stream began updating the movement immediately upon reception of the displaced target information.

When was this updating first expressed in the movement itself? The kinematic data seem to suggest that this depended on the type of jump involved in the trial. Analysis of PV revealed a small (25-30mm/s) but significant increase in PV on single-target jump trials. This increase is approximately a third of the magnitude of PV increase (80-90mm/s) that we see when comparing two stationary targets that are one position apart. In other words, if the movements on the perturbed trials had been initially programmed toward the displaced target position, we would have expected a PV increase three times the magnitude of the one that we observed. There are two ways to explain these PV results: 1) The movement on perturbed trials was being initiated toward a location approximately a third of the distance between the initial target location and its displaced location, or 2) The movement was being initiated toward the first target location and then being modified to some degree prior to the completion of the initial impulse. The first explanation seems highly unlikely simply because of processing time restrictions. The average time between the target jump and hand lift-off is approximately 45-50ms, which is insufficient time for the system to reprogram the movement. At a bare minimum, the system would require 100ms to perform such a modification (Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991). Thus, it would seem that on single-target trials the dorsal stream was starting to modify the movement prior to the completion of the initial impulse. Further modification was then occurring during the decelerative phase of the movement.

A similar PV increase was observed in double-target trials in which both targets jumped. The explanation for this increase is presumed to be the same as for the single-target trials described above.

Unlike the single-target and both-jump trials, the trials in which one of two targets jumped produced no significant effect of jump on PV. Although we might expect there to be no impact of a T2 jump on initial-impulse PV because T1 is remaining stationary, it seems puzzling that a T1 jump would produce no significant increase in PV when it did so in single-target and both-jump trials. A possible explanation for this outcome may have to do with the distance between T1 and T2 that arises after a T1 jump. On a T1-jump trial, T1 and T2 start off 5cm apart. Subsequent to the rightward T1 jump, this distance is reduced to 2.5cm. In order to maintain accuracy during the (now shortened) second leg of the movement, participants may be less inclined to increase velocity during the initial leg of the movement.

As the current study employs purely behavioural methods with healthy participants, we can not assert with certainty that the visuomotor processing under discussion is occurring in the dorsal stream. We can only infer that we were observing dorsal processing from the fact that participants made movement corrections to target perturbations of which they were unaware. There is considerable evidence to suggest that dorsal stream visual processing is not consciously accessible and that any consciously accessible visual information arises from ventral stream processes (see Milner and Goodale (1995) for a review). However, it does not follow from this that all non-conscious visual information is necessarily dorsal; we know, in fact, that ventrally processed visual information can be non-conscious – word priming studies, for instance, in which a masked word affects subsequent responding, clearly demonstrate non-conscious ventral processing. It is, therefore, possible that the current experiment's results reflect ventral processing. This, however, seems unlikely, as fast on-line

corrections to perturbed targets have previously been shown to rely on occipito-parietal regions of the brain (dorsal stream areas). Desmurget et al. (1999) used transcranial magnetic stimulation (TMS) on the left posterior parietal cortex and found that this disrupted the ability to correct fast aiming movements to perturbed targets. Similarly, Pisella et al. (2000) found that an optic ataxic patient with lesions to the posterior parietal cortex was unable to make fast automatic corrections to perturbed targets.

Still, we wished to confirm that the ventral stream was not responsible for the movement modifications observed in Experiment 1. Experiment 2 was designed to test the ventral stream's ability to respond to the same type of target perturbations employed in Experiment 1.

Chapter 3

Experiment 2

The logic behind the design of Experiment 2 was the following: If the dorsal stream operates only in real-time (Westwood & Goodale, 2003) or has, at most, a 2sec visual memory (Bridgeman, Peery, & Anand, 1997; Rossetti & Pisella, 2002), then a 3sec delay between the offset of the targets and the onset of the movement should force a ventrally-guided movement. Thus, if such a delay were added to the task used in Experiment 1, there would be a 3sec delay between the offset of saccadically-triggered 20ms target displacements and the onset of a movement to those same targets. Since the new position of the displaced target(s) would be visible only during the saccade – a period during which awareness of target displacement is suppressed – we hypothesized that ventrally-guided movements would be made toward the *initial* position of the target. Thus, the

delay introduced in Experiment 2 should eliminate the CE effect observed in Experiment 1.

Methods

Participants

Nine participants (3 male, 6 female) took part in Experiment 2. Ages ranged from 18-42. All participants were right-handed and had normal or corrected-to-normal vision. Participants were reimbursed \$20 for approximately 2.5 hours of participation. All participants gave informed consent, and the experiment was run according to the ethical guidelines set out by the University of British Columbia.

Apparatus and Procedure

The apparatus and procedure were identical to those of Experiment 1 except for the following modifications:

- A 3sec delay condition was added. One block of the experiment had no delay (this block was a direct replication of Experiment 1, except for the modifications listed below) and one block of the experiment had a 3sec delay between the saccade to the targets and the onset of a movement 'go' tone. Each block contained 240 trials, and the order of the blocks was counterbalanced.
- No single-target trials were included in Experiment 2.
- Bi-directional jumps were possible in Experiment 2 (Experiment 1 contained only rightward jumps). Thus, in Experiment 2, T1 could jump left or right, T2 could jump left or right, and on both-jump trials both targets could jump left

or right together. This manipulation was added to control for the possibility that a target perturbation simply prompts participants to bias their movements in a rightward direction. By including both forward and backward jumps, the number of jump types increased to six: T1 left; T1 right; T2 left; T2 right; both left; both right.

- The perceptual report was coupled to the pointing trials. After completing an aiming movement, participants reported whether a jump had occurred on that trial and, if so, which target had jumped: T1, T2, or both.

Analysis

Constant Error: As in Experiment 1, the comparisons of interest were known beforehand. We wished to compare CE (with respect to a target's initial position) for jumping targets on jump trials to CE for the same target on corresponding stationary trials. This meant that 8 different comparisons were carried out for each of the two conditions (no-delay and delay were analyzed separately): T1 forward vs. corresponding stationary; T1 backward vs. stationary; T2 forward vs. stationary; T2 backward vs. stationary; T1 forward when both jump vs. stationary; T1 backward when both jump vs. stationary; T2 forward when both jump vs. stationary; T2 backward when both jump vs. stationary. The Dunn (Bonferroni) method of planned contrasts was used, producing a per-contrast alpha level of .0063. As in Experiment 1, directional contrasts were carried out. (Jump effects, if present, were strongly predicted to be in the same direction as the target jumps.)

Unlike Experiment 1, contrasts were not carried out at each position (near, far), which would have required 16 contrasts per condition in Experiment 2. Rather, in Experiment 2 the CE values for the same types of trials were collapsed over position.

Perceptual Report: Since only double-target trials are included in Experiment 2, a type of trial for which four responses were possible ('no jump', 'T1 jumped', 'T2 jumped', and 'both jumped'), signal detection analysis was not applied. Hit rate values, alone, are presented for each of the 3 types of jump trial.

Results

The effects of the target jumps on CE in the no-delay and delay conditions are shown in figures 9 and 10, respectively. The no-delay condition CE effects are similar to those observed in Experiment 1: jumping targets bias the movement in the direction of the jump. Statistical analysis bears this out. All of the planned comparisons reached significance. Table 2 shows the t-values and corresponding p-values for each comparison.

Surprisingly, the delay condition did not eliminate these effects (fig. 10). In fact, the same set of planned comparisons revealed the same pattern of jump effects that were observed in the no-delay condition. Table 2 shows the t-values and corresponding p-values for each of these comparisons.

The concurrent perceptual report results are presented in table 3. Although the average overall hit rate is 'low' (.16) in both no-delay and delay conditions, the hit rates do vary considerably between trial types and between subjects. The average hit rate on both-jump trials, for instance, is much lower (.06) than the average hit rate on T1- and T2-jump trials (.22 and .21, respectively). This replicates the perceptual report findings of

Experiment 1, in which both-jump trials also had much lower hit rates than T1/T2-jump trials.

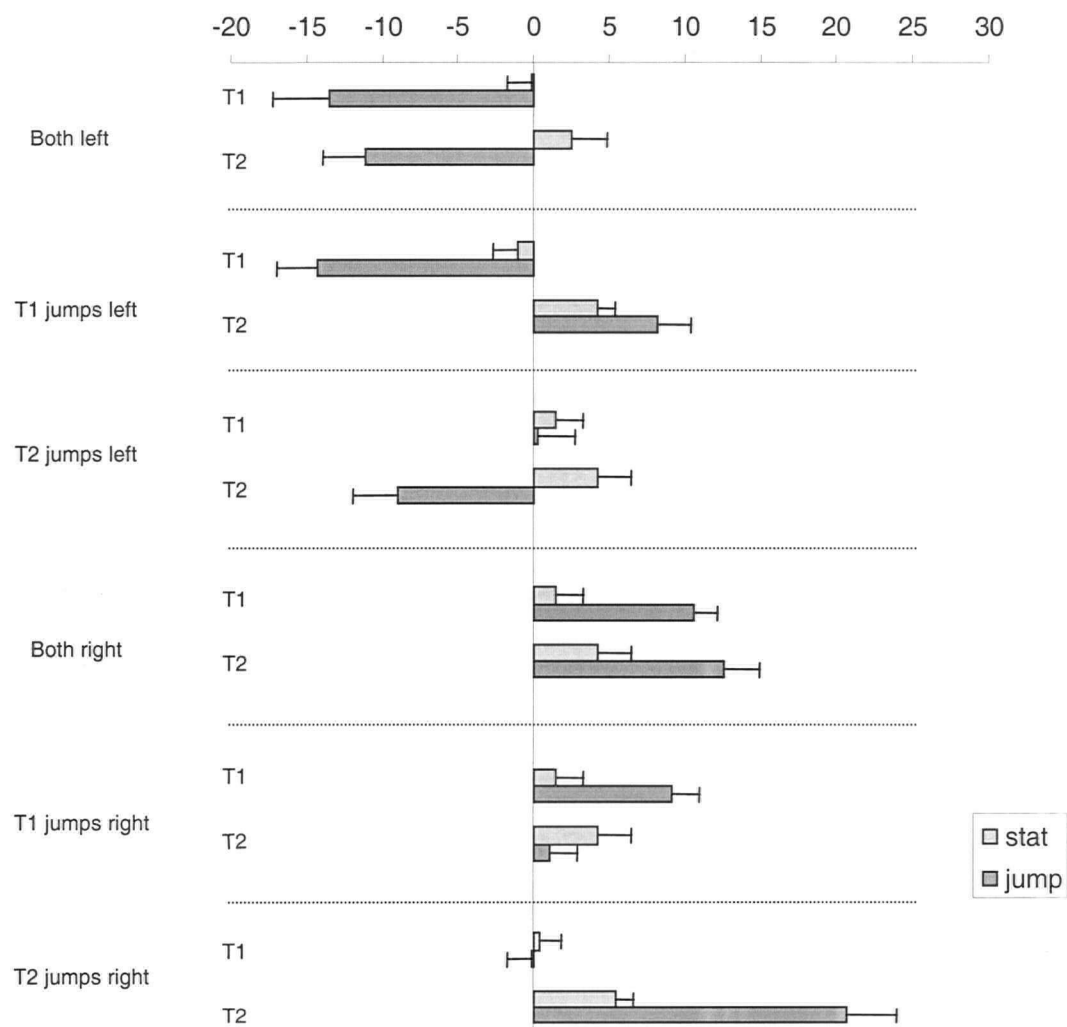


Figure 9. The influence of left and right target jumps on CE in the NO-DELAY condition of Experiment 2. Error bars represent standard error of the mean.

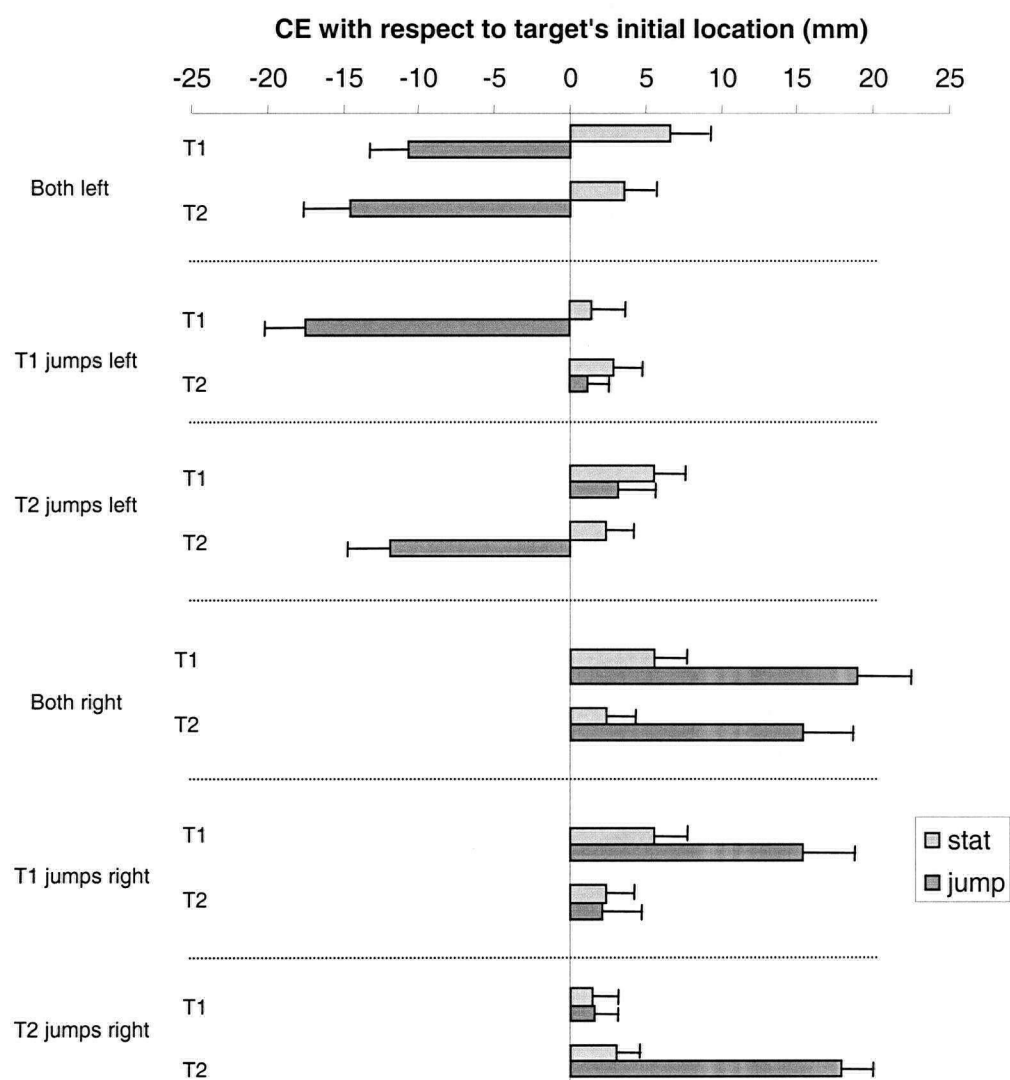


Figure 10. The influence of left and right target jumps on CE in the DELAY condition of Experiment 2. Error bars represent standard error of the mean.

Table 2. T-test analysis of the perturbation of effect in the NO-DELAY and DELAY conditions. All tests were one-tailed, and the per-contrast alpha required for significance was .0063.

NO-DELAY			DELAY		
	T1 stat vs. T1 jump	T2 stat vs. T2 jump		T1 stat vs. T1 jump	T2 stat vs. T2 jump
T1 jumps left	$t(8)=6.54, p=.00009$		T1 jumps left	$t(8)=7.09, p=.00005$	
T1 jumps right	$t(8)=-4.15, p=.0016$		T1 jumps right	$t(8)=-4.27, p=.0014$	
T2 jumps left		$t(8)=5.53, p=.00028$	T2 jumps left		$t(8)=8.97, p=.00001$
T2 jumps right		$t(8)=-5.13, p=.00045$	T2 jumps right		$t(8)=-6.76, p=.00007$
Both jump left	$t(8)=5.97, p=.00017$	$t(8)=8.19, p=.00002$	Both jump left	$t(8)=6.97, p=.00006$	$t(8)=7.64, p=.00003$
Both jump right	$t(8)=-5.75, p=.00022$	$t(8)=-4.64, p=.00084$	Both jump right	$t(8)=4.98, p=.00054$	$t(8)=-4.71, p=.00075$

Table 3. Perceptual report results for Experiment 2.

Subject	NO-DELAY			DELAY			OVERALL			Overall hit rate
	Hit rate on T1 jump trials	Hit rate on T2 jump trials	Hit rate on both jump trials	Hit rate on T1 jump trials	Hit rate on T2 jump trials	Hit rate on both jump trials	Hit rate on T1 jump trials	Hit rate on T2 jump trials	Hit rate on both jump trials	
1	0.47	0.69	0.03	0.44	0.60	0.13	0.46	0.65	0.08	0.40
2	0.07	0.03	0.00	0.18	0.06	0.00	0.12	0.04	0.00	0.05
3	0.72	0.53	0.00	0.53	0.43	0.00	0.63	0.48	0.00	0.37
4	0.07	0.03	0.00	0.07	0.03	0.04	0.07	0.03	0.02	0.04
5	0.26	0.30	0.17	0.41	0.23	0.14	0.34	0.27	0.16	0.25
6	0.23	0.10	0.20	0.03	0.24	0.10	0.13	0.17	0.15	0.15
7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.28	0.21	0.03	0.27	0.25	0.20	0.28	0.23	0.12	0.21
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mean	0.23	0.21	0.05	0.22	0.20	0.07	0.22	0.21	0.06	0.16

Discussion

Experiment 2 was originally intended to provide converging evidence for the postulated implications of Experiment 1, but it appears to do just the opposite. While the findings of Experiment 2's no-delay condition replicate both the motor and perceptual findings of Experiment 1, the findings of Experiment 2's delay condition force us to reconsider which visual pathway is responsible for these effects. They also call into question the validity of the perceptual report of target displacement as a measure of relevant ventral processing.

The most important finding of Experiment 2 is that a 3sec delay between the intra-saccadic target displacement and the start of the movement to the targets does not eliminate – does not even appear to *weaken* – the ability of the target displacements to bias the movement. This suggests that visual information acquired during the saccade is being stored and used to guide the movement on delay trials. Furthermore, information about the location of *both* aiming targets is being retained during this period: as in Experiment 1 and the no-delay condition of Experiment 2, participants selectively adjusted their movements to a displacement in either or both targets.

How do we explain the findings of Experiment 2 from a dual-systems perspective? Three potential explanations, with arguments for and against each one, are outlined below:

1. The dorsal stream is able to retain visual information for at least 3sec and is responsible for the effects in both the no-delay and delay conditions.

The only evidence that supports this explanation is the poor perceptual reporting observed in both the delay and no-delay conditions. If these reports are taken to accurately reflect awareness of target displacement, and if we posit that absence of such awareness is an indicator of the ventral stream's lack of involvement in guiding the movement, then it follows that the dorsal stream is responsible for the motor adaptations observed in both the delay and no-delay conditions.

Arguments against this explanation stem from previous research (Bridgeman, Peery, & Anand, 1997; and see Rossetti & Pisella, 2002 for a review) showing that sensorimotor/dorsal processing has, at most, a 2sec visual memory, and possibly much less (Westwood and Goodale, 2003).

2. The ventral stream is responsible for the effects in both the no-delay and delay conditions.

The similar patterns of motor bias observed in both the no-delay and delay conditions provide evidence in support of this explanation. If we accept that the 3sec interval precluded any dorsal stream involvement in the delay condition, the simplest explanation for the similarity of results in the no-delay and delay conditions may be that the same visual stream (i.e., the ventral stream) was responsible for both.

On the other hand, the poor perceptual report of target displacement in both conditions provides evidence against this explanation. If the ventral stream was not 'aware' of the displacements, how could it be responsible for the observed motor biases? (The potential weaknesses of this argument will be discussed later on.) Further evidence against this explanation is that previous research has shown that fast on-line motor corrections rely on posterior-parietal (dorsal) regions of the brain (Desmurget et al., 1999; Pisella et al., 2000). Thus, responding in the no-delay condition, in which target perturbations occurred on-line, must have required dorsal processing. This argument is a compelling one; however, given that the average MT to T1 in the no-delay condition was approximately 350-400ms and the average MT for the entire movement was approximately 600-700ms, there may have been sufficient time for ventral processes to influence the movement. The findings of Pisella et al. (2000), for instance, while showing that dorsal processing dominates for a 200-300ms movement, also suggest that ventral processes can impact a movement of 300ms or more. Indeed, the greater impact of a T2 jump than a T1 jump on the movement that we observed in the no-delay condition (and in Experiment 1) could be attributed to an accrual of ventral contributions as the movement

progresses. However, this same effect could also be attributed to the dorsal stream simply having more time to adjust the movement, independent of any ventral factor.

3. The dorsal stream was primarily responsible for the effects in the no-delay condition, while the ventral stream was responsible for the effects in the delay condition.

This explanation has the benefit of fitting with much of the previous research on dual-system processing, in that the on-line effects observed in the no-delay condition are attributed to the 'on-line' dorsal stream, while the off-line effects observed in the delay condition are attributed to the 'memory-capable' ventral stream. One line of research with which it would not fit, however, is the double-step literature suggesting that intra-saccadic target displacements are not accessible to the ventral stream.

A drawback to this explanation is its lack of parsimony. Given the similarity of the effects in the delay and no-delay conditions, and the lack of any evidence of a visual dissociation in the current results, explanation #3 seems unnecessarily complex. On the other hand, if both streams *do* have access to the same information (which, I will argue, was the case here), we would expect similar movement outcomes in dorsally-guided and ventrally-guided actions. In short, while the CE results provide no evidence of dissociation, they also provide no evidence against such dissociation. The most reasonable course, then, may be to interpret the findings in accordance with previous research on dual-system processing and memory-guided action.

Each of these 3 potential explanations for the current results relies on a different set of assumptions about behavioural measures of dual-system processing. Which explanation is preferred depends on our confidence in each of the assumptions.

Explanation #1 relies on two assumptions: 1) that perceptual report of target displacement measures a relevant parameter of ventral stream processing, and 2) that for the ventral stream to guide a movement, the individual must be consciously aware of the visual information used to guide that movement. There is a potentially major flaw in the first of these assumptions, in that perception of displacement might be completely irrelevant to the guidance of a movement. The only parameter of relevance to guiding a movement should be the current position of the movement target. This is related to a point that has been made previously by Post, Welch, and Bridgeman (2003), who argue that for any behavioural test of dissociation to be valid, the motor-response and the perceptual response must refer to the same physical parameter¹⁶. A double-step design in which the motor-response deals with a target's *final* position while the perceptual response deals with a *change* in target position does not meet this requirement.¹⁷

If perception of displacement is an irrelevant parameter, support for Explanation #1 is considerably weakened: we cannot confidently rely on poor perceptual report as evidence for a lack of ventral involvement. Furthermore, the second assumption underlying Explanation #1 is also dubious. As mentioned in the discussion of Experiment 1, absence of awareness does not necessarily imply absence of ventral processing (word-priming was cited earlier as an example of unconscious ventral processing). Thus, even if

¹⁶ The other requirement, according to the same authors, is that the motor response be visually open-loop.

¹⁷ This same criticism can, of course, be leveled at the current study, which employs just such a double-step design. For this reason, the perceptual report that we used is, as will be argued in the main text, of minimal value.

one could show that target displacement *was* a relevant parameter and so re-establish confidence in the first assumption underlying Explanation #1, poor perceptual report would still be insufficient: the ventral stream might be processing the parameter even if the participant cannot report it. In light of all this, Explanation #1 is probably the weakest of the three explanations.

Explanations #2 and #3 are less problematic, but they both rely on the assumption that the findings of previous studies on memory-guided action, none of which used a double-step paradigm, can be generalized to the current study. Westwood and Goodale (2003), for instance, examined size-contrast illusion effects on grasping in no-delay and various delay conditions, while Bridgeman, Peery, and Anand (1997) examined the motor and perceptual effects of the Roelofs Effect at various time delays. The very fact that these two studies (each using a different paradigm) did not arrive at identical conclusions about the time-to-decay of dorsal/sensorimotor representations¹⁸ does make it at least conceivable that the duration of the sensorimotor representation probed with the double-step paradigm could extend beyond 3sec. A follow-up experiment in which longer delay durations are included would help clarify this issue; we might find, for instance, that intra-saccadic target position persists for up 4sec in dorsal memory. That being said, it seems unlikely that a surviving dorsal representation would be responsible for the effects in the delay condition, effects which had not diminished relative to the effects in the no-delay condition. If a decaying dorsal representation were responsible for the effects in both conditions, we would expect to see a much stronger effect in the no-delay condition.

¹⁸ Westwood and Goodale argue for immediate decay; Bridgeman, Peery, and Anand argue for approximately 2sec of persisting representation.

To summarize, the value of the 3 explanations relies largely on how much credence is given to each of two measures: **perceptual report of displacement** and **delayed aiming performance**. Which is a superior measure of ventral stream processing? I have argued that the first measure is probably invalid and that this forces us to rely on the second measure. Consequently, Explanations #2 and #3 are more tenable than Explanation #1. Deciding between #2 and #3 is more difficult, although the preponderance of prior research would tend to favour Explanation #3.

If we tentatively accept the explanation that the dorsal stream is responsible for the effects in the no-delay condition while the ventral stream is responsible for the effects in the delay condition, the effects would then suggest that both streams are able to attend to two aiming targets simultaneously. This does support the original hypothesis that the dorsal stream can process two targets simultaneously, but further research is clearly needed to strengthen this finding.

Chapter 4

General Discussion

For the current study to show that the dorsal stream can process more than one target simultaneously, 2 lines of evidence were needed: 1) evidence of selective responding to displacements in one or both of two aiming targets, and 2) evidence that these responses were not being mediated by the ventral stream.

Experiment 1 provided strong evidence of selective responding, and possible evidence of an absence of ventral stream involvement. Participants consistently adjusted their movements in the direction of the target perturbations while their perceptual reports

of the same types of target displacements were poor. Potential problems with the perceptual report as a measure of ventral stream involvement, however, do exist (see the previous section), and so Experiment 2 was run as a further test of ventral stream involvement.

Experiment 2 introduced a 3sec delay between the saccadically-triggered target displacements and the onset of the movement. The delay was intended to eliminate any dorsal contributions to the movement, thereby isolating ventral control. The results of this manipulation were surprisingly similar to the results when no delay was used, suggesting that the ventral stream was able to use intra-saccadic information to guide the movement. The findings of Experiment 2, therefore, did not clarify the findings of Experiment 1, though they did inform us about ventrally-guided sequential aiming movements.

In short, the results of Experiments 1 and 2 are insufficient to confidently conclude that the dorsal stream can process two targets simultaneously. Experiment 1 is suggestive of such processing, due to the on-line nature of its task, but the results of the delay condition of Experiment 2 do little to substantiate or discredit this theory. Had we found an absence of a displacement effect in Experiment 2, we could have been more confident. However, the presence of a strong effect when there is a delay is an ambiguous outcome with regard to dorsal processing. It suggests that the ventral stream can process both targets, but does not speak to whether or not it did so when there was no delay.

Attention and Action

One conclusion in which we can be confident is that attention can be distributed between two targets during a sequential aiming movement. Our findings, therefore, confirm those

of Deubel and Schneider (2004), who used a letter discrimination task during a sequential aiming movement and found that discrimination was high at the two locations to which an aiming movement was directed. The current study extends their finding to show that the location information gleaned from both aiming targets can be used to immediately (or belatedly) update the movement.

Interestingly, the current study may also lend support to the Visual Attention Model (VAM). Recall that the VAM states that a common selection mechanism operates for both the dorsal and ventral stream. If the current study's no-delay and delay conditions reflected dorsal and ventral processing respectively, then we observed that processes in both streams were coupled to the two aiming targets. On-line movement updating reflected dorsal selection of both targets, while storage of the updated target locations in short-term memory reflected ventral selection of both targets. This is entirely consistent with VAM¹⁹.

Other issues

Although the current study failed to provide conclusive results regarding dorsal stream processing, it has raised some important issues in dual-system research that deserve further discussion.

First among these is the use of the double-step design as a tool for dissociating dorsal and ventral processing. While it can be used effectively for examining the 'automatic-pilot' characteristics of the dorsal stream (Pisella et al., 2000), I would argue that it should be used with great caution when coupled with a perceptual report of

¹⁹ Except for the tenet of VAM which states that only one target can be selected at a time, a feature of the model which, as Deubel and Schneider (2004) discuss, appears incorrect, as they've shown with their sequential aiming study.

displacement. Post, Welch, and Bridgeman (2003) have already pointed out the logical flaw inherent in such a design: the motor response measures a different parameter of the stimuli than the perceptual response does, so how can dissociation be inferred? I would further argue that not only does perception of displacement measure a different parameter than motor localization, but that displacement may be an *irrelevant* parameter when examining aiming movements. As the results of the delay condition of Experiment 2 showed, whether or not participants perceived displacement did not influence their guidance of a delayed (and presumably ventral) movement to the targets. A better perceptual report than the standard displacement report would be a report of final position, a parameter that is both consistent with the motor response and relevant to the movement. The problem with such a report is that it could not be used with double-step designs in which the target remains lit after the saccade is completed. In such cases, the ventral/cognitive representation of target location would simply be updated to reflect the new position, and the report would always be reasonably accurate. However, it could be used in a design like the current one, in which the target disappears prior to the completion of the saccade.

A second issue is how much access the ventral stream has to intra-saccadic information. Many studies, this one included, have proceeded under the assumption that ventral stream processing of a target is suppressed during a saccade, while dorsal stream processing remains intact (an assumption that derives primarily from previous double-step studies that showed suppressed awareness of target displacement). The effects observed in the delay condition of the current study, however, strongly suggest that the ventral stream *does* have access to intra-saccadic target information.

While visual sensitivity has certainly been shown to decline during a saccade (see Ross et al., 2001), it is important to show that the suppression applies preferentially to the ventral stream if we want to use a saccade as a tool to remove ventral input to movement guidance. Recourse to studies showing suppressed perception of displacement but intact motor guidance (e.g. Goodale, Pelisson, and Prablanc, 1986) is not sufficient, for reasons that have already been discussed.

Limitations of the current study

The design of the study was such that participants knew that the targets to which they were aiming would disappear before their hand could reach them. While there were good reasons for employing such a design, we cannot escape its lack of ecological validity. Rarely do we make movements in a natural setting to targets that disappear as soon as we look at them! Thus, the study may be limited in the extent to which we can apply its findings to normal attentional processing during action: Do people normally attend to more than one object during a sequential movement, or have we merely forced them to do so by removing the targets? The study has shown that the system is *capable* of such divided processing, and while it may be tempting to argue that the system only has such a capacity because the organism uses it to make reaching movements in the 'real' world, the capacity may have developed for entirely different purposes. Simply because a flexible visual brain is able to divide visuomotor attention in order to respond to a contrived laboratory task does not imply that it would ever do so under normal reaching circumstances.

A second limitation of the study is that its findings may be confined to pointing actions. Although the discussion has centered on the more general topic of 'dorsal' processing per se, the findings are technically limited to 'dorsally-mediated pointing actions'. It is possible, for instance, that sequential movements involving grasping do not exhibit the same attentional characteristics.

Future directions

One of the more intriguing issues that arose during this study was the possibility that visual information presented during a saccade can be used by the ventral stream. What kinds of information survive during the saccade? And of these, which ones are relevant to movement guidance? Furthermore, does suppression of subjective awareness imply suppression of a ventral representation altogether?

It is important, in exploring these issues, that future studies make a clear distinction between suppression of displacement and suppression of positional information. Indeed, the very issue of whether displacement information is important for movement deserves further investigation. The assumption has been that ventrally-guided movement requires 'knowledge' of displacement – a knowledge that relies on making a comparison between initial and final location. This requirement is never made of the dorsal stream, and one wonders why we impose it on the ventral stream. Suppression of displacement information during a saccade is probably about maintaining a subjectively stable visual world and may be achieved in large part through a retro-active constancy mechanism operating in the ventral system (Deubel, Schneider, and Bridgeman, 2002). However, it seems odd that we consider the ventral system so inept as to be unable to

dissociate knowledge of movement from knowledge of position. It seems even stranger that we assume that the system would deduce a target's current position not from the coordinates of the stimulus itself, but from the amount of perceived prior motion (or lack thereof). Consider how foolish it would be if someone, upon seeing the moon at its zenith but not having seen it move there, insisted that it was still upon the horizon.

If we hope to investigate individual processing streams in healthy participants, great care is required in selecting the appropriate methodology. The current study relied on a protocol (the saccadically-triggered double-step) that may not probe isolated dorsal processing as effectively as previously thought. Researchers who intend to employ the same protocol should, before anything else, ensure that it measures what it is intended to measure.

In the meantime, a different protocol may be required to successfully measure multiple-target processing in the dorsal stream. We need a way to rule out ventral stream involvement without relying on the problematic 'perception of target displacement'. One way to do this, which was mentioned in the discussion of Experiment 2, would be to require a report of a target's final position rather than a report of displacement. The shortcoming of this type of report is that it still only tells us what information the ventral stream has *access* to. It does not tell us whether the ventral stream actually used that information to guide the movement. (We may find, for instance, that final position of a perturbed target is well reported by participants, while it was still the dorsal stream that mediated any motor correction to the target.) A stronger design would be one that pits conflicting dorsal and ventral stream representations against each other such that the outcome of the movement itself indicates which representation was used. Thus, one could

use, for example, a sequential aiming movement protocol in which *perceptual* target perturbations are induced by shifting frames positioned around each of the two targets (i.e., simultaneous Induced Roelofs Effects). The use of the frame shifts would produce a change in the allocentric coding of the target positions without influencing the egocentric coding of the targets. This would allow us to introduce conflicting information about target position to the two streams (allocentric to the ventral, egocentric to the dorsal), and by observing the outcome of the sequential aiming movement we could infer which stream was carrying out the processing.

An alternative means of probing the dorsal stream's involvement in a multiple target task would be to temporarily 'deactivate' posterior parietal areas with TMS (Desmurget et al., 1999). If we were to find, for instance, that application of TMS eliminates corrections to both targets in a rapid sequential aiming movement, we could more confidently conclude that the motor corrections observed in the current study are a result of dorsal processing.

As further research clarifies the roles played by each visual stream in selecting action targets, programming movements to these targets, and modifying the movements en route, we will deepen our understanding of how we use visual information to interact with the world. Multiple-target processing is an important part of the puzzle, for many of the actions we carry out on a daily basis involve multiple objects and multiple movement components. The current study took a first step in examining how the two visual streams process the visual information that is used to program and update such movements.

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