Revealing interactive sensorimotor processes for trajectory formation in oculo-manual actions and isolated saccades.

REVEALING INTERACTIVE SENSORIMOTOR PROCESSES FOR TRAJECTORY FORMATION IN OCULO-MANUAL ACTIONS AND ISOLATED SACCADES.

BY

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Abstract

Trajectory formation is an important quality of human movement wherein the analysis of its kinematic structure often permits inferences regarding the underlying sensorimotor organization. The studies reported herein aimed to reveal how task-specific encoding of saccades contribute to two movement models.

We first examined saccades for changes in the evidence for online spatial corrections in response to different instances of visual tracking. Results from our first study indicated the sensorimotor operations associated with making timed series responses permitted unhindered operation of online corrections in predictive saccades. These saccades imposed a demand on spatial working memory without suffering diminished corrections typical of single delayed memory-guided saccades.

Next, we queried the role of ventral stream visuomotor processing, as well as the contribution of basic stimulus features to explaining known modulations of online saccadic corrections. Our results are consistent with the explanation that ventral stream contribution to target metrics influence trajectory kinematics, but did not induce diminished online corrections if vision of that illusory target was available at saccade onset.

Using another movement task, we examined how different saccadic tracking behaviours dissociated the contribution of various sensorimotor operations involved in oculomotor preparation and execution to eye-hand coupling. By observing changes in manual trajectory in an oculo-manual task, we contrasted the effects of saccadic

tracking in predictive and reactive modes, overt and covert, horizontal and vertical, spatially congruent or perpendicular axes of primary motion relative to eye-hand coupling.

From these data we concluded that saccadic encoding induced execution-dependent coupling, and optionally motor planning-dependent coupling when task constraints specified temporal synchrony between eye and hand movements. Moreover, eventual motor execution was a prerequisite for the emergence of oculomotor planning-dependent coupling effects. This implied no apparent contribution to the coupling dynamic as an exclusive function of shifts in the spatial allocation of attention without oculomotor output.

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Notation and abbreviations

antSac - Anti-saccade

dmgSac - Delayed memory-guided saccade

EOM - Extraocular muscles

FEF - Frontal eye field

IPL - Inferior parietal lobule

IRI - inter-response interval

ISI - Inter-stimulus interval

IT - inferotemporal cortex

LGN - Lateral geniculate nucleus

LIP - Lateral intraparietal area, sulcus

M1 - Primary motor cortex

mIPS - Midposterior intraparietal sulculs

mm - Millimetres

ms - Milliseconds

MT - Movement time

PM, PMC - Premotor cortex

pMT - Percentage of movement time

PPC - Posterior parietal cortex

PRF - Pontine reticular formation

SC - Superior colliculus

SEF - Supplementary eye field

SMA - Supplementary motor area

SPL - Superior parietal lobule

SWM - Spatial working memory

TMS - Transcranial magnetic stimulation

TTL - Transistor-transistor logic

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Chapter 1

Introduction

1.1 Scope of investigations

Human movement, as performed by individuals who are selected from a typically developed and healthy population, is a result of the brain's ability to create and send structured task-specific information to our body's musculature. A majority of movements are generally executed with the purpose of changing our body's configuration to a more desirable state. In order to do so objectively, efficiently, and effectively the brain implements control policies specific to the goal of each movement scenario. Different information is encoded in a variety of sensorimotor networks, and those which are required for mediating performance in a given task under a specific set of task-specific constraints are selectively recruited. As a consequence of functionally dissociable sensorimotor networks contributing different information to encoding a motor response, the respective contribution of these processes to the kinematics of the subsequent response are also often dissociable in their behavioural presentation. For this reason, both the spatiotemporal and cognitive constraints imposed on the performance of a given task often have a direct influence on the kinematic properties with which movement trajectories emerge.

A control policy embodies the overall operation and implementation of a set of sensorimotor functions that are collectively relevant for performing a given task (Diedrichsen, Shadmehr, & Ivry, 2010). Some cursory examples are those related to visuomotor transformations (Woolley, Rugy, Carson, & Riek, 2011), predictions of temporal precision (Joiner & Shelhamer, 2006; Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002) and other forms of motor planning (Grafton, Schmitt, Van Horn, & Diedrichsen, 2008), working memory (Ungerleider, Courtney, & Haxby, 1998), and visual target selection (Hutton, 2008). While these are just a few of the many factors that are dissociable in their contribution to the encoding and production of motor responses, their respective relevance to a given task is contingent on the type of movement goal that has been specified for that task. In fact, it is both the type of goal specified for which an action intends to achieve as well as the constraints under which that action is being executed that determines the neural footprint of a given task.

For defining the movement context within which we examine the effects of task constraints, basic classes of human movement are divided according to the nature of parameters that are optimized in execution. These goal variables quantify how a degree of success is represented in the performance. A primary distinction between two such classes is whether the execution of a movement is constrained for precision in either its spatial, or its temporal accuracy. In order to optimizing performance for minimizing error in one variable or the other, these two types of motor responses produce actions that have fundamentally different intrinsic kinematic structures.

This distinction is perhaps most clearly introduced in respect to manual actions. Reaching and aiming are examples of goal-directed actions wherein their end-point spatial error is the optimized performance variable. In contrast, when tapping one's finger to a metronome this action is optimized by achieving a timing goal, and not for spatial precision. Spatially-directed actions constitute a class of their own, including other types of movements such as saccadic eye movements. Saccades are also directed from one location to another with an emphasis on their spatial precision at the time of movement offset. Despite the obvious kinetic and metric dissimilarities between oculomotor actions and aiming with the upper-limb, their respective intrinsic kinematic structure is in fact rather similar. As a function of being directed to a spatial target, both actions evolve with a characteristic bell-shaped velocity profile (Bahill, Clark, & Stark, 1975; D. Elliott, Helsen, & Chua, 2001; M. T. Elliott, Welchman, & Wing, 2009). In contrast, the velocity profile of the fingertip trajectory in periodic tapping tasks is much different as a function of optimizing the temporal precision of the response with respect to an internal or external timing goal, irrespective of the finger's exact spatial location on the tapping surface (Balasubramaniam, Wing, & Daffertshofer, 2004; Balasubramaniam, 2006). In either case of goal-directed or timed movements, trajectory formation is often examined by means of its observed kinematics with the intention of determining how its structure emerges as a function of task-specific constraints on performance.

1.1.1 Problem statement

At this juncture, it is important to underscore that all studies conducted as a part of this dissertation research implemented a consistent approach in their methodology and aims. To be precise, the research problem that generalized to all the current studies was an examination of changing patterns in movement kinematics in response to task manipulations for dissociating the respective contributions of a number of sensorimotor operations. Overall, the merit of conducting these studies lies in their implications for refining current functional-anatomic models of sensorimotor organization, and to identify the factors that draw limits on their extension to a number of novel contexts.

In Chapters 2 and 3, the kinematic structure of saccade trajectories was examined for evidence of control processes that implement online spatial corrections. Previous work has shown evidence that the efficiency in the operation of online corrections is modulated by visuospatial constraints imposed on saccadic tracking (West, Welsh, & Pratt, 2009; Heath, Dunham, Binsted, & Godbolt, 2010; Heath, Weiler, Marriott, & Welsh, 2011). The two current studies intended to resolve further specificity in determining which sensorimotor operations are most relevant to modulating the implementation of online saccadic corrections.

The next section of research studies presented in Chapters 4 and 5 examined the trajectory of hand movements to reveal how their sensorimotor organization overlaps with that of concurrent oculomotor responses. An analysis of the hand trajectory was focused at revealing mechanisms of oculo-manual coordination by means of unintended coupling effects between concurrent eye and hand actions. These studies are partly an oculo-manual extrapolation of the seminal work showing unintentional coupling between the two upper-limbs during concurrent hand actions (E. a. Franz, Zelaznik, & McCabe, 1991; E. A. Franz, Zelaznik, Swinnen, & Walter, 2001; E. A. Franz & Ramachandran, 1998). The research problem specific to Chapter 5 and 6 studies aims to refine a general model of the functional organization of concurrent eye and hand actions.

1.1.2 Statement of overlapping content

The background section includes a review of current literature for presenting a complete and cohesive line of reasoning that justifies the methodology of our current studies with respect to their intended purposes and implications of their outcomes. This was written while attempting to avoid excessive overlap and repetition with the content included in the research chapters. Yet each research chapter is written with an independently sufficient introduction to merit its presentation in form of a report that has either been published or prepared for dissemination. Referencing the collection of studies relevant for a general background thus implicates some degree of overlap with content presented with the individual studies. While this is necessary, an attempt at avoiding repetition is made by focusing the general sections on the relevance of this information to the model of the overall research program, and less with respect to topic-specific discourse that is otherwise relevant only to the nuances of each research chapter.

Overlapping content between individual research chapters is only considerable for Chapters 2 and 3, and separately for Chapters 4 and 5. This overlap is only partial because the first two research chapters focus on the exclusive case of oculomotor control mechanisms for resolving spatial errors in the execution of saccadic eye movements. In a separate series of two studies, Chapters 4 and 5 are instead aimed at examining motoric coupling between eye and hand movements. Consecutive chapters in each of these two series are incremental. For this reason the background literature for Chapters 3 and 5 include some redundancy in their review of results from the chronologically preceding Chapters 2 and 4 studies, upon which they respectively extend.

In summarizing the content that most frequently overlaps between sections of this dissertation, all four research chapters develop their conclusions with the requirement of understanding many properties of oculomotor organization, specifically that which mediates saccadic responses. This topic is responsible for the largest portion of repeated content between all chapters of the dissertation. Of course, this content is delivered in each chapter with a focus tailored to that relevant for the associated study.

1.2 Research program overview

1.2.1 General background

The premise of the current research program is most significantly contingent on, and best introduced with respect to the control theory regarding the mechanisms of encoding actions that are directed to a spatial location. As alluded to previously, saccades fall within a class of spatially-directed actions —*goal-directed* action itself is a term implying a spatial goal —and are similar to manual aiming in their relative kinematic structure. Saccades are used in every visual tracking task in the current studies. As a goal-directed action, this classification imparts some general principles of sensorimotor organization in its own merit. This topic originates in a larger portion of control theory of goal-directed actions that has emerged from the analysis of trajectory kinematics with the case of spatially-directed arm movements (Woodworth, 1899).

Over a century of research on this topic has seen many different variations of aiming tasks (D. Elliott et al., 2001). A common point of enquiry for many of these studies has been directed at understanding how reaching performance is modulated as a function of manipulating task factors. When aiming with full vision of one's upper-limb and of the target, these factors are conducive to a few distinct types of control policies. In preparation for a reach, motor planning networks develop their best prediction of the task metrics to prepare the encoded movement, thus forming a feed-forward control policy (Beaubaton & Hay, 1986). Following movement onset, as the movement progresses visual feedback becomes available of the motion of one's limb and of its position relative to the target (Khan et al., 2006) from which a representation of error is formed and the action is updated online. This forms one instance of a feedback control policy. This latter phase, also referred to as the *homing* phase in reaching is characterized by discrete changes in trajectory direction as a function of a strong reliance on visual feedback (D. Elliott, Binstead, & Heath, 1999).

Evidence for these two forms of control strategies were revealed from the kinematic structure of reaching trajectory using two serially important analysis procedures (D. Elliott et al., 1999). The first indicator of online corrections is that position is significantly more variable at mid-trajectory measurements than at the eventual end-point. This alone does not suggest an active mode of online spatial correction is implemented in the trajectory, as it does not rule out a passive means of correction. However, a passive reconciliation of trajectory error would also inherently demonstrate ballistic properties.

To resolve this possibility, a regression analysis determines the degree to which hand position early in the trajectory predicts the eventual end-point. This is an indicator to determine whether or not the trajectory evolves in a ballistic manner. A high degree of correspondence between the hand position early in the trajectory relative to its end-point reflects little intervention from corrective mechanisms. This conclusion is based on the contention that online corrections would otherwise implement changes later on in the course of the trajectory. For example, smaller correspondence from a regression analysis indicates the subsequent trajectory evolved following an unpredictable path. This characterization of behaviour is be apparent in the final homing phase corrections to reaching actions irrespective of whether they are implemented in continuous and discrete modulations of the late-phase upper-limb trajectory (D. Elliott, Carson, Goodman, & Chua, 1991).

Until recently, this was considered a point of divergence in the comparison of saccades and aiming. Whereas aiming tasks clearly exhibit feedback-based control policies, this was not regarded to be true for saccades. Instead, the idea that saccades operated in a fully ballistic manner was generally accepted. The absolute reliance of saccades on feed-forward control was generally assumed since their duration, in addition to being very brief, was very tightly correlated to their extent (Bahill et al., 1975). The validity of a purely ballistic saccade trajectory model is questioned, in part because saccades demonstrate motor equivalence. This property implies they are similar to reaches in that their trajectory can evolve following one of many possible paths and arrive at the same end-point. More recent work examining the time-course of gaze position data throughout the evolving saccade challenges this ballistic theory. By adapting variability and regression analysis from aiming research to visual tracking tasks, the demonstration of analogous kinematic evidence for online corrections was extended to include saccades (West et al., 2009).

Subsequent to revealing the similar two-component operation of feed-forward and feedback processes for the control of both saccades and reaches, a logical question asks whether these two components emerge from a common functional basis? With the duality of prospective and retrospective control policies, goal-directed eye and hand actions seem most similar in their requirement for preparing and planning via feed-forward control. For example, a goal target is first identified from a visual representation that is later translated for encoding specific movement metrics.

To this effect, the perception-action model suggests that localization of a visual stimulus for visuomotor integration is a specialized process mediated by the dorsal visuospatial processing stream (Goodale & Milner, 1992). This model also recognizes a second ventral stream that is respectively specialized for perceptual assimilation of target properties in a qualitative sense. Whereas the dorsal stream is associated with posterior parietal cortex (PPC) function, primarily the superior parietal lobule (SPL), the ventral stream is correlated to a footprint in the inferotemporal cortex (IT). The encoded metrics representing a spatial target for a goal-directed action are postulated as being encoded in the dorsal stream for direct translation to the encoding the metrics of upper-limb (Chang, Dickinson, & Snyder, 2008; Desmurget et al., 1999), saccadic (Pierrot-Deseilligny, Müri, Nyffeler, & Milea, 2005; Müri & Nyffeler, 2008), and other motor responses (Rizzolatti, Fogassi, & Gallese, 1997).

An overlap of visuomotor integration in the dorsal processing stream as it serves the initial specification of target metrics for reaches and saccades is undoubtedly useful in a number of circumstances. In the case of reaching to grasp an object, saccades to the same target generally accompany the reach to facilitate performance by enhancing the acuity of resolving manual error with visual feedback (Land, 2009). Saccade-guided foveal vision provides the visual information which accounts for a large portion of the sensory feedback used to evaluate reaching performance online (Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Chua & Elliott, 1993). This fact is conducive to explaining the mechanism for feedback control in reaching, and also sources a critical divergence in its similarities in contrast to the control mechanisms for the saccades.

The mechanism of online feedback-based control for saccades is necessarily different in key aspects from that implemented for reaching. An important consideration when interpreting theories described by the action-perception model is in considering its origin was developed as a model of upper-limb aiming, and in combination with instances of pathological behaviour. So there are aspects of this model incompletely adapted to saccading. In its fundamental claims, online feedback for reaching is implemented through the *real-time* visuomotor integration via the dorsal stream (Goodale & Milner, 1992; Westwood D.A. & Goodale M.A., 2003). The same cannot be reciprocally extended to saccades since the visual information about the saccade end-point is not available until, of course, the saccade terminates. While evidence for fast retinal feedback does exist, it has only been demonstrated to account for unexpected changes in target position that occurred no later than the instant at which saccade onset was detected (Gaveau et al., 2003), and fails to explain resolving trajectory error that accumulates after this point. Other mechanisms of fast oculomotor feedback do exist, and likely involve subcortical oculomotor loops for fast evaluations of motor commands, specifically those that compare differences in their actual output versus their intended output (Angel, 1976; Soetedjo, Kaneko, & Fuchs, 2002).

A separation of the anatomical correlates of visual processing for action and those for perception is a primary distinction of the perception-action model, also referred to as duplex vision (Goodale & Westwood, 2004). Other theoretical perspectives, however, argue against this strict duality that functional-anatomic modularization is completely representative of its intended dissociation. One example of such thinking is the unitary representation model (V. Franz & Gegenfurtner, 2000), which suggests that the scale of the perceptual and motoric bias induced by a visual illusion is coupled in ways that are incompatible with the perception-aciton model (V. H. Franz, Hesse, & Kollath, 2009). Additional concerns regarding a strict functional dissociation of perception and action to ventral and dorsal streams of sensory and motor operations are raised in a review of evolving methodologies and (re)interpretation of the collective evidence (Schenk, 2010).

Both sides of this discourse generally agree that visual processing encompasses the integration of a range of specialized visuospatial information (Schenk, 2010; Goodale & Westwood, 2004). Criticisms are instead directed at the validity of asserting it is the integration of pre-processed signals that are respectively specialized for perception and action, and that these operations are represented respectively in IT and SPL brain regions. This debate is current and ongoing, with additional details found in recent reviews either supporting duplex vision theory (Westwood & Goodale, 2011) or in opposition of it (Schenk, Franz, & Bruno, 2011).

A point that garners a greater degree of agreement amongst researchers, and one that is perhaps of more relevance to this study is that different psychophysical demands of task variations are associated with different patterns of brain activity. This latter fact establishes that anatomical neural correlates validly distinguish some aspect of segregated function and encoded sensorimotor operations between SPL and IT networks. The thesis research herein draws attention to many instances of anatomical-functional modularization. In the sections below, references to ventral and dorsal stream processing are more relevant to distinguishing their anatomical correlates, and less so in regard to implications that the duplex vision theory imparts for dissociating explicit and segregated functions of perception and action.

In the context of goal-directed behaviour another unique distinction of saccades is that involuntary responses are dependent on a direct specification of target and saccade metrics by means of visuomotor integration. Reactive and reflexive saccades are similar cases of involuntary responses wherein their execution occurs following the presentation of the visual stimulus that triggered their response. Voluntary saccades are instead those made to target locations that are specified by endogenous means, or those which require an explicit modification of an involuntary response. A few examples of voluntary saccades include those to targets that are selected from a range of distractors, or to memorized or predicted locations. The functional division of voluntary and involuntary cases of oculomotor responses is also supported by different neurophysiological networks correlated to their performance (Mort, 2003; Müri & Nyffeler, 2008; Brignani, Bortoletto, Miniussi, & Maioli, 2010). Referring to this visuomotor integration process as being *direct* implies specific properties of their organization according the views perception-action model (Westwood D.A. & Goodale M.A., 2003) that are challenged as not being any more functionally direct than motor parameters specified from operations of ventral stream (V. H. Franz et al., 2009). However, the dorsal stream includes populations of neurons which show much stronger evidence of target representation encoded in a *direct* retinotopic coordinate system (Snyder, 2000) than is associated with ventral stream visual processing.

Up to this point in reviewing background literature, contrasting the control of saccades and aiming has queried whether specific properties of their functional organization are common to both, or unique to either movement context. Another complimentary method for comparing the control mechanisms of ocular and manual actions is on the basis of the degree to which various sensorimotor processes either overlap or specialize in their respective coding of saccades and, or upper-limb movements. Despite previous mention that the division of dorsal and ventral stream visuospatial processing serves both the metrical target representations for goal-directed reaches and saccades, this overlap is broadly incomplete.

The control of manual actions and saccades is predominantly mediated by separate and specialized networks. Saccadic oculomotor control is a feat owing its behaviour to a network of brain areas specialized for this function (Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998; Melamed & Larsen, 1979; Sparks, 2002; Lawrence & Snyder, 2009; Schlag, Dassonville, & Schlag-Rey, 1998), and predominantly separate from those related to controlling upper limb movements (Kaas, 2012). At a macroscopic level this distinction remains mostly consistent in both their cortical and subcortical correlates of primary motor function —the superior colliculus (SC) and frontal eye fields (FEF) for saccades, and the primary motor cortex (M1) for manual actions. However, in the single-cell response characteristics of oculomotor and manual motor system neurons, both *effector-specific* brain regions have subsets of cells in primary (Mushiake, Fujii, & Tanji, 1996) and secondary (Pesaran, Nelson, & Andersen, 2010) motor, and parietal (Snyder, Batista, & Andersen, 2000) association cortices that demonstrate cross-effector[1] responsive properties. It is likely that a

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[1] In its traditional usage, *effector* implies a an interaction between one's movement and a consequent change in the state of the environment *effected* by an action. Our use of this terminology includes the extended meaning of effecting a movement, including the change of gaze state effected by saccades

regulated and selective integration and inter-regional propagation of signals encoded in these neurons contributes to a mechanism of implementing oculo-manual coupling.

In addition to a neurological substrate with cross-effector responsive characteristics as a mediating factor of oculo-manual coordination, the context and constraints under which a task is performed also modulates the expression of overlapping eye and hand action representations. The time-course of eye and hand coupling dynamics in coordinated aiming-saccading paradigms provide evidence that the feed-forward dependent components of their coordinated actions are reliant on overlapping motor plans (Donkelaar, Siu, & Walterschied, 2004; Kattoulas et al., 2008). More specifically, in a coordinated eye-hand aiming task, despite saccades being executed before their manual counterpart to the same target, the saccade metrics scaled as a function of the pre-cued kinetic requirements of the impending arm movement. An eye-hand coupled representation in the feed-forward specification of movement metrics is the likely explanation of this cross-effector effect

As alluded to previously the neurophysiological footprint of saccades are different according to the tracking paradigm that used to engage their responses. The case of separate control networks for voluntary and involuntary saccadic tracking is one good example that is also relevant here. It then stands to infer that overlapping representations of encoded eye and hand movements might also change as a function of the tracking paradigm.

The above reviews draw many parallels, contrasts, and interactions between the control architecture of eye and hand movements to develop a conceptual model of the relative functional organization of saccades, goal-directed upper-limb actions, and how they might interact. In relation to the focus of the dissertation studies, two specific reasons to have introduced this general control theory in regards to manual and oculomotor actions are as follows. Firstly, chapters 2 and 3 present studies that test the extension of control theory from goal-directed aiming to predict how online corrections in saccades are modified by task manipulations. Further detail is included below in the topic-specific introduction to these studies along with hypotheses and outcome predictions for each.

A second reason for which the general introduction has situated manual aiming and saccading in the common context of goal-directed actions is because it implies a certain degree of overlap in their control architecture. In the case of intentionally coordinated goal-directed reaching and saccading, a number of studies explore the overlap in mechanisms that encode eye and hand movements for concurrent actions to explain their correlated performance measures (Donkelaar, 1997; Snyder, Calton, Dickinson, & Lawrence, 2002; Gueugneau, Crognier, & Papaxanthis, 2008; Cohen & Rosenbaum, 2007; Lünenburger, Kutz, & Hoffmann, 2000; Kattoulas et al., 2008). Chapter 4 and 5 studies digress from these investigations in their aims to investigate mechanisms of oculo-manual coupling that operate as a function of sensorimotor operations unrelated to mediating intentional spatial coordination. The basis for understanding isolated and coordinated goal-directed action is important to the formation of these studies, and is elaborated in the following topic-specific reviews to these research chapters.

1.2.2 Online spatial corrections in saccades

Differentiating the mechanisms for feedback-based corrections in eye and hand movements leads to a clear divergence wherein only the latter operates as a function of integrating online visual feedback. It may then seem to be an illogical approach to use control theory developed by means of manual motor behaviour in aiming tasks as a foundation for formulating and guiding studies related to feedback-based control in saccades. The later movement phase in aiming that demonstrates the onset of secondary submovements for correcting trajectory errors was originally referred to as the *current control* phase. The important role for visuomotor integration in the current control of aiming is not disputed (Glover & Dixon, 2001; Khan et al., 2006; Glover, 2004; D. Elliott & Khan, 2010). Yet this does not preclude the additional importance of feedback from other sensory modalities, like proprioception (Sarlegna & Sainburg, 2009), or that relating efference copies (Angel, 1976; Pelisson et al., 1986; Lewis, Gaymard, & Tamargo, 2013). Both examples of these feedback mechanisms are relevant for oculomotor and manual motor control, thus resurrecting the importance of considering parallels in the control theory for aiming and saccading as it relates to their online corrections.

Returning to the similarities between the representations of gaze and upper-limb, as is upper-limb proprioception represented in the somatosensory cortex gaze position is also reflected by ocular proprioception and represented in the sensorimotor cortex (Balslev, Albert, & Miall, 2011). Yet the potential use of these signals for online corrections in saccades are limited by afferent transduction delays. Despite ocular proprioception feedback having a much faster integration as compared with that of the limbs on the simple comparison of the distance of neuronal signal transduction from sensor cells to control networks, even faster solutions exist as putative mechanisms for online corrections in both saccades and reaches.

In either manual or oculomotor actions, efference copies are formed by the retrograde-projecting motor commands from motor neurons[2] back to their higher-order control processes in their sensorimotor networks (Angel, 1976). These loops acquire efficiency in their ability to evaluate the quality of the executed motor commands without having yet been effected by the target muscle groups. The direct upstream integration of the outgoing motor commands allows for an estimation of the actual movement metrics produced (Wolpert, Miall, & Kawato, 1998; Glover, 2004), relative to those that were intended and corrupted by motor noise in execution, an inherent quality of oculomotor (Beers, 2007) and manual actions (Wolpert, 2007). Whereas the cerebellum is generally implicated in this process regardless of effector (Wolpert et al., 1998), local loops exist between the cerebellum and subcortical oculomotor-specific networks like the SC and the pontine reticular formation (PRF) of the brainstem (Kato, Grantyn, Dalezios, & Moschovakis, 2006; Quaia et al., 2011) that exhibit relevant operations for refining the coding of sensorimotor metrics (Lewis et al., 2013).

Even though saccades and reaches differ in their use of sensory feedback for their online guidance, other similar mechanisms of implementing corrections to their emerging trajectory is adequate reason to extend and test the control theory of saccades from that developed in aiming tasks. Irrespective of the precise mechanism of implementing saccadic corrections, and irrespective whether these corrections are discrete or continuously applied, the kinematic evidence from variability and regression analysis are used to investigate their influence in making amends to movement trajectory.

The research studies presented in Chapters 2 and 3 were conducted as incremental

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[2] Another processes related to fast feedback is that of corollary discharge. This is distinguished from efference copies in that that corollary discharge includes the interactions between a larger set sensorimotor operations that are interconnected at many levels within the control hierarchy (Crapse & Sommer, 2008)

extensions of a series of work demonstrating the diminished evidence and efficacy of online corrections in goal-directed movements to memorized locations. In the case that a target is presented briefly and then masked with a subsequent delay interval before movement onset, the accuracy of manual or oculomotor responses is decreased as the delay interval preceding their execution increases (Rolheiser, Binsted, & Brownell, 2006). A related research group also showed a decay in accuracy when reaching to remembered locations is consistent with a reduction of the evidence for online corrections (Heath, Westwood, & Binsted, 2004). When reaching to memorized target locations, there was a higher correspondence between limb position and the movement end-point at all times in the trajectory as compared with visually-guided reaching. One further extension replicated evidence for diminished efficiency in corrections to delayed memory-guided saccades (dmgSac) (West et al., 2009). In these three works, the explanation for a decrement in accuracy and performance measures when moving toward memorized target locations most commonly allude to the overlap of spatial working memory (SWM) and ventral visuospatial processing networks (Westwood D.A. & Goodale M.A., 2003). Testing these claims, and refining the accuracy of their contentions is a common point of enquiry for both of the following two studies.

Chapter 2 Irrespective of the exact relation of SWM and the degree to which it overlaps with the dorsal or ventral visual processing streams, the Chapter 2 study specifically queries whether an outright dependence on SWM for sourcing the metrics of the goal location is responsible for degrading the operation of online saccadic corrections. In the context of voluntary saccades, the supplemental contribution of motor planning is selectively engaged when performing series of reciprocal saccades between two constant target locations in a motor timekeeping task (Joiner & Shelhamer, 2006; Richardson & Balasubramaniam, 2010; Schubotz, Friederici, & Cramon, 2000). The pacing for responses is cued by alternating the visibility of left and right targets at regular intervals. These stimuli are normally tracked with predictive saccades, an inherent property of which is that their onset occurs prior to target visibility. Importantly, a predictive time-course implies their trajectories are encoded prior unmasking the visual target, with their metrics being derived from a representation stored in SWM.

Hypotheses In contrast to dmgSac responses, the tracking paradigm for evoking predictive saccades implicates two factors, response repetition and timing prediction. Whereas the former is congruent with habituation and facilitation of SWM function, the latter is associated with a contingency on preparatory coding in planning. The hypothesis for this study commits the prediction that enhanced task representation by means of either of these preceding factors might bear the potential to support efficient online corrections in saccades despite a reliance on SWM.

Chapter 3 The outcome of the Chapter 2 study bears some relevance to the formation of the Chapter 3 research model. A brief review of the conclusions drawn from Chapter 2 results follows that diminished corrections observed in single dmgSac response tasks are perhaps a cost associated with SWM, but one that is recoverable by other means outside the context of single delayed responses. The recovery of efficient online corrections in predictive saccades emerged for a few possible reasons. The serial nature of repeating reciprocal saccades might have caused a habituated and enhanced operation of SWM (Mennemeier et al., 1994). Alternatively, it is also possible that the additional recruitment of networks for motor timekeeping might facilitate the performance of SWM by mechanisms related to prediction and planning.

In addition to the results of Chapter 2, a dissociation that remains unresolved from previous work (West et al., 2009) is whether SWM implements its costly effect for deteriorating online corrections in dmgSac responses from its overlapping representation with the ventral visuospatial processing stream. As adapted from reasoning that has previously been applied in other studies (Rolheiser et al., 2006), rather than SWM itself imposing a performance cost on corrections, this second explanation suggests the deficit arises as a function of the ventral stream's specialization for encoding visual properties that are not optimally conducive to visuomotor integration.

Moreover, one additional context of saccadic tracking is relevant to consider in the formulation of the Chapter 3 research paradigm. Anti-saccades (antSac) are those that require, in the following order, a cue from a peripheral visual stimulus, a suppression of the reflexive and directed coded response to the unmasked target, a vector-inversion to estimate the relative position of a virtual target location horizontally opposite to that cued directly by the stimulus, and finally a saccade to that estimated extent in the hemifield opposite from that in which the target was initially revealed. Responses in antSac conditions showed that online corrections operated with less efficacy than compared to visually-guided control responses.

In Chapter 3, two experiments test parallel theories for explaining these preceding trends in oculomotor function. One theory tested in the first experiment is whether degraded corrections in antSac and dmgSac conditions could be a by-product of degraded metrics, either a result of storing metrics in SWM or specifying them with uncertainty from inaccurate estimations. In other words, we test the theory that diminished online corrections do not necessarily result from encoded response representations that are mediated by any specific network or visual processing stream, but rather because the representation itself suffers corruption. The first experiment in Chapter 3 tests this theory by means of corrupting the perceptual representation of target metrics with uncertainty from presenting saccadic targets as Gaussian blobs.

Hypotheses - Experiment 1 Gaussian blob targets induce a degree of uncertainty in the spatial localization of the target's location. Should degraded modes of online corrections be explained by the corruption of the encoded sensorimotor representation with spatial uncertainty, saccades to Gaussian blob targets are expected to exhibit online corrections with diminished efficacy congruent with decreased certainty in the resolved location of the target location.

The second experiment in Chapter 3 digresses from the theory tested in the first experiment and instead queries the relevance of the ventral stream processes, other than those related to SWM, as they contribute to the operation of online saccadic corrections. When a regular solid dot saccadic target is presented in the visual periphery, the dorsal stream often encodes a response with directly interpolated metrics from its perceptual representation. Illusory targets, however, lead to actions that are biased by the discrepancy between actual and perceived extent of the eccentricity at which the target is located in the periphery (Glazebrook et al., 2005). The perception and motor consequences of biased metrics from visual illusions is associated with the integration of ventral stream function (Weidner & Fink, 2007), lending support for the possibility to cue saccades with a dependence on ventral processing without implicating SWM.

Hypotheses - Experiment 2 M*ü*ller-Lyer targets with wings-in and wings-out configurations should induce amplitude biases in saccadic responses relative to responses to control targets. While the direction of the illusion should result in opposite biases in response amplitude, the hypothesis stands that responses made to either wings-in or wings-out stimuli will show similar decreased evidence for online corrections. Confirming this hypothesis would support the explanation for diminished corrections in saccades as a function of ventral perceptual functions that are not optimized for visuomotor integration.

1.2.3 Eye-to-hand coupling

The preceding sections have contrasted many similarities and differences between ocular and manual motor behaviour, and in their respective overlapping or specialized neural correlates for control. A topic receiving less detailed attention thus far in the introduction to this thesis research has been the degree to which the respective performance measures of eye and hand actions correlate to one anther when performed concurrently (Donkelaar, 1997; Donkelaar et al., 2004; Snyder et al., 2002; Gueugneau et al., 2008; Cohen & Rosenbaum, 2007; Lünenburger et al., 2000; Kattoulas et al., 2008). In explanation of the mechanisms that lead to the observed patterns of oculo-manual coordination, these studies demonstrate clearly that eye-hand coupling emerges in a predictive manner. This implies an overlap in the feed-forward motor planning of concurrent actions is at least in part responsible for their coupling.

These conclusions, however, are specific to the case of goal-directed eye and hand responses. Concurrent aiming and saccading task paradigms have objectively served the investigation of oculo-manual coupling in tasks requiring intentional spatial coordination. Yet this narrow context incurs limitations in dissociating other sensorimotor mechanisms of oculo-manual coupling that are unrelated to mediated an intended mode of spatial coordination. To this effect, an exemplary question that coordinated reaching and saccading studies have not answered is whether the encoding of spatial goals for both eye and hand movements is itself process that serves as a necessary requisite for eye-hand coupling.

The studies in Chapter 4 and 5 are aimed at making this distinction, among others. A novel movement task paradigm was required to answer the cursory question whether motor planning-dependent coupling between concurrent eye and hand actions can emerge in the case that a spatial goal is not specified for at least one of the two actions. For this purpose, a necessary criterion of a novel task is that it must cause an overlapping representation in motor planning for the concurrent eye and hand actions without an explicit spatial parametrization of both eye and hand response. In the process of conceptualizing an appropriate motor task, the precluding fact that all saccades are inherently goal-directed necessitated that any suitable task must dissociate the role of spatial goals by implementing the manual component of the concurrent task in a way that avoids explicitly specified spatial parameters for its respective performance.

As compared with the explicit spatial optimization of manual aiming, another specialized mode of sensorimotor control is engaged to optimize the temporal precision of other movements. For example, when tapping one's finger on a tabletop surface in time with metronome cues, the fingertip trajectory emerges as a function of the temporal error of the response with respect to the external pacing stimulus

(Balasubramaniam et al., 2004; M. T. Elliott et al., 2009). In other words, finger tapping is served by a sensorimotor control strategy that implicates no relation to a spatial goal, or to maintaining spatial precision during execution. So the idea of examining concurrent saccading and finger tapping responses for evidence of coupling is one that also supports resolving whether eye-hand coupling emerges without the requisite of interacting spatial goals specified for both eye and hand actions.

In brief, the following introductions respective to Chapter 4 and 5 studies are contingent on first confirming that viable eye-hand coupling effects were indeed produced in this novel task paradigm. These studies determined that eye-hand coupling is not exclusively dependent on interacting spatial goals. This point is included here as it must first be acknowledged to make sense of the task variations included below. In addition to demonstrating the viability of eye-hand coupling in this saccading and finger tapping task, a larger portion of these studies are in fact aimed at determining how visual and spatial topological task constraints can alter the sensorimotor encoding of the motor responses with the consequence of evoking different patterns of oculo-manual coupling. In general, saccades performed concurrently with finger tapping caused trajectory deviations in the fingertip that were spatially congruent with the saccade's respective metrics.

Chapter 4 The study presented in this chapter was conducted with the intention of dissociating oculo-manual coupling as a phenomenon that emerges based on the contribution of a number of sensorimotor processes. In the context of bimanual coordination there is a clear division of coupling effects relating to different levels of the control hierarchy. A common division of these coupling effects is whether they emerged as a function of overlapping representations in motor planning (Heuer, Spijkers, Kleinsorge, Loo, & Steglich, 1998; Heuer, Spijkers, Kleinsorge, & van Der Loo, 1998; E. A. Franz & Ramachandran, 1998) or later during execution (Carson, 2005). The relevance of motor planning to oculo-manual coupling has already been ascribed in the context of goal-directed saccading and reaching (Donkelaar et al., 2004).

Relative to oculo-manual coupling, execution-dependent coupling in bimanual coordination is a specialized case because of its reliance on direct cortico-cortical connections between homologous motor areas in either hemisphere, and its relation to the pyramidal corticospinal neuromotor tract (Carson, 2005). For this reason, a putative network for explaining an analogous case of execution-dependent oculo-manual coupling is not immediately obvious, but this challenge does not preclude the possible existence of such effects.

To make the dissociation of motor planning-related or execution-dependent contributions to oculo-manual coupling, two complimentary experiments were conducted as a part of this study. The primary distinction between these tasks is the method of engaging saccadic tracking. In experiment one, predictive saccades and finger tapping were executed synchronously in a coordinated motor timekeeping task. In this case, both the eye and hand responses imposed overlapping demands on motor planning.

Hypotheses - Experiment 1 The primary hypothesis of experiment one contended that any observed patterns of eye-hand coupling are perhaps mediated by motor planning or execution-dependent mechanisms, a dissociation of which is permitted only by contrasting these results with those from the second experiment.

Next, a second experiment engaged reactive saccadic tracking. This second form of saccadic responses imposed no overlapping demand on motor planning with that implicated for encoding manual responses when repeating the concurrent finger tapping task.

Hypotheses - Experiment 2 As compared with the predictive saccadic responses in experiment one, the second hypothesis contended that the reactive saccades would be executed without imposing any respective demands on motor planning and thus do not overlap at this level of the control hierarchy with the preparation of finger tapping responses. In this case, patterns of eye-hand coupling would not be expected to reflect any contribution from motor planning, and instead represent the subordinate effect of execution-dependent processes that are necessarily conserved in performing reactive saccading concurrently with finger tapping.

Overall, the research model used in Chapter 4 provided a selective dissociation of the overlapping demands that eye and hand responses placed on their shared and isolated control networks. Contrasting any apparent differences in the patterns of oculo-manual coupling in either experiment thus reflected the contributions of either motor planning or execution-related processes to the coordination dynamic.

Chapter 5 The research model used in this chapter was an extension of that developed in Chapter 4. Accordingly, the design of the Chapter 5 research study was partially contingent on the results of the previous study. In brief review of the Chapter 4 results, a successful dissociation was made in separating the contributions of motor planning and execution-dependent mechanisms to eye-hand coupling. In general, saccades were made in either the left or right horizontal direction, often causing a spatially congruent deviation in the fingertip trajectory.

In the case of coupling effects that operated with a dependence on motor planning, the interference effect produced in the fingertip trajectory presented in unimanual responses with either the left or the right hand. However, the pattern of eye-hand coupling observed consequent to reactive saccading indicated that execution-dependent coupling mechanisms operated with a compatibility effect between the saccade direction and the responding hand. Rightward reactive saccades caused only a rightward deviation in right hand responses, and leftward reactive saccades caused a leftward deviation in the left hand. The results from Chapter 4 provided a preliminary demonstration of novel forms of eye-hand coordination not previously revealed in other literature. Chapter 5 included a follow up experiment that applied a range of incremental variations to this task for testing a number of predictions.

A preliminary extension was aimed at resolving whether the observed motor planning-dependent eye-hand interference was a function of the encoded motor response, or instead related to the tightly coupled process of shifting one's attention between target locations. Shifts in the spatial allocation of attention are known to reflect the operations of a tightly correlated set of brain regions that overlap with functions of oculomotor encoding (Juan et al., 2008; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Smith & Schenk, 2012).

Hypotheses - 1 If the eye-hand coupling effects observed previously were not exclusively a function of saccadic motor coding and were partially or fully dependent on shifting the spatial allocation of one's attention, the first hypothesis stated that covert and overt modes of visual tracking would induce similar interference in the fingertip trajectory.

Additionally, this experiment tested a putative explanation for the compatibility effect that was observed in the presentation of interference from horizontal reactive saccades relative to the responding hand. One theory contended that execution-dependent coupling between the eyes and hands was a result of information sharing within only one hemisphere. This explanation was consistent with the predominant contralateral control of the upper limbs (Kaas, 2012) and contraversive control of horizontal saccades (Schlag et al., 1998).

Hypotheses - 2 If the compatibility effect between reactive horizontal saccades and finger tapping was explained by the respective division of their representations in either hemisphere, the second hypothesis in experiment two predicted that vertical reactive saccades should interfere with responses from either limb as a function of their specification requiring the collaborative interaction of both hemispheres.

A final extension of this task was conducted to query whether the motor planning-dependent interference that we observed might otherwise integrate its effects in manner that scales with the magnitude of the encoded metrics of the fingertip movement that becomes corrupted. The interference from horizontal saccading was shown to manifest in the horizontal axis of the finger tapping trajectory, which was not the primary axis of tapping motion. It stood to reason that the relatively small magnitude deviations in fingertip position from saccadic interference was a function of integrating the spatial bias relative to the magnitude of the encoded hand action, of which the representation of horizontal fingertip trajectory was minimal.

Hypotheses - 3 If the motor planning-dependent interference in fingertip position from predictive saccades was implemented by means of biasing the metrics of finger tapping trajectory as it was specified in motor planning, we hypothesized that the influence of predictive saccades that are instead directed in parallel, not perpendicular to the primary axis of fingertip trajectory might induce a larger scale interference effect as a function of biasing metrics that are encoded for a larger scale action. This predicted a modulation of peak velocity in the fingertip during its acceleration toward the tapping surface that would become faster when concurrent saccades are executed in the same direction, and slower when saccades are directed in an opposite anti-parallel direction.

1.2.4 Summary

The human oculomotor system is remarkably flexible in its ability to produce a range of behaviours. Different forms of saccadic tracking are engaged in response to task-specific demands. Importantly, different modes of saccadic responses are differentially served by a variety of sensorimotor processes, a relationship that is well documented by a number of neuroimaging studies. To take advantage of the dissociation of various sensorimotor functions for various modes of saccadic tracking, the studies herein used a range of manipulations to the stimulus presentation protocols for examining how the task-specific encoding of saccades related to oculomotor and manual instances of trajectory formation. In either the case of examining saccadic trajectory in isolation for inferring the operation of online corrections (Chapters 2 and 3), or fingertip trajectory for inferring mechanisms of spatial interference sourced in concurrent saccadic responses (Chapters 4 and 5), the utility of observing these performance variables in a variety of visual tracking paradigms was derived from its implications for dissociating the roles of a number of sensorimotor processes as they each contributed to the emerging movement trajectories.

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Chapter 2

The time course of online trajectory corrections in memory-guided saccades

2.1 Citation & Author Contributions

Under the guidance of the senior authors JL and RB, the main author of this article and thesis, BR was the lead investigator involved directly in all steps from the initial project formulation to the final dissemination. The second co-author RA assisted with data collection as a junior lab member in completion of undergraduate thesis requirements.

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RESEARCH ARTICLE

The time course of online trajectory corrections in memory-guided saccades

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Abstract Recent investigations have revealed the kinematics of horizontal saccades are less variable near the end of the trajectory than during the course of execution. Converging evidence indicates that oculomotor networks use online sensorimotor feedback to correct for initial trajectory errors. It is also known that oculomotor networks express saccadic corrections with decreased efficiency when responses are made toward memorized locations. The present research investigated whether repetitive motor timekeeping influences online feedback-based corrections in predictive saccades. Predictive saccades are a subclass of memory-guided saccades and are observed when one makes series of timed saccades. We hypothesized that cueing predictive saccades in a sequence would facilitate the expression of trajectory corrections. Seven participants produced a number of single unpaced, visually guided saccades, and also sequences of timed predictive saccades. Kinematic and trajectory variability were used to measure the expression of online saccadic corrections at a number of time indices in saccade trajectories. In particular, we estimated the minimum time required to implement feedback-based corrections, which was consistently 37 ms. Our observations demonstrate that motor commands in predictive memory-guided saccades can be parameterized by spatial working memory and retain the accuracy of online trajectory corrections typically associated with visually guided behavior. In contrast, untimed memory-guided saccades exhibited diminished kinematic evidence for online corrections. We conclude that motor timekeeping and sequencing contributed to efficient saccadic corrections. These results contribute to an evolving view of the interactions between motor planning and spatial working memory, as they relate to oculomotor control.

Keywords Saccades · Feedback · Oculomotor control · Motor timing · Spatial working memory

Introduction

Saccadic movements of the eyes are among the fastest and most frequently occurring movements executed by humans. Satisfying both the speed and accuracy demands of oculomotor control is often quite difficult. As a result, the precision of saccades is imperfect, and few neural mechanisms exist to correct for spatial errors. To correct gaze position immediately following an inaccurate saccade, secondary corrective saccades toward the proper target location are made frequently (Prablanc et al. 1978). If a discrepancy between the target and gaze recurs consistently, future saccade plans are updated via gain adaptation (Noto and Robinson 2001). Recent work that investigated saccades on a finer timescale of error correction showed that the oculomotor system corrects for impending visual errors while the saccade is still being executed (Gaveau et al. 2003; West et al. 2009; Heath et al. 2010, 2011). These *online* changes to saccade trajectory resolve accruing spatial errors before

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movement termination. In the current experiment, we investigated the influence of motor timekeeping on the kinematics of online saccade corrections.

Saccadic eye movements are in a class of goal-directed actions that are directed toward a spatial goal. Often, goal-directed actions exhibit qualities that are invariant across effectors. For example, the relative kinematics observed in both manual aiming and saccading are remarkably similar. One methodology used for investigating the spatiotemporal dynamics of online corrective process in goal-directed actions involves a comparison of trajectory kinematics. It is commonly observed that spatial errors do not completely accumulate from movement onset to termination in rapid manual aiming (Khan et al. 2002) and saccading movements (West et al. 2009). When comparing repeated execution movements that have similar amplitudes, there is a large variability in effector position during early phases of the movement that is corrected for prior to arriving at the target. This leads to a characteristic and significant decrease in variability from mid-trajectory to the end. Online saccadic corrections are interesting phenomena since they occur at a fast rate, as early as 30 ms after the initiation of the saccade (West et al. 2009). Small amplitude saccades are completed in less time, so corrections are only observed in longer duration saccades.

Online saccadic corrections are expressed optimally when the movements are guided by a visible target. Memory-guided saccades are controlled differently since they are directed to a location where a target has previously been seen and is not visible when saccades are executed. When executing memory-guided saccades, the saccade motor command metrics are generated based on a target representation stored in spatial working memory (SWM). In the specific case of single memory-guided saccades, online corrections are implemented with decreased efficiency relative to visually guided saccades (West et al. 2009). This task involved showing a visual target only briefly, and saccades to the remembered location were made after a short delay.

Predictive saccades could also be considered as a class of memory-guided saccades when there is no visible target when they are initiated. Such predictive behavior is commonly observed in motor timekeeping tasks. For example, saccades arrive at target locations prior to the onset of target visibility when the movements are sequenced to periodic time intervals. Thus, predictive saccades provide a novel context in which to investigate online trajectory corrections. In the present study, we aimed to observe the expression of online corrections in predictive saccades. We hypothesized the expression of online corrections would be modulated by imposing a periodic motor timekeeping goal on sequences of saccades. One reason to predict that timekeeping will influence saccadic trajectories is that some models of timekeeping define an elementary overlap with short-term memory resources (Staddon 2005). This is relevant to predictive saccades because their motor commands are parameterized by metrics stored in spatial working memory. Furthermore, it has also been demonstrated that repeated execution of a motor action contributes to potentiation of spatial working memory (Awh and Jonides 2001). It is possible that the aspect of sequencing in itself promotes ideas of greater cortical recruitment for anticipatory planning, which can even be done in parallel for consecutive goals (Heide et al. 2001; Baldauf et al. 2008). Consequently, with many possibilities for overlapping function, we reasoned that sequenced and periodic execution might facilitate online trajectory corrections in saccades.

Materials and methods

Seven undergraduate students (two men, five women, *M* age = 20.86 years, SD = 0.69, range 19–22 years) were recruited from the McMaster University student population. All participants gave informed consent to participate in the experiment and were naïve to the purposes of the study. All participants had 20/20 vision either naturally or corrected. The following experimental protocol was approved by the Research Ethics Board of McMaster University.

Apparatus

The data acquisition apparatus used in this study was the EyeLink II (SR Research, Osgoode, Ontario) eye-tracking system. We used this head-mounted system to sample gaze angle at a rate of 250 Hz. This system recorded gaze data with a dedicated host PC running proprietary DOS-based software. Experimental stimuli were presented using the Experiment Builder (SR Research) software on a display screen (CRT monitor, 640 × 480@125 Hz resolution) attached to a Windows XP (TM)-based PC. Saccading targets were presented on the computer screen as white circles, which subtended approximately 0.4° of visual angle (∼5 mm). In order to cue saccades to predetermined amplitudes, participants sat with their heads located 65 cm from the display screen. The distance between saccade targets and the position of gaze direction was measured in degrees of visual angle.

Procedure

Participants made horizontal saccades to locations on the display screen, which were cued by visual targets in either a "control" condition or a "timed" condition. Saccades were executed to target amplitudes of 4°, 8°, 12°, 16°, and 20° of visual angle. To show the sequence of conditions visually, the following procedures are also illustrated in Fig. 1.

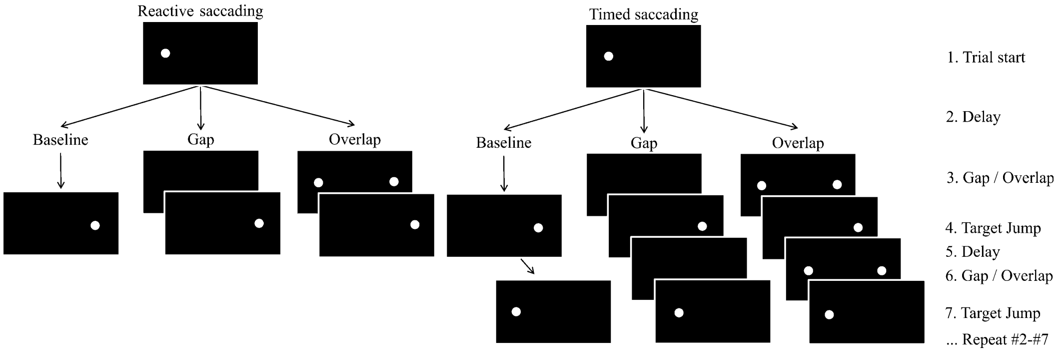

Fig. 1 Illustration of the procedure used in our experiment. Timed saccading cueing protocol is pictured on the *right*, and reactive saccading cues are presented in the control condition and pictured on the *left*. In the *baseline* condition, target jumps had no temporal gap or overlap and toggled visibility synchronously. Consequently, steps 3 and 6 do not apply to *baseline* trials. In reactive saccading trials, the delay at step 2 was randomly set between 750 and 1,500 ms. After step 4, the reactive trials are terminated. In timed trials, delay in step 2 and 5 is represented by the duration of the inter-stimulus interval (ISI), at 500, 750, 1,000, and 1,500 ms. In these trials, targets were switched back and forth for 26 jumps total, then the trials were terminated

In the control condition, participants made reactive saccades in response to the onset of a visual target. Our control procedure was performed exactly using the specifications of the visually guided reactive saccading conditions used in previous research (see experiment 1; West et al. 2009). At the beginning of a trial, participants maintained fixation looking at a static target on the display screen. When the eye tracker detected a steady fixation for one second, a pseudorandom delay between 750 and 1,500 ms was imposed prior to the onset of the saccade target. This target would appear at one of the aforementioned amplitudes, either to the left or to the right of the fixation target. When participants saw the target appear, they quickly executed a saccade toward the target location and the trial was terminated shortly thereafter. Fifteen saccades were collected in both rightward and leftward directions, and data were collapsed for this factor in analysis.

In the timed saccading condition, targets were either visible on the left or on the right side of the screen. Pacing for saccades was cued by alternating the visibility of left and right visual targets at regular time intervals. Since saccades were made reciprocally in both directions, we referred to the fixation target as the location where gaze was fixated before a saccade, and the saccade target as the location to where each saccade is directed. In other words, during a sequence of movements, the saccade target of one saccade is effectively the fixation target for the next. Saccade cues were presented at 4 pacing rates (inter-stimulus intervals—ISI), 500, 750, 1,000, or 1,500 ms. These particular time intervals were chosen because they are associated with entraining periodic saccades to a rhythm such that initiation is accomplished by predictive timekeeping and not by visually guided reactive behavior (Joiner and Shelhamer 2006). We have used these techniques previously and replicated predictive responses using similar cueing methods (Richardson and Balasubramaniam 2010). In the case of timed saccading alone, our analyses refer to *ISI* as the 4-level analysis factor within timed saccading trials. Our analyses instead use *pacing condition* when referring to the comparison of control condition reactive saccades against timed saccades. Each timed trial consisted of cueing 26 consecutive saccades in alternating directions, and data were collapsed across rightward and leftward directions.

We also manipulated target visibility using the gap paradigm (gap task) for both timed and reactive saccading tasks. Gaps in target visibility were used for manipulating the excitability of the oculomotor system in the time window immediately preceding saccade onset. When the eyes are not in motion, they are in fixation, and omnipause neurons are responsible for inhibiting activity in saccade-related burst neurons (Sparks 2002). Changing the visibility of a fixation target thus modulates the level of inhibition on saccade-related oculomotor output. The gap task manipulation had three conditions: in the baseline condition, the fixation target toggled synchronously with the saccade target. In other words, as the fixation target extinguished the saccade target appeared at the same instant. Here, the oculomotor system must increase activity in saccade-related burst neurons in parallel with decreasing the activity in omnipause neurons. In the gap condition, however, occlusion of the fixation target preceded the onset of the next saccade target by 200 ms. Similar gap conditions have been used in many experiments to demonstrate that active fixations are more quickly disengaged prior to onset of the saccade target, which leads to faster saccade latencies (Saslow 1967). In the overlap condition, the fixation target continued to be visible until 200 ms after the onset of the saccade target. Imposing this overlap in visibility directly opposes the intention of imposing a gap. An overlap is associated with longer response latencies, which are consequent to extending the duration of inhibition on the saccade-related neurons. Previous research failed to demonstrate an influence of the gap effect on the trajectories of visually guided saccades (West et al. 2009). However, we included the gap, overlap, and baseline conditions to assess whether this manipulation influences oculomotor performance differently when saccades are initiated by means of internal sensorimotor timekeeping. Overall, the timed saccading trials consisted of 4 ISI × 3 Gap Task × 5 Target Amplitude factorial designs. Control saccading did not include the pacing rate factor, and data were acquired for a 3 Gap Task × 5 Target Amplitude factorial model.

Data analysis

Data processing was carried out with in-house developed scripts written for MATLAB (Mathworks, Natick, MA). Gaze position, velocity, and acceleration time series were extracted for each trial. To better identify the gaze position at a finite time scale, MATLAB's *resample* function was used to upsample gaze data by a factor of four, which equated one sample to one millisecond. Similar interpolations have been used with the same intention in other research (van Beers 2007). Saccades were identified using velocity and acceleration thresholds. The onset of saccades was determined as the first sample to exceed both 30º/s and 8,000º/s^2. The termination of saccades was then marked by the first sample where velocity was less than 30º/s. Saccades were excluded based on one heuristic. When the saccade amplitude was greater than 2.75º visual angle error away from the cued amplitude, that saccade was excluded. This criterion is approximately the mean plus three standard deviations of the expected variability in saccade amplitudes as reported from saccades in previous research (West et al. 2009). The rate of exclusion was approximately 1 in 6 saccades and was consistent between both timed and control conditions. By definition, our inclusion criteria effectively constrain the analysis to accurate saccades. Since the intention of this experiment is to attribute the mid-saccade trajectory variability to corrective processes, we can only infer that variability is potentially representative of corrections if the saccade is accurate.

Each remaining saccade was examined using a kinematic analysis. Gaze position was extracted at five relative indices of movement completion: 20, 40, 60, 80% movement time (MT), and the endpoint. At these time markers, we computed the distance gaze had travelled from the location where the saccade was initiated. This was done for each saccade for ultimately comparing trajectory variability at all MT indices. For the variability analysis, kinematic data from the saccades in each trial condition were pooled for calculating the standard deviations of gaze distance traveled at each kinematic marker. Next, a regression analysis involved computing the proportion of explained endpoint variance as the square of the Pearson product-moment determined the strength of correlation between the gaze positions at all MT index and the eventual saccade endpoint. This process yielded the R^2 coefficient of determination, which describes how well mid-trajectory gaze predicts the locations where the saccades are terminated. High R^2 at early (i.e., 20, 40% MT) saccading indicates that the trajectory is largely ballistic thereafter. This implies that from that those time indices onward in time, the saccade proceeds deterministically to termination with no kinematic evidence of intervening processes. To the contrary, low R^2 are interpreted as evidence that saccadic corrections may be amending gaze trajectory. When values of R^2 are low at early MT, this implies the determinism of the trajectory is hampered because corrective processes affect the kinematics emerging at later phases of the movement. These R^2 data were also organized according to the time at which they occurred prior to saccade termination. In this format, an iterative outlier was used to estimate the minimum delay required to implement feedback-based corrections. The exact procedure will be described in the discussion.

Results

Descriptive statistics presented in Table 1 confirmed that participants performed the saccading tasks within the expected metrics. In the present data, there were no statistically significant effects or interactions when comparing saccade amplitude in all reactive and timed pacing conditions, and as a function of the gap task. A significant main effect of pacing condition ($F_{(4,\,24)} = 5.67$, $P < 0.05$) was observed on movement duration, while there were no significant pairwise comparisons after applying Bonferroni corrections. These tests confirmed that saccadic accuracy and basic performance metrics were similar across all the experimental conditions. The remaining analyses focused on two main determinants of performance: temporal and spatial. To confirm that participants were successfully tracking the stimuli with predictive saccades, we measured the millisecond latency (i.e., asynchrony) between the initiation of saccades and the timing of onset of target visibility. Next, spatial analyses examined the kinematics of saccade trajectory to demonstrate evidence of online feedback-based corrections.

Saccading latency

Saccade latency indicated whether responses were initiated in anticipation of target onset, or instead as externally cued reactions toward the visual target. The absolute minimum latency for exogenously cued reactive saccade is approximately 80 ms. Thus, one can infer that responses executed

Table 1 Descriptive statistics of basic saccade metrics

Pacing interval	4°		8°		12°		16°		20°	
	M	SD	M	SD	M	SD	M	SD	M	SD
Amplitude										
500 ms	3.39	0.19	7.18	0.28	11.35	0.46	15.10	0.43	19.37	0.53
750 ms	3.49	0.28	7.37	0.24	11.41	0.36	15.32	0.49	19.26	0.52
1,000 ms	3.48	0.24	7.28	0.25	11.31	0.49	15.38	0.48	19.37	0.38
1,500 ms	3.34	0.21	7.11	0.32	11.17	0.41	15.13	0.55	19.32	0.60
Reactive	3.46	0.27	7.23	0.19	11.14	0.14	15.04	0.26	19.01	0.20
Movement time										
500 ms	27.67	2.04	42.73	4.84	53.64	6.21	61.15	7.37	68.68	8.22
750 ms	27.96	2.14	44.33	5.78	53.33	5.49	65.23	11.16	73.72	13.67
1,000 ms	28.25	2.97	44.60	6.97	55.49	7.25	65.61	13.18	74.30	16.10
1,500 ms	28.14	2.69	42.75	3.82	55.15	7.11	64.35	9.37	74.36	11.63
Reactive	25.42	1.65	39.22	4.73	48.76	4.58	56.10	5.54	62.84	4.90

with a shorter latency are made in anticipation of a stimulus through a voluntary motor plan. It is important to demonstrate predictive behavior in the current task because it implies that responses were guided to the target location by metrics stored in spatial working memory. A 5 Pacing condition (4 ISI + reactive saccades) × 3 Gap Task × 5 Saccade Amplitude repeated measures ANOVA was used to investigate trends in the latency data. Figure 2 shows the mean latency at all pacing conditions and saccade amplitudes. The main effects of pacing condition ($F_{(4,\ 24)} = 111.28$, $P < 0.001$) are quite clear, in that reactive saccades are well above the reference line for the fastest sensory reactions. This plot also confirms that saccade latency is representative of predictive tracking in all ISI levels of timed saccading.

There was also a significant main effect of saccade amplitude ($F_{(4, 24)} = 8.97$, $P < 0.001$) where saccade latency decreased at longer amplitudes. However, with Bonferroni corrections, there were only significant differences when comparing 4° saccades ($M = -0.84$, 30.53) against 12° ($M = -26.57$, $SD = 27.78$, $P < 0.005$) and 20° ($M = -32.86$, $SD = 34.20$, $P < 0.05$). While this effect demonstrates a modulation of saccade latency with the movement amplitude, we maintain that reactive saccades in the control condition were initiated in response to external sensory cueing, and saccades in the timed condition were predominantly initiated by means of sensorimotor prediction.

It is also expected that saccading latencies would vary according to the gap/overlap task. We confirmed a significant effect of gap task condition ($F_{(2,\ 12)} = 36.59$, $P < 0.001$). This effect is consequent to a facilitation of saccade onset latency during gap trials. Post hoc comparisons show that latency during gap trials ($M = -84.90$, $SD = 27.79$ is less than Baseline ($M = 13.21$, $SD = 29.54$, $P < 0.001$) and Overlap ($M = 7.92$, $SD = 46.38$, $P < 0.005$).

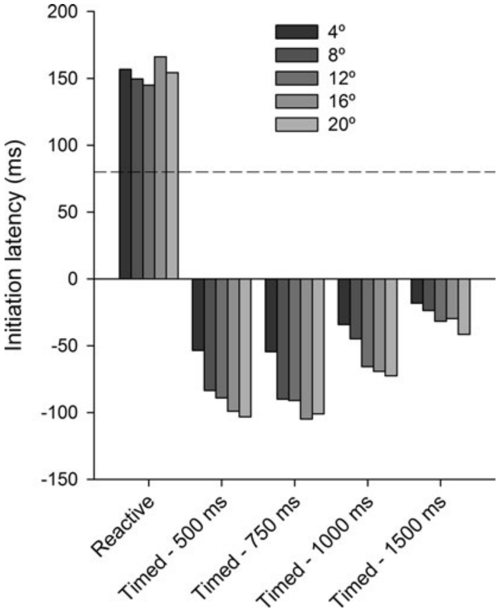

Fig. 2 Millisecond (ms) saccade latency as a function of all pacing conditions and saccade amplitude. Shortest possible latency for visually guided saccades is approximately 80 ms and is marked with a reference line. This plot confirms the predictive nature of saccades at all 4 ISI pacing rates

Since saccadic motor commands are actively inhibited during ocular fixation, the above effect of gap task indicates this inhibitory drive was reduced when the fixation target disappeared 200 ms prior to the onset of the saccading target. Here, we confirmed a perceptually mediated change in excitability of the saccadic oculomotor networks. Since predictive and reactive saccades are initiated by different means, we might also expect to see differences in the way saccade kinematics are modulated by perisaccadic oculomotor excitability.

Lastly, saccade latency also interacted as a function of pacing condition and gap task ($F_{(8,48)} = 4.03$, $P < 0.05$). However, no consistent trends allude to conceptually important differences. In the context of our current investigation, it is solely important that we confirmed responses were predictive in all instances of timed saccades and reactive in all instances of control saccades. From this section of the analyses, we validate our intended classification of timed saccades as a predictive subclass of memory-guided saccades. This classification labels them as definitively different from reactive saccades made in the control saccading task.

Saccade trajectory variability

Next, we examined the data for evidence of online error corrections in the kinematics of saccade trajectories. To do this, gaze position at early and late phases of each saccade was examined in a variability analysis. Our experimental design comprised of one untimed control condition and 4 levels of timed conditions. Preliminary analysis of the control data aimed to replicate evidence for online corrections in reactive saccading trials. Subsequently, the same trends were demonstrated in the timed saccading data. Here, we were also concerned whether ISI pacing rates influenced the expression of online corrections. Lastly, we compare the expression of online corrections between reactive and timed saccades.

To corroborate our observations of trajectory kinematics in reactive saccades with those reported in related literature (West et al. 2009; Heath et al. 2010, 2011), we performed a 3 Gap Task × 5 Saccade Amplitude × 5 Percent MT repeated measures ANOVA on kinematic variability. Figure 3a is a plot of the significant interaction between saccade amplitude and percent MT ($F_{(16,\ 96)} = 11.13$, $P < 0.001$). Both factors also have significant main effects: saccade amplitude ($F_{(4,\ 24)} = 33.56$, $P < 0.001$) and percent MT ($F_{(4,\ 24)} = 25.50$, $P < 0.001$). This interaction successfully replicates a common observation that instantaneous trajectory variability increases continually from initiation to termination in saccades of short amplitude (4°). However, in longer amplitude saccades (12°–20°), the variability is maximal around 60% MT and significantly decreases as the saccades near termination. From this, we infer that some sensorimotor process operates in longer saccades—but not in shorter saccades—to resolve initial trajectory variability so that saccades end at a consistent target location.

The R^2 coefficient of determination measured from these reactive saccades also corroborates observations in the aforementioned studies. Values of R^2 approaching 1 indicate a high correlation between the gaze position at MT indexes and the saccade endpoints. These high values indicate a trajectory is ballistic, and values approaching zero are interpreted as evidence that sensorimotor processes intervene and alter the course of the movement. Main effects of the saccade amplitude ($F_{(4,\ 24)} = 14.59$, $P < 0.001$), percent MT ($F_{(3,\ 18)} = 326.81$, $P < 0.001$), and an interaction between these factors ($F_{(12,72)} = 10.42$, $P < 0.001$) all reached significance. Figure 4a is the interaction plot of these factors, which illustrates that small amplitude saccades are increasingly correlated with their movement endpoint beginning very early in their execution. Conversely, longer amplitude saccades do not become highly correlated with their endpoint until the latest phase of their execution, 80% MT. More importantly, the R^2 regression analysis supplements the variability analysis: the trajectory kinematics in longer saccades become deterministic in the same time window when variability in gaze position decreases. While the variability analysis cannot distinguish whether variability arises from different paths of ballistic trajectories, the regression analysis provides an account of the proportion of endpoint variance explained by gaze position earlier in the trajectory. Together, these findings replicate the expected evidence for a sensorimotor process that controls online corrections in reactive saccades.

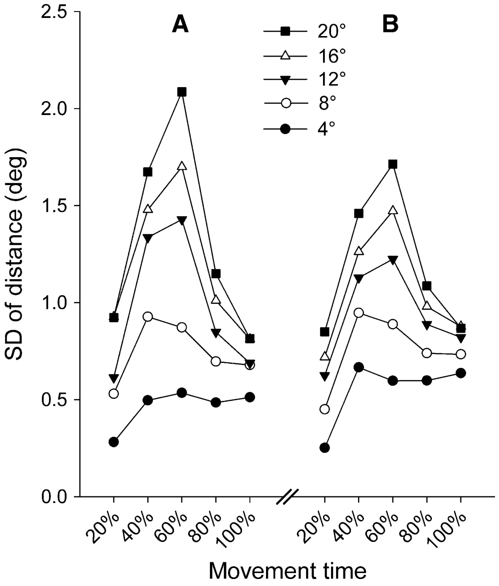

Fig. 3 Interaction plot for the variability of the gaze trajectory at all MT indices for saccades of all amplitudes. Data collected from reactive saccades in the control condition (**a**) and from timed saccade measures averaged across all ISI pacing rates (**b**). This plot demonstrates that shorter saccades generally increase in variability from their onset to termination, whereas larger saccades have a maximal variability measured at 60% MT that decreases significantly by the movement endpoint

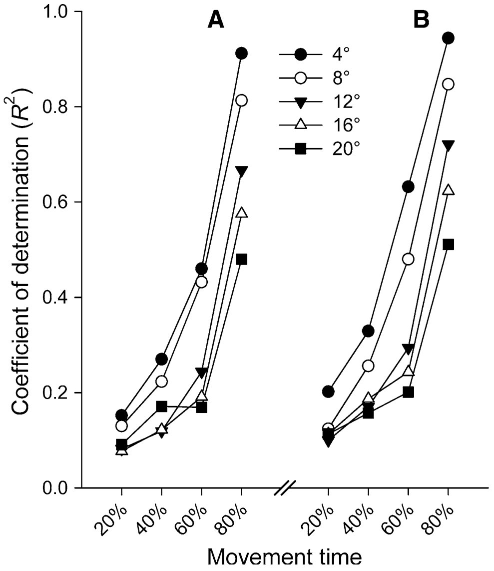

Fig. 4 Interaction plot for the coefficient of determination R^2 at all MT index for saccades of all amplitudes. Data from reactive saccading in the control condition are shown on the *left* (**a**) and from timed trials that were averaged across all ISI pacing rates on the *right* (**b**). R^2 is a measure of how well the position of the trajectory predicts the final endpoint. Higher R^2 is associated with an open-loop ballistic trajectory. This *plot* shows that small amplitude saccades raise quick from their onset to having large R^2, which suggests the trajectory is mostly ballistic. Conversely, larger saccades do not increase to similar levels of predictability until later 80% MT. This reflects the intervention of online saccadic corrections mid-trajectory

Timed saccading

Within the timed saccading tasks, the same measures were analyzed with a 4 ISI × 3 Gap Task × 5 Saccade Amplitude × 5 Percent MT repeated measures ANOVA. First, we consider timed saccades at all ISI pacing rates as representing a homogenous sample of predictive saccading behavior. In this case, when collapsed across the ISI factor because neither kinematic variability nor R^2 regression measures showed significance in main effects of or interactions involving the ISI pacing. Figure 3b illustrates data from all instances of timed saccading where the interactions between saccade amplitude and percent MT for kinematic variability ($F_{(16,\ 96)} = 5.04$, $P < 0.001$) reached significance. This interaction, main effects of saccade amplitude ($F_{(4,\ 24)} = 24.78$, $P < 0.001$), and percent MT ($F_{(4,\ 24)} = 17.49$, $P < 0.001$) replicate trends in trajectory variability that were observed during reactive saccading. These results reproduce the kinematics observed in reactive saccades, where only the kinematics in longer saccades decrease in variability from midway through their execution to the endpoint. Additionally, Fig. 4b shows that trajectories in timed saccading also express evidence from R^2 regression analyses indicating that shorter saccades are highly ballistic and longer saccades are not. This is supported by main effects of saccade amplitude ($F_{(4,\ 24)} = 56.49$, $P < 0.001$), percent MT ($F_{(3,\ 18)} = 339.41$, $P < 0.001$), and an interaction between these factors ($F_{(12,\ 72)} = 20.97$, $P < 0.001$) all reached significance.

A result unique to the R^2 regression analysis in timed saccades is the significant main effect of gap task ($F_{(2,12)} = 5.88$, $P < 0.05$). This effect occurs such that mean R^2 in the baseline condition (synchronous target onset/offset) appeared to be lower than R^2 in overlap and gap conditions. However, applying Bonferroni corrections in post hoc pairwise comparison nullified this effect. Furthermore, the gap task conditions also interacted significantly with percent MT ($F_{(6,36)} = 3.36$, $P < 0.05$). Post hoc comparisons revealed that saccades made in the baseline condition had significantly lower R^2 than gap and overlap conditions only at the 40 and 60% MT markers (both $P < 0.05$). Here, we briefly revisit the topic that our investigations into saccade latency revealed that saccades in the gap condition had short latencies. This represents a more highly excitable state in the oculomotor system as compared with longer latency behaviors in baseline and overlap trials. We also hypothesized that changes in basic oculomotor excitability might interact with predictive saccading behavior in timed trials differently than in reactive saccading behavior observed in untimed control trials. Since gap and overlap task performance were equivocal in R^2 regression analyses, while baseline and overlap were equivocal in latency measures, we argue the mechanisms behind a modulation of saccade latency, and R^2 regression measures seem unrelated.

Untimed reactive saccading versus timed predictive saccading

Next, we collapse the timed data across all levels of ISI pacing rates and compare the reactive and timed saccading data to see if the kinematic evidence for online corrections is expressed differently. These data were tested in a 2 Pacing condition (reactive/timed) × 3 Gap Task × 5 Saccade Amplitude design. In reflection of the trends observed in both timed and reactive saccading data subsets, kinematic variability analyses revealed significant main effects for saccade amplitude ($F_{(4,\ 24)} = 37.22$, $P < 0.001$), percent MT ($F_{(2,\ 24)} = 22.51$, $P < 0.005$), and an interaction between these factors ($F_{(4,\ 24)} = 10.62$, $P < 0.005$).

Now that this interaction has been reported consistently in all instances of saccading, here we report post hoc tests. Interpreting this interaction is simplified when discussing it in terms of progression of a saccade from beginning to completion. To correct for multiple comparisons, we are making only 4 comparisons per level of saccade amplitude: 20–40%, 40–60%, 60–80%, and 80% to the endpoint. At a corrected significance of $P < 0.013$, short 4° and 8° saccades increase consistently and significantly from 20% MT to their endpoint. All longer saccades between 12° and 20° increased in variability consistently and significantly only from 20% MT to 60% MT. These longer saccades also significantly decreased in kinematic variability from 60% MT to 80% MT and to the saccade endpoint.

A significant interaction between gap task and percent MT ($F_{(8,\ 48)} = 4.24$, $P < 0.018$) was also observed in the kinematic variability. Post hoc test significant at $P < 0.0167$ applies here, and the results indicate that kinematic variability measured at the saccade endpoint is significantly higher in gap trials ($M = 0.81$, $\mathrm{SD} = 0.09$) than overlap ($M = 0.70$, $\mathrm{SD} = 0.09$) and baseline ($M = 0.72$, $\mathrm{SD} = 0.06$) trials. However, this is of little importance since the interaction between saccade amplitude and percent MT suggests that saccades in all instances of the gap task demonstrate evidence for online saccadic corrections.

Lastly, we observed a significant interaction between the 2 pacing conditions and the 5 percent MT indices ($F_{(4,24)} = 9.17$, $P < 0.001$). With only 1 pairwise comparison being made at each level of the percent MT factor, significance was maintained at the initial uncorrected $P < 0.05$. Post hoc tests reached significance at 60% MT where reactive saccades ($M = 1.32$, $\mathrm{SD} = 0.34$) were significantly more variable than were timed saccades ($M = 1.18$, $\mathrm{SD} = 0.36$). Interestingly, at the saccade endpoint, reactive saccades ($M = 0.70$, $\mathrm{SD} = 0.06$) were significantly less variable then timed saccades ($M = 0.79$, $\mathrm{SD} = 0.10$). Reactive saccades thus demonstrate a larger reduction in variability prior to saccade termination. However, the latent interaction between saccade amplitude and percent MT is the source of evidence for online saccadic corrections. The 3-way interaction between pacing condition, saccade amplitude, and percent MT factors narrowly missed significance when adjusting for sphericity with Greenhouse-Geisser corrections ($F_{(16,96)} = 2.09$, $P = 0.133$). Consequently, the failure of reaching significance in the 3-way interaction with pacing condition warrants caution when inferring whether the trends in the kinematic variability are different in reactive and timed saccades. The R^2 regression analyses were also examined for an effect of pacing condition. Saccade amplitude ($F_{(4,\ 24)} = 55.51$, $P < 0.001$), percent MT ($F_{(3,18)} = 437.98$, $P < 0.001$), and their 2-way interaction ($F_{(12,\ 72)} = 25.61$, $P < 0.001$) were all significant. This has been consistent in all instances of saccading, and here, we report post hoc comparisons. Mean R^2 data suggest that small saccades have a predictable trajectory (high R^2) from very early in the movement through to the end. At values above $R^2 = 0.3$, saccades are increasingly ballistic and 4° saccades surpass the R^2 value of 0.3 as early as 40% MT ($M = 0.30$). Contrasting this, 8° saccades pass the R^2 value of 0.3 at 50% MT ($M = 0.46$), and 12° ($M = 0.69$), 16° ($M = 0.60$), and 20° ($M = 0.50$) saccades do not pass the said value until 80%. These data suggest the mid-trajectory variability in longer saccades is not a result of passive dynamics in variable ballistic saccades. This is inferred when considering that mid-trajectory variability is reduced prior to movement completion and also that R^2 values in the early phase of saccading are significantly lower as compared with R^2 nearing the movement endpoint.

We also observed significant differences in timed versus reactive saccading ($F_{(1,\ 6)} = 6.82$, $P < 0.05$). However, we interpret this with caution because of the very small changes in between the two marginal means. Reactive saccading trajectories ($M = 0.32$, $\mathrm{SD} = 0.04$) had significantly lower R^2 than in timed saccading ($M = 0.36$, $\mathrm{SD} = 0.05$). The observed power for this effect is only 59% at $\alpha = 0.05$. The mean difference of 0.04 is also quite small, especially compared with the experimental effects observed elsewhere (e.g., $\sim M_{\mathrm{diff}} = 0.2$, see Heath et al. 2010). Another consideration is that R^2 is often equated between two conditions at very early and late percent MT indexes but is significantly different only at the middle 40–60% MT indices. Thus, truly robust effects between the timed and reactive saccading conditions would have been expected to express themselves with more power through an interaction with percent MT. Our data did not reach significance for this interaction ($F_{(3,\ 18)} = 1.95$, $P = 0.19$).

The distribution of R^2 values as a function of their time from saccade termination was also examined. This approach has been used in previous literature to estimate the minimum delay for implementing online corrections (West et al. 2009). The R^2 values are presented without distinction from what amplitude condition they were collected, only when they were measured relative to the saccade's end. Figure 5 plots these data for a few experimental conditions. The idea behind this analysis was to identify the time furthest preceding saccade termination at which R^2 could be measured and represent substantial predictability. Figure 5 illustrates the increasing R^2 as the measures near saccade termination. Here, an iterative outlier procedure compared each data point against the mean plus 2 standard deviations ($M + 2 \times \mathrm{SD}$) of all previous points to determine the time at which saccades become increasingly correlated with their endpoint. This procedure was run separately for all gap task conditions in timed trials, in the control reactive saccades, and also separately for 1,500 ms ISI timed saccades. The distinction of the gap task was preserved in timed saccading data because of the aforementioned significant interaction between gap task and percent MT for R^2 in timed saccading. Furthermore, we chose to isolate data from 1,500-ms ISI trials, because they had the longest memory delay period between successive movements. This

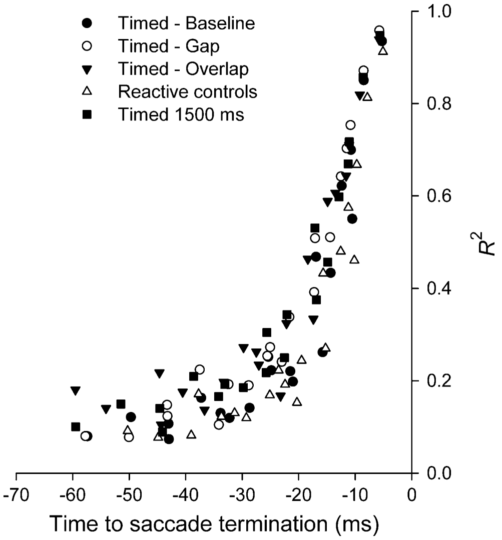

Fig. 5 Proportion of explained endpoint variance R^2 plotted as a function of the time before saccade termination. The iterated outlier procedure operates on this dataset and measures the point at which R^2 values first increase significantly as saccades approached their termination. Descriptive table of data that accompanies this plot is in Table 2

planned contrast was made to maintain consistency with previous research that has shown memory delays of this duration hinder the implementation of online saccadic corrections in single memory-guided saccades. Data for all conditions shown in Fig. 5 are provided in Table 2.

In comparison with previous delay estimates (West et al. 2009), our control data revealed a 37-ms delay for reactive saccades, ~7 ms slower than in comparison with the aforementioned study. It is not surprising to see an offset when comparing numbers from separate research groups. Our measures differ in two basic ways: our data were initially sampled at a lower rate and resampled to a finer timescale. Moreover, we performed the iterative outlier with more data points by including R^2 measures at 4 levels of percent MT, whereas previous work used only 3. The iterative outlier procedure seems partially responsible in itself, where the feedback estimate in the overlap condition is ~10 ms faster yet there is also a marked increase in the critical and threshold R^2 values. Using a $M + 2 \times \mathrm{SD}$ heuristic seems to be less sensitive for these data. Since it is an absolute value of R^2 that describes the nature of the trajectory as predictable, or not, consistency in the threshold R^2 value in turn determines the consistency of labeling what value of R^2 represents the time at which the trajectory becomes predominantly ballistic. As such, if we instead tested the iterated outlier using a manually imposed threshold of $R^2 = 0.16$ averaged from threshold values in the other timed saccading conditions, the estimate increases to ~33 ms. This value is closer to the estimates in the other saccading conditions. In ideal circumstances, an iterated outlier assumes stationarity in the data prior to the index at which a marked increase in value is to be identified. Since the initial stages of any movement would naturally be expected to have a lasting but small effect on the later phases of the movement, the data are inherently non-stationary. Future investigations could perhaps explore more accurate methods to identify a break point of a piecewise fit in data like these, which inherently show broad variability in short tails of the distribution.

Discussion

This study investigated the combined role of periodic timing and motor sequencing as they related to the implementation of online feedback-based trajectory corrections. We first confirmed that our participants were engaged in predictive visual tracking in the timed saccading conditions. By confirming anticipatory behavior, we concluded that saccades were initiated via internal sensorimotor planning whereby saccade metrics were parameterized by a task representation in spatial working memory. As expected, anticipatory behavior was preserved across all of the ISI, saccade amplitude, and gap task conditions. Importantly, this differed significantly from the large positive latencies observed in all variations in reactive saccading. These observed differences in temporal dynamics call for a separate classification of reactive and predictive saccades as visually guided and memory-guided behavior, respectively.

Subsequent analysis examined spatiotemporal dynamics of saccade kinematics. Kinematic variability in saccade trajectories results from compounded errors in sensory and motor functions (van Beers 2007; Khan et al. 2006). Without processes that make online corrections, such errors would

Table 2 Results from R^2 iterative outlier

	Reactive	Timed			
		Baseline	Gap	Overlap	1,500 ms
Threshold R^2 value	0.10	0.14	0.18	0.24	0.18
Critical R^2 value	0.17	0.16	0.22	0.27	0.21
Estimated implementation delay (ms)	37.71	37.24	37.52	29.75	38.59

accrue throughout the course of execution, leading to maximal movement variability measured at the endpoint (Messier and Kalaska 1999). As expected, we found evidence for online corrections in long amplitude saccades that were similar in reactive and predictive contexts: variability reached a maximum at 60% MT and decreased significantly at the endpoint. This observation replicates similar observations made in single visually guided and memory-guided saccading tasks (West et al. 2009; Heath et al. 2010, 2011). Further support for corrective mechanisms was corroborated with a regression analysis where we tested how accurately gaze position at MT indices predicted the endpoint. For larger amplitude saccades, the correlation between gaze position and endpoint was strong only at later phases of execution. This contrasts shorter saccades, where the coefficient of determination between MT indices and endpoint is high from early phases of saccading through to the endpoint. We observed similar trends in predictive and reactive saccades. This also led to an equivocal estimation of feedback delays in all instances of predictive and reactive saccading. In comparison with other literature, it is most relevant to contrast oculomotor behavior in 1500-ms ISI timed saccading with that in reactive saccading. Our estimate of the minimum delay to implement corrections is ∼37 ms in both cases. Previous research (West et al. 2009; Heath et al. 2010) demonstrated that single memory-guided saccades exhibit slowly implemented (∼50 ms delay) online corrections that also have reduced expression (higher R^2). From our observations, we infer that spatial working memory-related effects that hindered online corrections in single memory-guided saccades are mostly recovered when making predictive saccades in timed sequences.

In designing the methods, we made an explicit attempt to be consistent with other research that investigates spatial working memory. Accordingly, our tasks imposed memory delays between 500 and 1,500 ms, which are within a range commonly used in goal-directed motor tasks. Memory delays in this range provide ample time for spatial working memory to decay in the quality of metrics that are stored (Rolheiser et al. 2006) and also to exhibit a memory-related cortical recruitment (Brignani et al. 2010). In other words, our study provided visual cueing in the time window immediately prior to saccade onset that was similar to what participants would have seen in a typical single memory-guided saccading task. This lends support to the conclusion that timed sequencing is the only novel influence imposed in our task that is acting on the sensorimotor dynamics.

In sum, we concluded there are only negligible differences in the kinematic evidence for online trajectory corrections when saccades are performed reactively to visible targets or in timed sequences in anticipation of target onset. This led us to reason the combined processes of motor timekeeping and sequencing were responsible for maintaining a fast and efficient mode of trajectory corrections. Despite periodic saccades being parameterized by metrics sourced in spatial working memory, online corrections to their trajectories operated as efficiently as was observed in visually guided reactive saccades. It is thus of particular importance that we tested control behavior in reactive saccades and then compared the measures in order to find appropriate evidence for online corrections in timed saccades.

General discussion and Neurophysiological implications

In order to understand the contribution of the present experiments to developing models of sensorimotor brain functions, one first requires a brief review of oculomotor networks and their putative online control systems. Saccadic motor efferents originate subcortically from the superior colliculus (SC) and the pontoreticular formation (PRF) in the brain stem (Sparks 2002). Feedback-based corrections are likely integrated near the source of motor output, in subcortical structures (Kato et al. 2006; Gaveau et al. 2003). The state of the oculomotor system is monitored using a combination of feedback modalities, all of which contribute to the registration of gaze position (Bridgeman and Stark 1991). Proprioception from extraocular muscles (EOM) (Weir et al. 2000), low latency visual afferents from the retina (Gaveau et al. 2003), and corollary discharge sourced from oculomotor control centers (Kato et al. 2006; Guthrie et al. 1983) are all mechanisms potentially contributing to saccade trajectory changes on a fast timescale. The coding of feedback via these pathways might contribute to the construction and integration of forward models of saccadic control, potentially implicating the cerebellum (Wolpert et al. 1998; Quaia et al. 2011). Subcortical oculomotor networks are also known to be tightly coupled with the thalamus and early sensory areas of visual processing, particularly the lateral geniculate nucleus (LGN) (Reppas et al. 2002). So, one or a combination of these networks could lend support to feedback (via sensory integration) or feedforward (via corollary motor discharge) models of closed-loop online control. However, a complete understanding and parsing of modality-respective contributions to trajectory corrections remains elusive.

One might suppose our protocol lends support for corrections based on fast visual feedback networks: it stands to argue that predictive saccades were partially guided by low-latency visual information when targets became visible in the perisaccadic time window. Such an argument would follow a notion that target onset may have occurred during the course of the saccade. According to observations made by Gaveau et al. (2003), changes in target visibility during a saccade was often perceived and resulted in online corrections prior to termination of the saccade. However, data from this study do not support the idea that transient visual feedback is used for trajectory guidance in our tasks. For example, the movement time of 20° saccades is approximately 70 ms. When executed in the 500-ms ISI condition, saccades of this amplitude had a mean latency of approximately -100 ms. Consequently, we ascertain that saccades in this condition were terminated prior to the onset of target visibility. However, 20° saccades in the 1,500-ms ISI condition had a mean latency of approximately -40 ms, and target onset would have occurred while the saccade was in mid-flight. Importantly, we observed a significant main effect of ISI on latency, but no effect of or interaction involving ISI in the kinematic variability and regression analyses of timed saccading. This led us to refute that a transient visibility of visual targets was at least not solely responsible for the online corrections.

An important factor to consider when discussing candidate oculomotor feedback integrators is the speed of neuronal signaling. The rate of afferent propagation from the retina to the central nervous system limits the likelihood that the neocortex integrates online performance feedback for mediating efferent signals. Yet the latent possibility of a top-down cortical source of online saccadic corrections is not excluded. From a behavioral standpoint, cognitive manipulations in our current study and other seminal works (West et al. 2009; Heath et al. 2010, 2011) modulate online oculomotor corrections. With regard to the contributions of cortical and subcortical networks, the following sections are a non-exhaustive discussion of possible explanations for task-dependent changes in oculomotor behavior.

Task representation in the cortex

When saccades are directed toward visible targets in our immediate environment, the "real-time" hypothesis (Westwood and Goodale 2003) suggests that dorsal stream visual processing is specialized for integrating object metrics into the motor system. In the other case that saccades are directed to memorized locations, the movement goal is no longer parameterized directly from this real-time percept. Instead, saccade metrics must be first translated from a non-metric qualitative memory in the ventral visual-processing stream (Haffenden and Goodale 2000). West et al. (2009) postulated this ventral representation is used less efficiently for feedback-based corrections as compared with a native dorsal representation. This is supported by the fact that reciprocal and single memory-guided saccades are more variable in their execution than are visually guided saccades (Rolheiser et al. 2006).

This reasoning is founded in the perception–action model of visual processing (Goodale and Milner 1992), a limitation of which is the absence of a neurophysiological distinction for motor parameterization by planning or by real-time visual integration. Predictive saccades observed in our study were guided by a short-term, spatial working memory (SWM) representation of the target and did not show a characteristic performance decrement associated with single memory-guided saccades. Less efficient online corrections in single memory-guided saccades were explained by a delay of ventral stream interpolation of target metrics. Interestingly, the perception–action model fails to explain how predictive saccades can rely on SWM yet be equivocal in their performance to reactive saccades. It is therefore possible that saccades operate outside the classical behaviors used to construct the perception–action model.

Our study is not alone in elucidating motor behavior in goal-directed tasks that is at odds with the perception–action model (Glazebrook et al. 2005). A more favorable approach for applying theoretical sensorimotor processing models to the current study is situated in the planning-control model (Glover 2004). In addition to the specialized dorsal and ventral visual processing streams, the planning-control model also incorporates a "third stream." This model is more compatible with the current behavioral results because the third stream accounts for differences in the neuroanatomical correlates implicated in motor planning and online control processes. These two processes are distinguished as separate functions of the inferior parietal lobule (IPL) and superior parietal lobule (SPL), respectively. Using this framework, one can easily adapt the model to the results of our current study. One supporting example suggests that it is important to consider the role of the IPL because this area has been ascribed functions related to saccade planning and maintenance of memorized spatial coordinates (Brignani et al. 2010; Schluppeck et al. 2005). The planning-control model also accounts for a source of collateral projections to the motor system from the IPL and SPL. In the case of memory-guided saccades, it is possible to account for differences in the performance of single and repetitive saccades if SWM integrates differently into sequence planning via these networks.

These arguments have been framed with the assumption that SWM is established equivocally between the short-interval timed saccades in our study and other single memory-guided saccades. From an alternative standpoint, it is possible that motor planning was unrelated, and instead, the act of repeating movements in a sequence enhanced the representation of saccade metrics in SWM through habituation. In this case, the quality of memorized saccade metrics would decay in quality at a slower rate, thus contributing to improved execution and online control. The entrainment of sensorimotor networks with repetitive movements has been shown to persist based on prior context, including selective activity in the posterior parietal cortex (Jantzen et al. 2004).

This might reflect neural activity related to the maintenance of task goals. If modulation of memory habituation is the source of the observed differences in memory-guided saccading behaviors, and this is fundamentally different from distinguishing the contribution of planning movements in a sequence. Recent work in this field (Heath et al. 2010, 2011) has distinguished between effects of response suppression and vector inversion in anti-saccading. Future studies could be targeted at isolating the differential role of SWM maintenance and sequence planning in their contribution to online corrections in saccades.

Task representation in subcortical regions

As mentioned in the previous paragraph, the entrainment dynamics of repetitive movements have a lasting effect on cortical recruitment. There are also similar entrainment effects noted in subcortical structures including the thalamus, which also has known roles for integrating corollary discharge of saccade motor commands (Bellebaum et al. 2005). It is likely that other subcortical areas might be responsible for the observed enhanced performance in timed saccading. When making saccades to predictable locations, as the probability of specific locations of visual stimuli increases, there is a priming effect on the activity of neuronal activity in the SC (Basso and Wurtz 1998). Enhancement effects of the kind noted here reflect some level of potentiated task parameters, possibly reflecting the role of neurons in the SC. Determining whether low-level responses are caused locally through interaction with other subcortical networks or reflect top-down modulation is a general question we pose and hope to see solved in future research.

Conclusions

We hypothesized that some form of functional overlap in task-relevant resources—between spatial working memory, sensorimotor timekeeping processes, and sequence planning networks—would lead to differences in saccadic corrections. We have provided evidence that imposing a temporal expectation structure on repetitive saccades facilitates the integration of task-relevant sensorimotor information for online oculomotor control. More specifically, we have demonstrated that repetitive motor timekeeping in saccade sequences influences the fundamental operations of the oculomotor control system. This was based on observations that predictive saccades expressed enhanced online corrections when compared with suboptimal behaviors exhibited in untimed single memory-guided saccades.

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Chapter 3

The emergence of saccadic trajectory in response to illusory stimuli and spatial uncertainty

3.1 Citation & Author Contributions

This study was carried through from project formulation to the reporting and dissemination of results by the primary author, BR who operated under the guidance of the supervising and senior author JL.

Richardson BA, & Lyons J (in prep, July 2013)

3.2 Abstract

Just as any human movement is performed with a natural variability, saccadic eye movements demonstrate a degree of motor equivalence wherein comparing the trajectory of multiple saccades to a given amplitude target reveals gaze position is more variable mid-trajectory than at the saccadic end-point. An increasing body of evidence is building to suggest that online spatial error corrections are implemented to

reconcile this early trajectory variability so that the eye position at the offset saccades is aimed at the intended target location. Online corrections seem to operate most efficiently with visually-guided stimuli. In contrast, delayed memory-guided saccade (dmgSac) and anti-saccade (antSac) responses reveal a diminished efficacy of these corrections. In the current study, alternative visual stimulus paradigms were employed in two experiments for testing hypotheses that aimed to determine the reason diminished corrections emerge in some scenarios. Experiment one tested the hypothesis that both dmgSac and antSac tasks result in target and/or saccade metric representation that lack precision. To emulate this effect by other means than those used in previous studies, we used Gaussian blob targets to induce perceptual uncertainty in target position. While Gaussian blobs did influence the metrics of the produce responses, it did not change the expression of online corrections. Experiment two then tested the theory that a dependence on the ventral visuospatial processing stream was responsible for diminished corrections. Here we examined saccades that were directed to illusory M*ü*llyer-Lyer targets, which exert a perceptual and motoric bias on saccade responses that is founded in the discrepant encoding of target metrics by networks in the dorsal and ventral visuospatial processing streams. We hypothesized responses to illusory targets would exhibit diminished corrections for this reason, but our results provided evidence for an opposite trend. In the case of saccading to illusory targets, we observed larger scale interventions from online corrections that altered the course of saccade trajectory more severely than was the case in saccading to non-illusory targets in a control condition. These results suggested the illusory effects emerging from the ventral stream do not necessitate a poor mode of online control, and might instead introduce a greater variability that must be corrected for.

3.3 Introduction

Both saccadic eye movements and manual aiming with the upper limb are members of a range of goal-direction actions. The defining characteristic of their common basis is that their execution is optimized by minimizing spatial error at the instant of movement offset. Both saccades and manual aiming movements have velocity profiles that are roughly bell-shaped. Deviations of their trajectory away from completely symmetric acceleration and deceleration phases can be analyzed for evidence of different mechanisms that integrate task-relevant information and contribute to the accuracy of performance. Often times, various mechanisms exert their respective effects to trajectory formation on different time-scales as the movement progresses to completion —*c.f.* (Elliott & Khan, 2010).

This was first a point of investigation into manual aiming wherein a primary distinction in control policies was that fast corrections from feedforward mechanisms are dependent on planning and prediction, and these are integrated with slower feedback strategies based on perceptual-motor integrations (Elliott, Helsen, & Chua, 2001). Similarly, with the emergence of finer resolution measurements of eye position during saccadic execution, the ageing idea that saccades are fully ballistic (Becker & Fuchs, 1969) has been challenged by a number of studies. Exemplary evidence against the case of ballistic saccades includes fast retinal feedback that modifies the programming of saccadic commands in response to unexpected changes in target amplitude occurring at the instant of saccadic onset (Gaveau et al., 2003). Aside from mechanisms correcting for external perturbations, the oculomotor system naturally produces motor commands with inherent variability for which other modes of closed-loop control are implemented to correct.

Saccades demonstrate motor equivalence. The analysis of a number of saccades to a target located at a constant eccentricity reveals a higher spatial variability in eye position during the early and middle phases of execution despite a comparatively lower variability in end-point spatial error. A certain amount of this variability emerges as a function of normal sensorimotor noise (Beers, 2007), and while it peaks near the halfway-point of the movement it is largely corrected for prior to saccade termination (West, Welsh, & Pratt, 2009). This property of saccades provides evidence that a mechanism of online correction exists for reconciling even natural variability in saccadic trajectories, and for optimizing end-point accuracy.

An important consideration when querying mechanisms of oculomotor control is that saccades can be produced in many different natural and experimental scenarios. The importance of this is demonstrated by manipulations of a visual tracking task that modulate the efficiency of implementing these spatial error corrections. For example, fast corrections observed during stimulus-guided saccades operate with an approximate delay of 30 ms. Yet, if single saccades are instead directed to a memorized location the implementation of online corrections is slower, and contribute to trajectory formation only after a 50 ms latency following the movement onset (West et al., 2009).

Decreased evidence for closed-loop control in the case of memory-guided actions is a finding that is congruent with similar studies using manual aiming models (Heath, Westwood, & Binsted, 2004). Collectively these findings suggest that actions whose parameters are encoded from a goal representation stored in spatial working memory (SWM) are not conducive to efficient online modes of spatial error correction. This costly imposition on SWM was discussed as perhaps being related to a delayed interpolation of metrics from the ventral visual processing stream. In many cases of manual actions the ventral stream is considered to be less specialized than the dorsal stream for visuomotor integration (Westwood D.A. & Goodale M.A., 2003).

In extension of these findings, previous work from our lab (Richardson, Ratneswaran, Lyons, & Balasubramaniam, 2011) used a periodic saccadic tracking task to elicit series of predictive saccades using reciprocal targets. Predictive saccades are also inherently memory-guided, and implicate other mechanisms for predictive control in addition to SWM. Motor planning is required for entraining the timing of responses to regular intervals with exogenous pacing cues (Joiner & Shelhamer, 2006). From predictive saccades, we observed a mode of online corrections that was equally efficient as compared with that observed in stimulus-driven responses from a full vision reactive tracking protocol. These findings extended the results and conclusions from the other research group (West et al., 2009), and we suggested that inefficient online corrections are not always a necessary cost of being directed to targets encoded in SWM. Instead, the additional recruitment of motor planning, or a habituation effect of target metrics that emerged from the reciprocal nature and series production of responses in our task was perhaps the factor responsible for recovering the efficient corrections.

Another series of studies (Heath, Dunham, Binsted, & Godbolt, 2010; Heath, Weiler, Marriott, & Welsh, 2011) has also demonstrated that the compatibility of visual stimuli and saccade direction can modulate the implementation of online corrections. Anti-saccades are those that are made in a centre-out tracking task and directed with an equal magnitude but opposite vector into the visual hemifield contraversive to the unmasked visual stimulus. Since visual space is encoded for visuomotor integration in a very direct manner (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002), the costly process of inverting a response vector opposite to the directly cued stimulus leads to a saccade whose online corrections also show diminished efficacy (Heath et al., 2011).

The exact mechanism of the vector inversion process is not completely revealed in its own domain. This fact limits the depth of conclusions one can derive regarding why its process influences the implementation of online corrections in saccades. Potentially, vector inversion involves the frontal eye fields (FEF) and lateral intraparietal area (LIP), as shown in non-human primates (Munoz & Everling, 2004) —the LIP human analog is often regarded as the midposterior intraparietal sulculs (mIPS) (Vesia, Prime, Yan, Sergio, & Crawford, 2010; Levy, Schluppeck, Heeger, & Glimcher, 2007). Yet the exact reason why vector inversion causes saccades to exhibit increasingly determinate behaviour consequent to diminished operations of closed-loop intervention to an otherwise ballistic trajectory remains elusive.

In a similar framework, another question remains as to the reason why single memory-guided saccades in a delayed execution task showed diminished intervention of online error corrections. While our previous study indicated that the diminished control is recovered when making predictive memory-guided saccades in series, it is unclear whether this recovery of efficient behaviour was served by mechanisms related to motor planning or the repetitive nature and potential habituation of the target representation. To build on this model we report herein the result from two other forms of visuospatial manipulations to this task paradigm with the intention of providing incremental evidence for answering these questions.

A potential factor shared between delayed memory-guided saccades (dmgSac) and anti-saccades (antSac) that might explain their diminished online corrections is an inherent degree of uncertainty in encoding the spatial metrics of targets and, or the consequent saccades. It is known that the accuracy of both saccades (West et al., 2009) and reaches (Heath et al., 2004) to a memorized location degrades increasingly over time as a function of decay in the quality of their representation (Rolheiser, Binsted, & Brownell, 2006). An equally degraded representation in motor networks is also a potential manifest, and from affecting these areas could putatively effect online corrections. The coding of saccades is known to emerge from population averages of neurons that are individually tuned to a spatial location. This ensemble-coding is shown in non-human primate models of neuronal recordings from multiple brain areas, including oculomotor structures such as the superior colliculus (SC) (Opstal & Goossens, 2008; Lee, Rohrer, & Sparks, 1988; Van Gisbergen, Van Opstal, & Tax, 1987), FEF (Schlag, Dassonville, & Schlag-Rey, 1998), and also in oculomotor-nonspecific networks such as the parietal cortex (Fattori, Breveglieri, Raos, Bosco, & Galletti, 2012; Platt & Glimcher, 1997). In both cases of dmgSac and antSac responses, it is perhaps the case that the encoding of saccades and their suboptimal online corrections are a result of a more coarsely tuned population average in one of these areas. Should this be the case, we hypothesized that any other factors known to modulate such patterns of encoding target and saccade metrics might also induce similar decrements in the performance of online corrections.

In the first experiment conducted as a part of our current research, we approached this task with saccades to targets whose visual properties caused their perceptual representation to become increasingly corrupt with uncertainty in their encoded metrics. One method we had considered to accomplish this feat involved the use of distractor targets. This manipulation is associated with the incomplete suppression of the distractor target's directionally tuned representation in the FEF, and also with a congruent curvature in the consequent saccadic trajectory (McPeek, 2006). The use of distractor targets, however, confounds the investigation with relation to a strict focus on the encoding of target metrics because the added complexity of target discrimination and the cognitive demands of making a choice might also influence online corrections in by other means (Schall, 2001). So, to query whether perceptual uncertainty in the coded target location is itself a factor that modulates the implementation of online corrections we arrived at the conclusion that a more objective approach for manipulating visual stimulus properties would be with variations in the width of luminance contrast envelopes.

To be more specific, we presented targets as Gaussian blobs with increasing levels of spatial dispersion and decreased contrast with respect to the background. The effect of blurring visual stimuli in the periphery is consistent with a congruent increase in the uncertainty for resolving spatial position in perception (Levi & Klein, 1990; Levi & Tripathy, 1996). In further support that blurring is relevant for modulating the eventual encoding of saccades, Gaussian blobs placed in close proximity to one another are spatially resolved such that saccadic end-points are functions of a centre-of-gravity optimization, irrespective of whether the contrast gradings that need to be resolved are applied by means of target luminance or chrominance contrast envelopes

(Cellini, Schutz, & Gegenfurtner, 2010). In the case that decreased efficiency in online corrections for dmgSac and antSac is a superior function of a deteriorated target representation consequent to imprecision induced by their respective visuospatial task constraints, we hypothesized the outcome of this first experiment would show diminishing evidence for online corrections in saccades with increasing uncertainty in the target position.

Our second experiment tested an additional hypothesis that an imposition on the ventral visuospatial processing stream was potentially responsible in its own merit for a suboptimal implementation of online spatial corrections to saccades. The two experiments we conducted would not provide results that are inherently mutually exclusive. Explanations for diminished spatial corrections that are framed as separate functions of the acuity of target metrics and, or a reliance on the ventral stream are viable in their own merit.

The second experiment was an incremental extension of our previous results (Richardson et al., 2011). Our conclusions did not exclude the ventral stream from being a source of slow corrections, as was initially theorized by the authors of the work with dmgSac responses (West et al., 2009). Rather our previous study indicated that the performance limitations inherent to the dmgSac task were recovered or circumvented by overlaid effects of motor planning, or for reasons related to the production of series of reciprocal responses. So this second experiment in the current study was conducted to account for a reliance on the ventral visuospatial processing stream, while using a model other than dmgSac responses to impose a demand on the ventral stream, without implicating motor planning or series responses.

To do this, saccades in this second experiment were directed to the far end of a linear stem that included wings at its far extent. These wings were oriented inward or outward to induce a M*ü*ller-Lyer illusion. As a basis for comparison, the absolute metrics of simple non-illusory control targets are known to be coded for in the dorsal visuospatial processing stream, implicating the superior aspects of the posterior parietal cortex (PPC) (Goodale & Westwood, 2004). Conversely the biased target metrics induced by the M*ü*ller-Lyer illusion is associated with perceptual biases emerging from interpolating metrics from the encoded qualitative target representation. This illusory processes is mediated by areas around the intraparietal sulcus (IPS) (Weidner & Fink, 2007). Parietal areas bordering the IPS are closely connected with the temporal lobe for integrating information from the ventral visuospatial processing stream (Goodale & Milner, 1992). There is no doubt this illusion paradigm modulates the saccadic programming in biasing their overall amplitude (Bruno, Knox, & Grave, 2010). So we put forth the hypothesis that any functions of diminished online corrections related to the ventral stream coding of target metrics should also present themselves as a function of saccading to M*ü*ller-Lyer targets. Both wings-in and wings-out cases of the illusion, but not control saccading implicate a corruption by coding in the ventral stream. Consequently, diminished corrections when tracking illusory targets would be expected to be equivalent when comparing responses made to M*ü*ller-Lyer wings-in and wings-out targets, despite their amplitude-biasing effects being opposite in their predicted manifest.

3.4 Materials, methodology and procedure

In accordance with permission from the McMaster Ethics Research Board for the current procedures, we recruited two separate groups of healthy and typically-developed participants for the first ($N = 10$) and second ($N = 7$) experiments. Informed consent was received from participants, who were naïve to the purpose of the study, had normal or corrected to normal vision, and performed the task in a number of 30 to 60 minute sessions depending on their convenient availability, totalling approximately 2.5 hours.

3.4.1 Apparatus

Research participants performed an oculomotor tracking task in response to visual cues presented on a 21" wide-screen LCD monitor. Gaze angle recordings were made with the EyeLink II (SR Research, Osgoode, Ontario) eye-tracking system at a sampling rate of 500 Hz. Visual stimuli were coded and presented during experimentation using Experiment Builder (SR Research) software on a 21" wide-screen LCD computer display at a resolution of 1920 × 1080 @ 60 Hz connected to a PC running Windows XP (TM). The visible display area of the 1920 horizontal pixels was 534 mm, equating to a 0.278 mm dot pitch. Participants were seated 60 cm from the display screen, centred horizontally with the display screen, and these measurements were used with basic trigonometric relationships to compute the gaze angle in degrees.

3.4.2 Task procedure

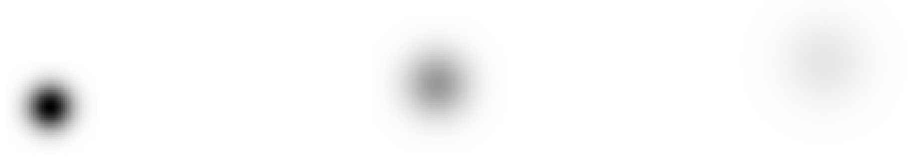
The general stimulus presentation protocol for both experiments was similar, with the primary manipulation exerted by means of altering the appearance of the visual stimuli. A centre-out tracking task was employed where at the beginning of each trial participants were required to maintain steady fixation on a central dot for one full second before a saccadic target was unmasked in the periphery. Following the fixation period, the saccadic target was presented to cue horizontal saccadic responses either to the left or the right of the central fixation. Five amplitudes of saccades were cued to targets at 4°, 8°, 12°, 16°, or 20° eccentricities outward from the centre, and in either direction. This eccentricity manipulation is captured by the TargAmp-n factor in our analysis, with n representing one of these target eccentricities.

Experiment 1 - Gaussian blobs In this first experiment, three levels of increasingly blurred targets were used for the Blob-m experimental factor, where m represents one of three progressively blurred targets from 1 to 3. The graphics we used for these three levels of Blob factor targets are shown in Figure 3.1. The parameters of the Gaussian function used to generate these stimuli are presented in Table 3.1.

Table 3.1: Gaussian blob target properties

Target	**Total angle subtended**	**SD of Gaussian**	**Grayscale peak**
Blob-1	1	0.17	100
Blob-2	1.5	0.25	40
Blob-3	2	0.33	10

Total angle subtended and the standard deviation (SD) of the Gaussian function are reported in degrees of visual angle, and the grayscale peak is darkest point of the image expressed as a percentage of total black, as coded for by 8-bits of depth in the luminance contrast.



(a) Blob-1 (b) Blob-2 (c) Blob-3

Figure 3.1: Visual comparison of the range of Gaussian blobs used as visual cues

Overall, in experiment one there were 3 × Blob conditions, combined with 5 × TargAmp and 2 × TargDir conditions, that were each repeated 35 times for examining multiple iterations of each saccading conditions. Since previous studies have indicated no effects or interactions contingent on the relative left or right direction of these responses (West et al., 2009; Richardson et al., 2011) the direction factor was included to avoid preparatory activity related to a target located in a known hemifield, while within-subject averages were taken to collapse across this direction factor before submitting data to other ANOVAs.

Experiment 2 - M*ü*ller-Lyer targets As a point of comparison for behaviour directed to illusory targets, a control target was presented as a solid black-filled and hard-edged circle, similar in size to a common LED approximately 5 mm width on the screen that subtended approximately 0.5° of visual angle. Moreover, the two complimentary wings-in and wings-out form of the M*ü*ller-Lyer targets were used, for which the factor MLTarg-*o* exists where *o* being either *in*, *out*, or *c* for "control". The wings spanned 100 px, which was equivalent to subtending approximately 2.6° of visual angle. Being a centre-out saccading task, when the MLTarg was unmasked one end of the target stem began at the central fixation point and extended laterally in the horizontal axis by a distance determined by the current trial iteration's TargAmp.

Participants were instructed to saccade to the peripheral end of the target stem. The characteristic M*ü*ller-Lyer wings were added to the end of both ends of the stem. Again in combination with the 5 × TargAmp and 2 × TargDir, the 3 × MLTarg conditions were repeated 35 times each.

3.4.3 Data Analysis

Time-series of eye position data were analyzed in MATLAB (Mathworks, Natick, MA) using analysis scripts developed in-house. In replication of up-sampling methods used previously (Richardson et al., 2011), the temporal resolution was increased by using MATLAB's *resample* function to interpolate position by a factor of two, to 1000 Hz. Eye movements were detected by standard means where saccade onset was acquired from the gaze time-series as the first sample exceeding both 30°/sec velocity and 8000°/sec ^{2} acceleration in the direction of the target. Offset was the first sample where the absolute velocity of the eye irrespective of direction was less than 30°/sec in every subsequent sample in a 10 ms window. Outlier saccades were excluded when the end-point exceeded +/-3° of error in amplitude from the mean amplitude of each participant with respect to each condition. These procedures assured the analysis of saccades made to completion, and only of those that were intentionally directed to visual stimuli. This also minimized potential overlap between TargAmp conditions, whilst avoiding potentially wrongful exclusion based from amplitude-modulating effects of varying stimuli. Across both experiments the average number of successful saccades collected in each condition was ($M = 27.50, SD = 1.26$).

Dependent measures

Similar methods of analysis were used for both experiments. Eye position was initially mapped onto screen coordinates, and their horizontal deviation from the central target at each sample was converted to degrees of visual angle by applying right-angle trigonometry. The data time-series in the horizontal axis of eye position was extracted for saccadic responses and subject to a few analysis techniques, which considered the saccade onset position to be 0° and progress to its end-point at p° away from the starting, where p is the final amplitude of a given saccade at the instant the saccade crossed the offset velocity threshold criteria. In other words, the gaze position at the onset of the saccade was subtracted from the time-series of gaze position samples during its motion.

The time-series of each saccade was divided into another experimental factor to examine how the eye position changed as it progressed to completion. After the saccade onset, the total movement time was divided into four intermediate levels, indicated by q for values of 20%, 40%, 60%, and 80% of total MT, as well as EP as is synonymous for the saccade end-point. pMT-q is the experimental factor subjected to statistical analysis that permits an examination of how the saccade trajectory evolves throughout its progression. A variability analysis was performed for every condition of saccading by taking the standard deviation of gaze position (SDpos) at each of these pMT levels and averaged across all iterations of a given condition. Subject means of these data were submit to repeated measure ANOVA models with 5 levels of pMT in conjunction with the other experimental factors.

To extend the variability analysis, the proportion of explained end-point variance (R^2) was also computed. For all saccades in a given condition from each subject, the Pearson product-moment correlation coefficient (r) was computed at all four intermediate levels of the pMT factor (pMT-20 to pMT-80) as the eye position in a given saccade at pMT-q can predict the ultimate movement end-point. The square of this value resolves the degree to which the position of the eyes during a given saccading condition explains variance in its distribution of end-points, also known as the coefficient of determination. Lower R^2 indicates there is little variance explained by saccade position. This implies that from the time the R^2 measurement was made there are other factors such as online corrections that alter the course of the evolving trajectory, causing it to exhibit an end-point that is not predictable as would otherwise be the case from a ballistic trajectory. Conversely, high R^2 values indicate the trajectory evolves in a determinate fashion where the end-points have a higher explained end-point variance when measured early in the trajectory. This latter case is associated with actions where no corrective processes change the course of the trajectory as it is emerging, implying a lower degree of online intervention. It is this R^2 measure which validates inferences that the reconciled mid-trajectory peaks in SDpos by the end-point is a function of intervening processes. Passive reconciliation of motor equivalence in saccades would exhibit higher R^2 values consistent with ballistic trajectory.

A few trends in the these measures are predicted based on the natural idiosyncrasies of the current task. In measuring the proportion of explained end-point variance at varying levels of pMT, one implication is that as the saccade becomes closer to its termination there is less time for any intervening factors to exert and integrate spatial changes in the trajectory to decrease the R^2 value. As a result, R^2 is expected to increase with pMT. Previous research (Heath et al., 2010, 2011) has demonstrated their main *task* factor, either making anti- or pro-saccades, resulted in a significant main effect for *task* as well as its interaction with pMT. The interaction between these two factor emerges as natural function of movements becoming more correlated to their end-points the closer they get.

In fact the full range of TargAmp-4 to TargAmp-20 conditions included in our study has been shown previously (West et al., 2009; Richardson et al., 2011) to include short saccades that show no intrinsic evidence of online corrections, since their variability does not decrease from any earlier point in their trajectory to that at their end-point. This is partly responsible for significant interactions between TargAmp and pMT, but this two-way interaction also emerges as a natural function of larger amplitude saccades having a longer distance left to travel to their end-point at any given level of pMT relative to shorter saccades. This interaction, is not always reproduced (Heath et al., 2010, 2011) as those studies included only two levels of target eccentricities, similar to our TargAmp-12 and TargAmp-16. Since these studies (Heath et al., 2010, 2011) provided evidence for modulating online corrections in R^2 measures in an ANOVA, to maintain proper power and sensitivity to our Blob and MLTarg task factors, we considered only the TargAmp-12 and -16 conditions our ANOVA of R^2 data. More information about a priori power is included in the relevant section below.

Despite R^2 values from TargAmp-4, -8, and -20 conditions not being used in the R^2 ANOVA, that data is not totally excluded from use or analysis by other means. R^2 values from all five levels of TargAmp can be plotted as a function of their average time before the saccade offset the measurements were made, separately for each TargAmp conditions. As opposed to grouping R^2 values by pMT which obfuscates their absolute time of measurement, this method allows a complimentary analysis of the ballistic nature of the trajectory as it emerges as a function of the time available for processes to alter its course. As used previously and described in other works (West et al., 2009; Richardson et al., 2011), an iterative outlier procedure is best suited to compare the increasing R^2 values as they approach the saccade termination. Specifically, the pre-termination latency —not to be confused with saccadic onset latency as is reported in our descriptive statistics of saccade metrics —of the first R^2 value which exceeds the mean plus two standard deviations of the previous and smaller values is an estimate of the time taken for corrective processes to implement. This measure provides a threshold value and time estimate of the implementation delay of online corrections to saccades.

Statistics

Analysis models All data descriptive of saccade metrics as well as those from which we can we acquire evidence for online corrections are entered to a fully within-subjects repeated measures ANOVA. With the exception of R^2 analysis considering only two TargAmp levels, all other levels are fully examined across all five TargAmp levels.

Main effects and pairwise comparisons are reported with significance values adjusted by means of Bonferroni corrections at $p < 0.05$. Post-hoc tests of interactions are completed in regard to planned comparisons to query how Blob or MLTask task factors might alter the expression of online corrections. In general, the t-test decomposition of interactions that contribute to examining how our main Blob and MLTarg task conditions influenced saccading behaviour are corrected for multiple-comparisons at a moderately conservative level discussed below on a case by case basis.

A priori power We based an a priori power analysis for our current sample sizes using effects observed in previous studies (Heath et al., 2011) that have applied tracking task modifications similar to those used here, and been sensitive to statistical differences. The power analysis applies to pruning the factorial combinations of our experimental conditions for a statistical model that has sufficient power to determine significance in the experimental factors that modulate the R^2 data. It is in these data that inferences are made about the degree to which a trajectory shows evidence for online corrections, and evidence that corrections are modulated by the main task manipulations.

From this previous work (Heath et al., 2011), the authors demonstrated diminished online control through a statistical main effect of *task* in R^2 data between anti- and pro-saccading conditions F(1,11)=24.47 with $n = 12$ participants. This computes to an effect size of $\hat{f} = 0.999$. Given the number of groups compared in their task, this mandates an a priori requirement of $n = 6$ participants for replication. Whereas their task (Heath et al., 2011) included only two levels of *task* (pro- and anti-saccading) both our two current experimental designs include three levels of *task* each, Blob-1, -2, and -3, as well as MLTarg-IN, -OUT, and -CTL. Consequently a priori power analyses based on the same effect size indicates a requirement of only 5 participants to replicate as our study includes an additional level of the main task independent variables being compared. Our sample sizes of $n = 11$ and $n = 7$ for experiments one and two should provide the sensitivity needed to show similar results should they exist consequent to our task. The main effect of Blob in experiment one, and of MLTarg in experiment two on R^2 data that are the most important factors to consider for interpreting our results, and our statistics are optimized for elucidating these trends.

3.5 Results

3.5.1 Descriptive statistics

A primary query in our analysis is for determining whether participants performed the saccading task to the expected metrics, and whether the task conditions altered basic measures of compliance to the task instructions.

Saccade amplitude Saccade end-point data and its variability is presented in Table 3.2 for both experiments at all five levels of TargAmp. As expected, we found significant effects for TargAmp in both experiment one $F_{4,36} = 7270.362$, $p < 0.001$, $\eta_p^2 = 0.999$ and two TargAmp $F_{4,24} = 8738.911$, $p < 0.001$, $\eta_p^2 = 0.999$.

In both studies we also found a main effect of the primary target manipulations on amplitude, which are illustrated in Figure 3.2. In experiment one, a main effect of Blob $F_{2,18} = 16.711$, $p < 0.001$, $\eta_p^2 = 0.650$ showed a trend of slightly decreasing amplitude from Blob-1 to Blob-3. Additionally, the illusion induced from the M*ü*ller-Lyer targets in experiment two induced the expected bias in amplitude, where a main effect of MLTarg $F_{2,12} = 94.774$, $p < 0.001$, $\eta_p^2 = 0.940$ revealed the shortest saccade amplitude in the wings-in condition, the longest in the wings-out condition, and a moderate relative amplitude in response to the control target conditions. Mean saccade amplitude at all levels of Blob were tested to be different from one another (all $p \leq 0.045$), and similarly at all levels of MLTarg (all $p \leq 0.004$) with Bonferroni corrected significance predetermined at $p <0.05$.

Saccade amplitude data demonstrated that despite a small-scale change in amplitude consequent to the three levels of Blob targets, generally their performance was rather similar as the mean difference between blob conditions at a given TargAmp level was well within one standard deviation. In respect to experiment two, the mean difference between the amplitude of saccades to illusory targets from those to control targets at a given TargAmp over one standard deviation of the mean, but still only a fraction of the difference in target eccentricity between TargAmp conditions. This confirmed the general integrity of our data grouping, specifically that the MLTarg did not cause so much scaling in the saccade amplitude such that saccades of similar amplitudes are considered at different levels of TargAmp by our statistical model.

Table 3.2: Saccade amplitude, Experiment × TargAmp

	4°		8°		12°		16°		20°	
MLTarg-	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
In	3.18	0.44	6.97	0.63	10.81	0.67	14.57	0.70	18.14	0.76
Control	4.01	0.24	7.90	0.32	11.69	0.42	15.35	0.51	18.80	0.67
Out	4.52	0.36	8.52	0.46	12.25	0.38	15.84	0.61	19.41	0.53

	4°		8°		12°		16°		20°	
Blob-	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
1	3.97	0.28	8.01	0.41	11.76	0.42	15.31	0.20	18.82	0.31
2	3.94	0.29	7.88	0.45	11.67	0.36	15.24	0.30	18.88	0.33
3	3.89	0.22	7.85	0.42	11.58	0.42	15.21	0.26	18.70	0.32

N.B. Values are reported in degrees of visual angle

Saccade onset latency In regard to the primary effects of task stimuli we imposed in either experiment, the Gaussian blobs presented in experiment one caused latency to increase significantly with more severe blurring and spatial dispersion of the target,

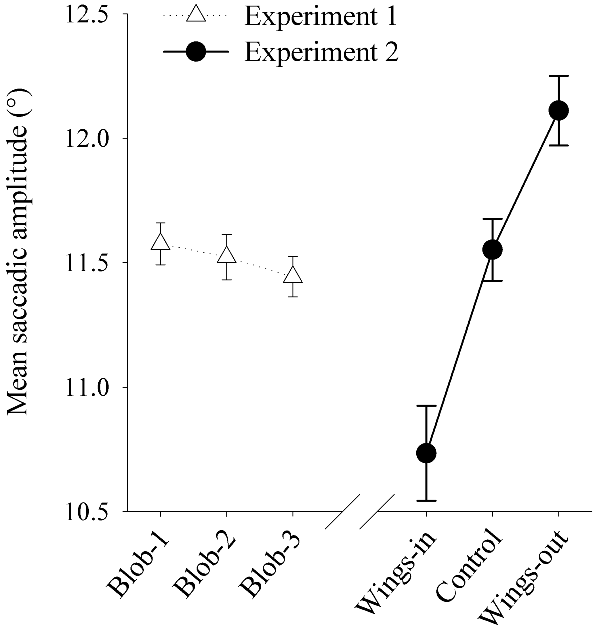
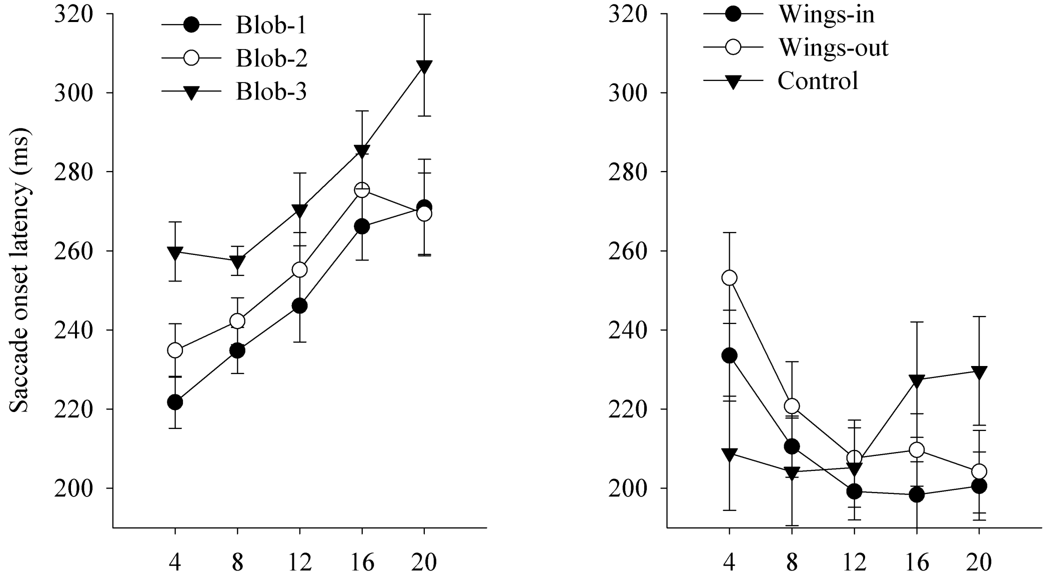


Figure 3.2: Saccade amplitude data illustrating the significant main effect of Blob in experiment 1 (left), and for MLTarg in experiment 2 (right). Mean saccade amplitude at all levels of Blob are different from one another (all p <0.04), and similarly at all levels of MLTarg (all p <0.005). Error-bars are plotted from the standard error of the mean.

at best from Blob-1 ($M = 247.95, SD = 22.76$), to Blob-2 ($M = 255.390, SD = 22.72$), and Blob-3 ($M = 276.057, SD = 22.93$) $F_{2,18} = 36.640$, $p < 0.001$, $\eta_p^2 = 0.803$. Also in experiment one, a significant effect of TargAmp emerged from a trend for increasing latency with increasing amplitude $F_{4,36} = 16.866$, $p < 0.001$, $\eta_p^2 = 0.652$. Pairwise comparisons from this effect of TargAmp shows latency is lower at TargAmp-4 than at -16 and -20, at TargAmp-8 is lower than at -16 and -20, at TargAmp-12 is lower than -16 and -20 (all p <0.05), and no difference reaching significance between TargAmp-16 and -20.



(a) Experiment 1 (b) Experiment 2

Figure 3.3: Saccade onset latency for the five levels of TargAmp, which are marked on the abscissa in units of degrees of visual angle, and its two significant two-way interactions with the tracking task factor, either Blob or MLTask in experiment one and two, respectively. Error bars plot the standard error of the mean.

An interaction of Blob × TargAmp also reached significance $F_{8,72} = 2.383$, $p < 0.024$, $\eta_p^2 = 0.209$, of which a visual inspection is shown in Figure 3.3a to highlight that Blob-1 and Blob-2 consistent increased in a roughly linear manner from TargAmp-4 to -16, whereas Blob-3 increased from TargAmp-8 to TargAmp-20. The non-linearity in latency data at TargAmp-4 and -20 from the three Blob targets might perhaps be attributed to known functions whereby contrast *detection* is facilitated in the periphery. Specifically trends in detection thresholds are known to change according to the combination of target eccentricity and the *SD* of the blurring function applied to the stimulus (Levi & Tripathy, 1996).

While such a modulation of detection thresholds is otherwise unrelated the decreasing spatial acuity in the periphery (Levi & Klein, 1990), this modulation of response latency by the Blob factor indicated our stimuli did in fact induce an important psychophysical change in the tracking behaviour. This provides a validation that our stimuli provided degrees of blurring that spanned a behaviourally relevant range of values.

From experiment two data, a main effect of the MLTarg factor did not reach significance in modulating saccade onset latency. As in the first experiment, we observed a main effect of $F_{4,24} = 26.717$, $p < 0.001$, $\eta_p^2 = 0.817$ but its interpretation means very little as the TargAmp factor also reached significance for its interaction with MLTarg $F_{8,48} = 34.902$, $p < 0.001$, $\eta_p^2 = 0.853$ (Figure 3.3b). A visual inspection of this interaction suggests that latency of saccading to control targets increased above TargAmp-12, whereas those to either wings-in or -out illusory targets decreased with increasing amplitude. It is interesting to note in this latency data that there were similarly emerging trends with increasing TargAmp for either illusory target condition. In contrast, this trend seemed to be opposite to that which emerged in response to control targets. This provided some evidence that the determinant of latency was contingent on whether or not the responses were performed to illusory or control targets, which provides cursory evidence that illusions induced a different mode of control as we intended it to, irrespective of wings-in our wings-out conditions.

3.5.2 Variability analysis

Experiment 1 - Gaussian blob targets These first spatial variability analyses included all five levels of the TargAmp factor. Gaze variability, as measured as the standard deviation of position (SDpos) as saccades progressed to completion at time points indicated by the pMT factor. Analysis of this data was important for determining that SDpos shows a mid-trajectory peak, followed by a significant decrease to the end-point to ascertain that online corrections were likely active to reconcile early variability before termination.

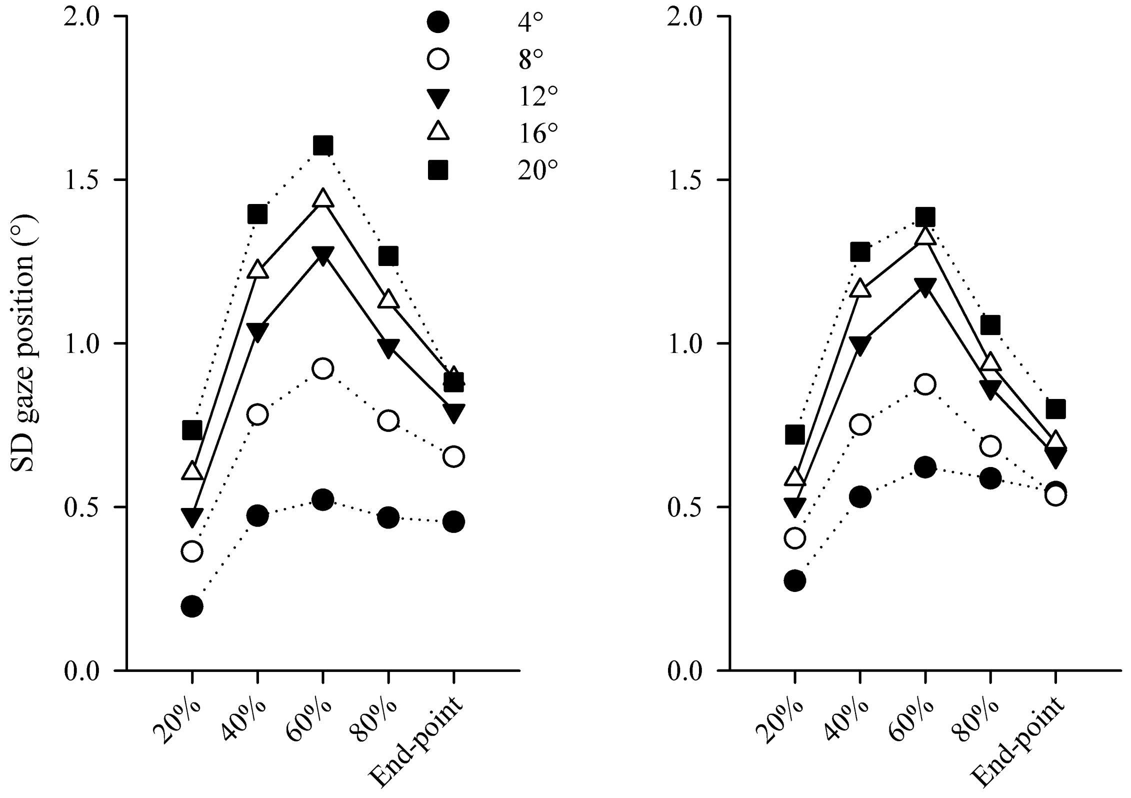
Main effects of TargAmp $F_{4,36} = 88.479$, $p < 0.001$, $\eta_p^2 = 0.908$ and pMT $F_{4,36} = 43.148$, $p < 0.001$, $\eta_p^2 = 0.827$ were complimented by their interaction also reaching significance TargAmp $\times$ pMT $F_{16,144} = 12.911$, $p < 0.001$, $\eta_p^2 = 0.589$. This trend is expected as previous research (West et al., 2009) has shown little evidence for significant reduction in variability at pMT-EP from earlier in a trajectory's time course when making small amplitude movements at TargAmp-4 and -8 that are not long enough in duration to permit online corrections. When considering TargAmp-12 and greater, we observed the expected reduction from peak SDpos at pMT-60 to the saccade end-point. This interaction is plotted for experiment one in Figure 3.4a.

The two-way interaction illustrated in the aforementioned figure was further supplemented by a nearly significant three-way interaction in combination with the Blob factor $F_{32,288} = 1.1436$, $p = 0.066$, $\eta_p^2 = 0.138$ (not illustrated). While this effect was only found to be approaching significance, we did consider this interaction for decomposition in limited breadth for the following reasons. First, our current statistics were not optimized for sensitivity to three-way effects, a limitation that emerged simply because our research model was directed a priori for adequate power in the Blob or MLTarg effects of regression analysis data. To that extent, the ANOVA of regression data itself included only TargAmp-12 and TargAmp-16 factors of the five total levels. The second reason we proceed with a limited breadth post-hoc enquiry to this three-way interaction is because we can do so in a justifiably pruned set of tests, using only the TargAmp-12 and -16 conditions. These two data sets are shown with solid lines in Figure 3.4a.

Relative to the peak SDpos at pMT-60 in both TargAmp-12 and -16 responses, it is necessary to demonstrate a significant decrease in SDpos from pMT-60 to pMT-EP in order to support the notion that mid-trajectory variability is corrected for before saccadic offset. This trend was significant for Blob-1 and -2 conditions separately investigated at TargAmp-12 and -16 eccentricities (all $p \leq 0.001$). For Blob-3 the similar comparison showed a decrease from pMT-60 to pMT-EP for TargAmp-16 trials was true to $p = 0.006$, and for TargAmp-12 $p = 0.016$. This conformed to maintaining significance using our initial criterion of p <0.05, adjusted here to p <0.25 since two tests were performed as a function of each TargAmp level. For example, TargAmp-12/pMT-60 vs. TargAmp-12/pMT-EP, and TargAmp-16/pMT-60 vs. TargAmp-16/pMT-EP at each level of the Blob factor.

Overall, these decomposed data suggest the three way interaction between Blob × TargAmp × pMT provided no consistent effect of the Blob factor in SDpos measures specific to the TargAmp-12 and -16 conditions. This was consistent with its small overall effect size (η_p^2 <0.3). The implication of this decomposition process was for inferring that saccades at TargAmp-12 and -16 eccentricity conditions for Blob-1, -2 and -3 all demonstrated significant reconciliation of mid-trajectory variability by their end-point, which we confirmed.

Experiment 2 - M*ü*ller-Lyer targets A replication from trends seen in experiment one was apparent in main effects for TargAmp $F_{4,24} = 20.101$, $p < 0.001$, $\eta_p^2 = 0.770$, pMT $F_{2.178,13.068} = 38.514$, $p < 0.001$, $\eta_p^2 = 0.865$ and their significant



(a) Experiment 1 (b) Experiment 2

Figure 3.4: Standard deviation of gaze position (SDpos) for both experiments, decomposed according to the interaction of pMT × TargAmp. This figure shows the trend for variability to peak mid-saccade near pMT-60. Post-hoc statistics are discussed in the results for the TargAmp-12 and -16 conditions only (solid lines), as these two target eccentricities are the only ones analyzed in the regression analysis. Overall the data in this plot demonstrate cursory evidence that a correction mechanism reconciles mid-trajectory variability in saccade position. Post-hoc tests of this data show that the SDpos decreases significantly from its peak at pMT-60 by the time the saccade terminates at pMT-EP. The tests not included in post-hoc comparisons here, and later in further regression analysis procedures are marked by dotted lines.

interaction TargAmp x pMT $F_{16,96} = 7.209$, $p < 0.001$, $\eta_p^2 = 0.546$ are data plotted in Figure 3.4b. While a three-way MLTarg × TargAmp × pMT was not significant $F_{32,192} = 1.076$, $p = 0.368$, $\eta_p^2 = 0.152$, post-hoc tests in a partial decomposition of this interaction sensitive to both the 12° and 16° target eccentricity conditions showed in both cases that mid-trajectory variability at pMT-60 was greater than at that the end-point of the saccade. Results were all confident to p <0.025, surviving corrections for two comparisons made within each level of TargAmp. In sum, the SDpos results from experiment two demonstrated a consistent reduction in variability from mid-trajectory to the saccade end-point in all MLTarg factor levels for TargAmp-12 and -16.

3.5.3 Regression analysis

Experiment 1 - Gaussian blob targets The ANOVA with R^2 data considered only the TargAmp-12 and -16 conditions for consistency with previous research and statistical sensitivity, and expected effect sizes. As expected, in experiment one we found a significant main effect of pMT $F_{2,18} = 103.849$, $p < 0.001$, $\eta_p^2 = 0.920$ and of its two-way interaction with TargAmp $F_{2.34,21.10} = 6.283$, $p = 0.005$, $\eta_p^2 = 0.411$, shown in Figure 3.5a with solid lines. The increase in R^2 as pMT progressed is one that was anticipated, and the interaction of these two factors was potentially expected regardless of our novel task manipulations with the Blob factor. As saccades approached their end-point the comparatively shorter TargAmp-12 saccades were closer to their end-point for every level of pMT as compared with TargAmp-16 saccades, meaning they are naturally expected to have a higher correlation to their end-point as was the case illustrated in Figure 3.5a.

These two factors also reached significance in their three-way interaction between Blob × pMT × TargAmp $F_{6,54} = 3.277$, $p = 0.008$, $\eta_p^2 = 0.267$. This interaction potentially indicated that our primary task manipulation of presenting different Gaussian blob targets altered the course of how saccades are correlated to their end-point. To examine this possibility directly, post-hoc tests were applied separately for responses at each level of TargAmp and pMT. This provided the best modelled investigation to compare whether R^2 changed as a function of Blob-1, -2, or -3 target presentation. None of these tests reached significance, suggesting there were no discernible effects whereby blob targets altered the degree to which mid-trajectory gaze position predicted the eventual end-point. This was inherently substantiated by a small effect size of this three-way interaction, and no supporting significant main effect of the Blob factor $F_{2,18} = 1.449$, $p = 0.261$, $\eta_p^2 = 0.139$ as we would anticipate.

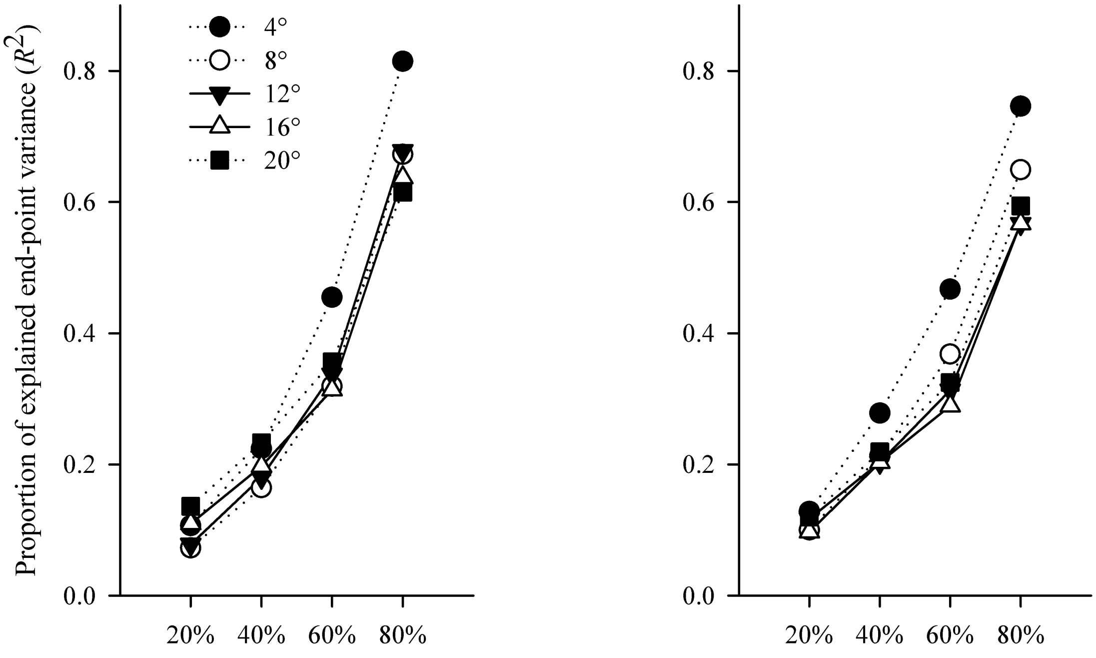
To this extent, in combination with the complimentary SDpos results, these R^2 data implied that no differences existed in the evidence for the efficacy of online corrections that varied with the degree of blurring imposed by the Gaussian blob targets. The iterative outlier procedure remains to identify whether these ultimately equivocal cases of online saccadic corrections are implemented with a similar delay.

Experiment 2 - M*ü*ller-Lyer targets As expected, R^2 increased while the saccades progressed to completion as was reflected by the main effect of pMT reaching significance $F_{1.395,8.368} = 112.938$, $p < 0.001$, $\eta_p^2 = 0.950$. The interaction of pMT with TargAmp did not reach significance, yet we included a plot of its decomposition in Figure 3.5b as solid lines. This permits a visual comparison against all other TargAmp conditions not included in the ANOVA (dotted lines) for situating the R^2 from TargAmp-12 and -16 in the general scheme of saccades as they related to target eccentricity.

From experiment two data we also observed a main effect of our primary manipulation, MLTarg $F_{2,12} = 5.037$, $p = 0.026$, $\eta_p^2 = 0.456$ and its interaction with pMT $F_{6,36} = 2.974$, $p = 0.018$, $\eta_p^2 = 0.331$. This would indicate that our MLTarg factor had a significant influence on R^2 data, possibly indicating a modulation of online corrections. This two-way interaction is plotted in Figure 3.6. Pairwise comparisons of the three MLTarg groups for decomposing the main effect of MLTarg indicated the MLTarg-OUT condition had significantly lower R^2 values, with a $(M = 0.120, SD = 0.035)$ mean difference score relative to the MLTarg-CTL trials. MLTarg-IN was not significantly different from MLTarg-CTL with $(M = 0.047, SD = 0.048)$ difference at emphp = 1.00, for which both tests significance was adjusted at p <0.05 with Bonferroni corrections.

Decomposing the above two-way interaction was more meaningful for the overall interpretation of the influence from our MLTarg factor. Post-hoc tests corroborated a consistent trend that saccades made in the MLTarg-OUT had a lower R^2 value at pMT-20 $t_6 = 3.285, p = 0.017$, pMT-40 $t_6 = 2.420, p = 0.052$, pMT-60 $t_6 = 2.958, p = 0.025$ and pMT-80 $t_6 = 3.370$, $p = 0.015$, with all but pMT-40 reaching significance without applying corrections for multiple comparison. Additionally, MLTarg-IN trials showed no significance in their difference from MLTarg-CTL at each level of pMT, despite mean R^2 being consistently lower at every level of pMT except for pMT-80 where they are nearly equal.

The implication of these data was their demonstration of a consistent trend for the lower R^2 in MLTarg-OUT versus MLTarg-CTL trials, suggesting that responses in the MLTarg-CTL trials exhibit a comparatively higher correlation to their end-point



(a) Experiment 1

(b) Experiment 2

Figure 3.5: The proportion of explained end-point variance (R^2) for experiment one and two, for the interaction of TargAmp × pMT. For situating the current data in as expanse a context as possible the R^2 data here is shown for all five levels of TargAmp, while the ANOVA results include only the TargAmp-12 and -16 illustrated here with the solid lines.

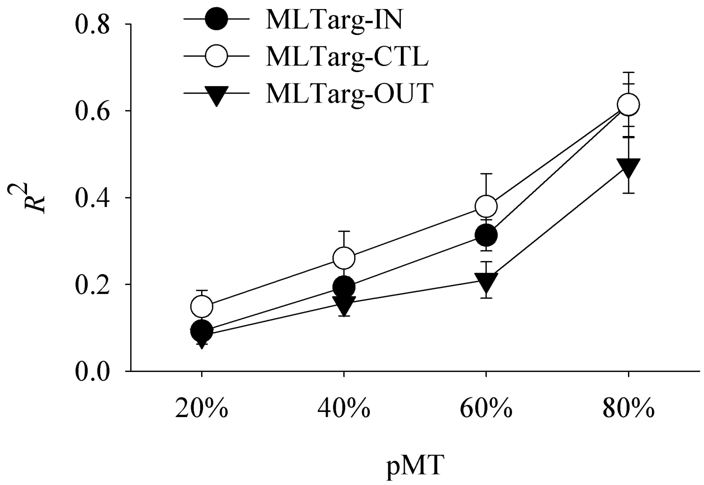


Figure 3.6: The proportion of explained end-point variance (R^2) for the significant interaction of MLTarg and pMT. MLTarg-OUT trials had a consistent trend of lower R^2 values in comparison to MLTarg-CTL trials, whereas MLTarg-IN trials did not reach significance in their difference from MLTarg-CTL trials. Error bars are plotted as the standard error of the mean.

throughout their execution. This extended to inferring that saccades to control targets showed less evidence for online corrections than do saccades to MLTarg-OUT targets, while non-significant but similar trend existed for MLTarg-IN trials as respectively compared with MLTarg-CTL. Initially we had hypothesized that experiment two could show whether a reliance on the ventral visual stream might induce a lower efficacy of online corrections. This current data provided evidence the opposite trend was true, and the full interpretation of our current data is included in the discussion section below.

Iterative outlier

Results from the iterative outlier procedure were used to estimate the time delay at which the processes operate that implement online corrections to saccades. These data are shown in Table 3.3 and plotted in Figure 3.7a and 3.7b for experiments one and two, respectively. The findings from these tests indicated equivocal estimates for this time delay, roughly 30 ms at all levels of the Blob factor in experiment one, and similarly for all MLTarg conditions in experiment two.

It is worth noting that the MLTarg-OUT data has a comparatively lower R^2, and initially a false threshold ($R^2 = 0.18$) is surpassed in this data at -40 ms despite the three subsequent R^2 values being under this threshold. Similar to the interpretation of a false threshold crossing as was made in previous work (West et al., 2009), the next threshold crossing was included for MLTarg-OUT in Table 3.3 as all but one subsequent R^2 value was above this more conservative threshold. This limit was similar to the thresholds obtained in data from all the other conditions. Overall, there were no discernible differences in the implementation delay of online saccadic corrections across any of the primary Blob or MLTarg conditions of both experiments.

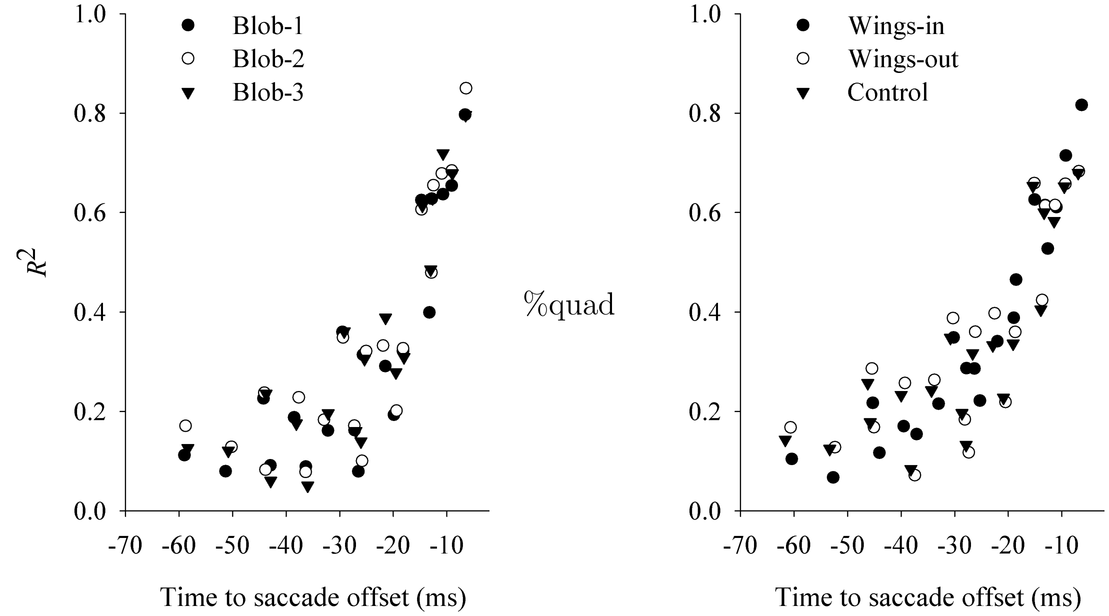
3.6 Discussion

Experiment 1 - Gaussian blobs In making our initial predictions for experiment one we reasoned that Gaussian blob targets would induce uncertainty in the resolved position of the targets. This, we suggested, would manifest in suboptimal modes of online corrections to saccadic eye movements if previous decrements observed consequent to anti-saccades (antSac) and delayed memory-guided saccades (dmgSac) emerged from a common basis that both have an inaccurate or degraded target representation. In our current study, we found no evidence to support this claim, and equivocal evidence for online corrections was replicated in all conditions of the Blob target factor.

Table 3.3: Data from iterated outlier procedures

Experiment	**Target**	**Feedback latency estimate**	**R^2 passed threshold**	**R^2-threshold**
1	Blob-1	-29.50	0.36	0.25
1	Blob-2	-29.39	0.35	0.29
1	Blob-3	-29.15	0.36	0.28
2	MLTarg-IN	-30.21	0.35	0.26
2	MLTarg-OUT	-31.11	0.23	0.19
2	MLTarg-CTL	-30.31	0.39	0.35

Nonetheless, we are confident that our Blob target manipulation had a significant bearing on the target representation assimilated by participants. This support builds from our results demonstrating the Blob did influence some aspects of saccadic performance, despite that influence having a manifest in performance variables other than those used to ascertaining the quality of online corrections. For example, we observed a consistent decrease in saccade amplitude to gaussian blobs with increased blurriness and spatial dispersion. Additionally, we observed a general trend of increasing latency from Blob-1 to Blob-3 consistent in its presentation in saccades made to TargAmp-12 and -16 target eccentricities. Both of these changes in descriptive saccade performance metrics suggested our target manipulation did in fact induce a viable psychophysical effect, albeit unrelated to online corrections. While our descriptive data provided



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(a) Experiment 1

(b) Experiment 2

Figure 3.7: Proportion of explained endpoint variance plotted as a function of the average time the measurement was made prior to saccade offset. Results from the iterated outlier procedure along with estimates of the feedback implementation delay are featured in Table 3.3

evidence that our task applied an objective and sensitive manipulation with the Blob factor, we concluded this was evidence for the case that it was *not* degraded target metrics that led to poor online corrections. Rather a different function of dmgSac and antSac protocols is responsible for explaining diminished online corrections.

Does this indicate with certainty that a degraded target representation is *not* responsible for a suboptimal mode of online corrections to saccades, whether it occurs as a function of the delay in dmgSac conditions or from an inaccurate vector inversion in antSac conditions? While our current results provide an important extension of other studies, additional factors should be considered for answering this question conclusively. One potential argument that our study must refute is that basic target features are extracted early in visual processing. An example of primary importance to the current study is stimulus edge-detection (Hubel & Wiesel, 1968), a factor we manipulate by using target contrast envelopes of various widths and peak intensities.

Within this context one may argue that features extracted at a low level might be those which were used for a range of downstream processing, see (Dyde & Milner, 2002). Since these low level operations represent a reduction in the complexity and dimensionality of the target into edges, this might be considered detrimental to the validity of our approach in that we reason that varying the contrast envelope of the stimulus should affect the breadth of population encoded representations of that target at all levels (*i.e.* from detection, to perception and action). However, our approach gains support in that the two forms of encoding stimulus parameters are not mutually exclusive, and the formation of signals representing detected edges doesn't preclude that lower level information regarding target contrast does not progress through lower visual processing to visuomotor integration.

Support for our interpretation was found in several areas of related research. Firstly, perceptual judgements such as size estimates are dependent on edge-detection in Gaussian-windowed targets and a function of integrating the contrast gradings of the whole target, not simply those local features which define the outer extent and boundaries of the target (Fredericksen, Bex, & Verstraten, 1997; Sclar, Maunsell, & Lennie, 1990). While this support was acquired from a perceptual task, there is accruing evidence processing streams for encoding a perceptual representation of a target and for encoding oculomotor goals are not separate entities (Bruno et al., 2010). This, of course, extends to tasks similar to ours, and implies that encoded motor actions and perceptual judgements have similar access to features of stimuli extracted from visual information in early visual processing (Grosbois, 2012).

In addition to these psychophysical results, our approach is further supported in studies examining, at the cellular level of encoding of vision, perception and action. The most robust accounts seem to indicate that as visual information progresses from early primary processing networks to late association areas, features are extracted and used to refine the representation (Sclar et al., 1990). Yet not all precision-confounding features of a target, such as contrast envelopes to induce ambiguous edges, or other allocentric properties to induce visual illusions [1] are filtered from the sensory and perceptual target representation prior to its integration into a motoric representation. This latter fact is demonstrated in that competing visual stimuli are encoded by location-tuned population averages in lower oculomotor networks, such as the superior colliculus (SC), and show evidence of conserving encoded metrics of both primary and distractor targets (Li & Basso, 2005).

Future studies may extend our current studies by returning to the paradigm of a dmgSac task. If we assume the perspective that a degraded representation of target metrics is not responsible for the diminished online corrections in dmgSac responses, then enhancing the function of spatial working memory (SWM) and storage of target metrics in a dmgSac task should not recover an efficient mode of online corrections. Transcranial magnetic stimulation (TMS) can be applied over the parietal cortex to temporarily enhance SWM (Yamanaka, Yamagata, Tomioka, Kawasaki, & Mimura, 2010). By applying active TMS according to these methods in conditions with a dmgSac task, examining trajectory should reveal a degraded mode of online saccadic

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[1] Gaussian targets are not always considered to be separate from illusory processes, see (Gori & Stubbs, 2006)

corrections similar to that observed in no-TMS or sham-TMS dmgSac condition (as previously demonstrated in West et al. 2009) if we are correct in rejecting the claim that a decay in target metrics is the reason why dmgSac tasks are associated with diminished corrections.

In further extension of the results from our current study, a TMS protocol aimed at enhancing SWM could also further disambiguate our previous results (Richardson et al., 2011). In this recent study we demonstrated that an efficient mode online corrections was restored for memory-guided saccades that were made to reciprocal targets repetitively at short periodic intervals. In comparison to a dmgSac task, our repetitive saccading task required both motor planning for making these responses while introducing the potential side effect of habituating target metrics through repetition. A TMS intervention would account for habituation effects by means of enhancing SWM separately from engaging motor planning networks, thus permitting the inference whether motor planning or target habituation was responsible for efficient online corrections in predictive saccades despite being directed to a memorized target location.

Overall, experiment one data did not provide evidence for concluding which factors of a dmgSac or antSac task were responsible for causing diminished online corrections. We provided cursory evidence for excluding the factor of uncertainty in spatial target position as an explanatory variable.

Experiment 2 - Müller-Lyer targets Experiment two was conducted to examine how illusory targets might modulate the implementation of online corrections to saccades. This manipulation was intended to examine saccades that were visually guided and that exhibited characteristics of being dependent on the ventral visuospatial processing stream. A dependence on the ventral stream was suggested to be a possible explanation for diminished online corrections in dmgSac tasks (West et al., 2009). A portion SWM's neural correlates (Awh & Jonides, 2001) do indeed overlap with those attributed with functions of the ventral visual processing stream (Goodale & Westwood, 2004). Moreover the discrepancy of target metrics from illusory targets from those encoded directly for visuomotor integration by means of the dorsal visual processing stream seem to be resolved in brain areas intermediate these two streams that mediate the conjunction of their signals (Goodale & Westwood, 2004; Weidner & Fink, 2007).

Presently we observed distinct trends in the descriptive saccade metrics that supported the case that responses were biased in the direction of the intended illusion (Figure 3.2, right panel). Importantly, we predicted that evidence that a modulation of online corrections of saccades should occur different from this amplitude scaling effect with the direction of the target wings. Instead we had predicted evidence for decreased corrections in both wings-in and wings-out MLTarg conditions, thus modulating R^2 in the same direction. Whereas we hypothesized that a reliance on the ventral stream induced by these M*ü*ller-Lyer targets would result in diminished online corrections and higher R^2 values in response to illusory targets, we found evidence for an effect to the contrary of our predictions. At least in the case of saccding to wings-out illusory targets, we observed significantly lower R^2 values relative to control saccading to non-illusory targets. This provides a case to argue that saccades made to MLTarg-OUT targets in fact show increased evidence for online corrections (Figure 3.6).

Contrary to this contention, an alternative explanation might argue the case that lower R^2 from MLTarg-OUT responses is a function of larger amplitude saccades induced as a function of the illusion's wing-direction sensitive effects. As mentioned previously in this paper, longer amplitude responses easily extend to implying an associated lower R^2 at a given pMT as compared with shorter amplitude saccades. For this reason the lower R^2 values with MLTarg-OUT might be argued to emerge as a function of a larger amplitude responses, and not from increased efficiency of online corrections as we suggested above. If this were true, however, one would also expect the effects of R^2 should have scaled with MLTarg from wings-in to wings-out targets congruent with the effect of the illusion as it biased saccade amplitude.

We build a defence against this alternative explanation as our results do not confirm this trend. R^2 values in MLTarg-IN conditions were not significantly different from that observed in control saccading, and would otherwise have been expected to have larger values in comparison to control responses to non-illusory targets since MLTarg-IN responses were significantly smaller in amplitude. Moreover the reduction in amplitude for MLTarg-IN responses was greater in magnitude than the increase in amplitude to MLTarg-OUT responses, relative to those made in the MLTarg-CTL condition. Furthermore, while this MLTarg-IN R^2 data did not reach statistical significance in its difference from R^2 in control responses, the non-significant trend in its means from pMT-20 to pMT-60 were opposite to that predicted by explaining R^2 effects by means of amplitude scaling (Figure 3.6). Collectively, these data provided a solid basis for arguing against this alternative explanation.

So how might one explain increased corrections in responses to illusory targets? We might speculate that illusory targets induced a mode of control dependent on the contribution of more factors than exclusively the ventral visuospatial processing stream. While we had initially predicted that the M*ü*ller-Lyer illusion implicated this ventral stream, and we do not reject this possibility here, we suggest additionally that colliding roles of ventral and dorsal visual processing might explain our results if both streams contribute differently, but act together in parallel for the generation of saccades. As compared with a dmgSac task that would perhaps impose an exclusive interpolation of saccade metrics from the ventral stream due to the complete masking of visual tragets, our current task maintains an independent component of establishing a direct representation for target metrics via the dorsal stream since it is inherently a visually-guided task, despite also including an illusory component.

An explanation for the seemingly paradoxical evidence for an increase in online corrections in the MLTarg-OUT condition would continue as follows. Efficient online corrections are potentially permitted as a function of our task using visually-guided responses, and at least a partial component of direct metric specification is encoded by means of the dorsal stream. The ventral stream's contribution to the specification of illusion-biased saccade metrics might induce increased error discrepant from that specified in the dorsal stream that are also eventually corrected for by online corrections. Consequently, should efficient online corrections reconcile error and variability in performance induced by the ventral stream's susceptibility to illusory targets, lower R^2 values for both MLTarg-IN and MLTarg-OUT conditions would be the predicted result of correcting for increased initial trajectory error induced by discrepant target representations implemented in parallel to one another.

Such assumptions are corroborated with lower R^2 in the case of MLTarg-OUT responses, and although not to a statistically significant degree a trend for lower

R^2 in MLTarg-IN responses is also apparent. We might reason this effect did not reach significance in MLTarg-IN relative to MLTarg-CTL responses as a function of a smaller change that might be expected in R^2 values, relative to the change expected in MLTarg-OUT for the following reason. Since MLTarg-IN responses are in fact smaller in amplitude than those to MLTarg-CTL, this naturally predicts that R^2 increases with a shorter amplitude. Since we observed a non-significant decrease in R^2, and no trend that was even remotely reflective of an increase, the underlying and expected increase of R^2 consequent to shorter amplitude responses could contribute to lessening the degree to which R^2 becomes reduced in MLTarg-IN by means of increased online corrections that reconcile additional error from illusory biases. Support from related research is found as it is certainly the case that multiple signals encoding different properties of target metrics arrive at oculomotor areas from different sources (McPeek, 2006). This contributes support to the idea saccade metrics are programmed and updated by means of parallel and interacting networks for visual integration, of which the dorsal and ventral processing stream are two such candidates in the case of this experiment.

Future studies may answer a complimentary question and query whether efficient online corrections are permitted as a general function of including a component of direct target and saccade metric specification in the dorsal stream. We suggest TMS is again a good intervention modality to make this distinction. In this case, using TMS to interfere with dorsal stream visuomotor integration for both visually guided saccades to illusory and non-illusory targets might predict a dissociation from our current results. If the mechanism we propose above successfully explains increased evidence for online corrections consequent to illusory targets, then a TMS-induced interference to dorsal stream processing should corrupt the integration of direct metric cues and deteriorate online corrections for both illusory and non-illusory targets. However, as we speculated the lower R^2 values in response to illusory targets emerged from increased error induced by the illusion, a TMS-induced effect to inhibit corrections would unmask the increased error induced by illusory targets and predict a larger proportional increase in R^2 values as compared with a more conservative increase in R^2 when correcting for comparatively lower error in saccades to non-illusory targets.

Final words Our current study provided results from two experiments, each of which was an incremental advancement to current literature pertaining to revealing factors that modulate online corrections to saccades. Whereas uncertainty in target localization as induced with Gaussian blobs was shown not to affect the emerging trajectory of saccadic responses, illusory targets did cause different trends in saccading behaviour relative to control responses. In this latter effect, our findings indicated that efficient online corrections to saccades are implemented even when saccading to targets that induce a spatial illusion. Further distinction of the visuospatial perceptual factors that have an effect on oculomotor networks when translated to saccade metrics requires very careful planning in future research. Many visuospatial manipulations have already been used to modify this task paradigm, such as those presented here and in previous work from our group and others' (West et al., 2009; Richardson et al., 2011; Heath et al., 2010, 2011). While the use of these visual cue manipulations has been unarguably useful in guiding the development of our understanding of online saccadic corrections up to this point, we advocate the advancement of this line of research with the application of other research modalities, such as TMS for permitting other types of inferences based on task facilitation and interruption, as opposed to those based exclusively on task representations relative to visual tracking and cognitive constraints.

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Chapter 4

An eye-to-hand magnet effect reveals distinct spatial interference in motor planning and execution

4.1 Citation & Author Contributions

This project was formulated by BR under the senior guidance of RB. BR was responsible for all of the data collection, analysis, and reporting for dissemination, with additional consultation and manuscript revisions provided by TC and JL.

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RESEARCH ARTICLE

An eye-to-hand magnet effect reveals distinct spatial interference in motor planning and execution

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Abstract An important question in oculomanual control is whether motor planning and execution modulate interference between motion of the eyes and hands. Here we investigated oculomanual interference using a novel paradigm that required saccadic eye movements and unimanual finger tapping. We examined finger trajectories for spatial interference caused by concurrent saccades. The first experiment used synchronous cues so that saccades and taps shared a common timekeeping goal. We found that finger trajectories showed bilateral interference where either finger was attracted in the direction of the accompanying saccade. The second experiment avoided interference due to shared planning resources by examining interference caused by reactive saccades. Here, we observed a lesser degree of execution-dependent coupling where the finger trajectory deviated only when reactive saccades were directed toward the hemifield of the responding hand. Our results show that distinct forms of eye-to-hand coupling emerge according to the demands of the task.

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Keywords Oculomanual coordination · Saccades · Sensorimotor timekeeping · Finger tapping · Motor overflow

Introduction

In daily activities, our brains direct our eyes to relevant targets in the environment. This is often done in parallel with a manual task that may or may not share a cooperative goal. To organize coupling suitable for a given task, the ocular and manual motor systems must share sensorimotor resources. An important challenge for researchers has been to model the encoding of motor planning and execution in multi-effector actions (e.g., Carson 2005; Carson and Kelso 2004; Grefkes et al. 2008; Swinnen and Wenderoth 2004). The topic of inter-effector coupling, for which the involuntary case is termed interference, is perhaps best introduced in the context of inter-limb coupling. An exemplary demonstration is the spatial magnet effect evoked by simultaneous action of the two upper limbs: when a circle is drawn with one hand and a line with the other, each movement is distorted in the direction of the other limb's trajectory (Franz et al. 1991).

Bimanual limb movements are susceptible to interference for a few reasons. During planning, the anticipatory encoding of one limb's action can influence the action of the other limb (Franz and Ramachandran 1998; Diedrichsen et al. 2006). Other coupling effects emerge during execution and are blanketed under the term *motor overflow.* Overflow describes effector crosstalk processes where motor commands interfere online during the execution of simultaneous movements. Two subclasses of overflow that have separate physiological correlates and are termed *associated* movements of non-homologous (dissimilar) limbs, or *irradiation* of motor commands to contralateral homologous (similar) muscle groups. It is important to distinguish these hierarchically organized mechanisms. Associated movements arise from intrahemispheric and transcallosal projections between cortical regions specialized for non-homologous effectors (Hoy et al. 2004). In contrast, incomplete decussation of the pyramidal corticospinal tract is the source of irradiation to contralateral homologous effectors (Carson 2005). In sum, interference between simultaneous limb movements is a combined function of crosstalk in action planning and two distinct types of interference that arise during the execution of motor tasks.

Defining a similar organizational model for oculomanual coupling is somewhat confounded by the different timescales of saccades and hand movements. Saccades are extremely fast and are completed in a fraction of the time required for upper limb motion. This minimizes their temporal overlap in coordinated tasks and limits the time available to integrate potential interference. Describing eye–hand interactions in a purely motoric framework is also difficult because the hand's actions often rely on visual perception and visuomotor transformations. Despite these paradigmatic caveats, it is apparent that oculomanual interactions emerge predictively due to overlapping motor planning resources (Kattoulas et al. 2008; Lünenburger et al. 2000; Snyder et al. 2002; van Donkelaar 1997, 2004). To our knowledge, oculomanual interference arising from motor overflow has not been clearly demonstrated. Although *irradiation* between eye and hand movements is not possible because the eyes and hands lack homologous muscle groups, an important question is whether the eyes and hands are susceptible to *associated* interference from the recruitment of common neural structures (i.e., motor overflow).

The brain structures responsible for ocular and manual motor control are predominantly specialized and separate (Graziano et al. 2002; Kalaska et al. 1997; Sparks 2002). While this regional motor specialization is evident in the activation of the frontal eye field and the primary motor cortex (Ferraina et al. 2002; Mushiake et al. 1996), it is incomplete at higher levels of the control hierarchy. Examples of brain regions that respond to multiple effectors are the premotor cortices, supplementary motor areas, supplementary eye fields, and posterior parietal cortices (Mushiake et al. 1996; Pesaran et al. 2010; Snyder et al. 2000; Levy et al. 2007). Compared to the primary motor areas, these secondary networks are associated with complex movement parameters like motor sequencing, learning patterns, and general functions of planning in both limb- and vision-centered reference systems (van Donkelaar et al. 2002).

The selective recruitment of these networks for reactive or predictive visual tracking is an exemplary case of how saccades are encoded differently depending on the behavioral context (Mort et al. 2003; Müri and Nyffeler 2008; Shelhamer and Joiner 2003). Predictive saccades require sensorimotor planning to model and implement a series of timed movement goals. Advanced temporal planning is not required for reactive saccades because they lack a predictable timing structure. This is a key factor in our study because reactive and predictive saccades recruit separate brain regions, and these regions might encode actions with varying levels of effector specificity and in different effector-centric coordinate systems. For this reason, we hypothesized that eye–hand interactions might also be different when reactive and predictive saccades are combined with a manual task.

In conjunction with these two types of saccades, our study assessed finger kinematics while participants executed periodic tabletop tapping. Saccading was performed in the horizontal axis while the tapping motion was vertical, and we hypothesized that the finger trajectory would deviate laterally in the direction of a concomitant saccade. Another noteworthy property of oculomanual control is that saccades are predominantly encoded in the hemisphere contraversive to their horizontal direction, whereas motor neurons projecting to the limbs arise primarily from the hemisphere contralateral to the associated limb. It is therefore reasonable to hypothesize that saccades in either direction might interact differently with the movements of either hand. For this reason, and for controlling potential handedness effects, our experiments included unimanual responses with both hands.

A prevailing model of discrete short-interval sensorimotor timekeeping posits that one timing network is entrained to externally specified intervals while timing output generalizes to motor and perceptual networks from a single reference signal (*c.f.* Hazeltine et al. 1997). Motor planning is necessary for timing responses with external pacing cues and we hypothesized that synchronous saccades and finger movements would share these planning resources and increase the likelihood of eye–hand crosstalk in motor planning (Experiment 1). Finger tapping was repeated in Experiment 2, but we used aperiodic visual stimuli to cue reactive saccades. In contrast to the first experiment, Experiment 2 was based on a dual-task design with independent goals for eye and hand movements. Research has shown that each goal in a dual task can be encoded separately in the brain (Charron and Koechlin 2010), that minimal temporal interference is observed when saccades and tapping are cued by different events (Sharikadze et al. 2009), and that predictive but not reactive saccades engage internal timing networks (Shelhamer and Joiner 2003). We reasoned that making reactive saccades in combination with periodic tapping would minimize common planning resources shared by both actions, thus enabling a dissociation of oculomanual interference that arises during motor planning and execution.

Our results demonstrated an eye-to-hand magnet effect wherein saccades attracted the finger trajectory in the direction of the eyes' motion. Interestingly, spatial interference affected both the left and right fingers when eye–hand responses were performed synchronously in Experiment 1, but we observed only weak oculomanual interference when saccades were directed to the hemifield of the tapping hand in Experiment 2.

Materials and methods

Participants and experimental apparatus

Nineteen healthy individuals were recruited from the local student body, consented to participate in the study, were naïve to the goals of the experiment, and received monetary compensation for their time. The following procedure was approved by the McMaster University Research Ethics Board. Participants sat comfortably at a table, kept the palms of their hands flat on the table with their index fingers pointing forward, and faced a computer display 60 cm away. Visual stimuli were presented on a 17-inch cathode ray tube monitor (640 × 480 @ 125 Hz) connected to a Windows XP PC workstation, and auditory stimuli were played through desktop speakers. The protocol was programmed and presented using the Experiment Builder software bundled with the Eye-Link II head-mounted eye tracker (SR Research Ltd., Osgoode, Ontario). The eye tracking system sampled gaze position at 250 Hz. Three-dimensional finger trajectories were recorded at 250 Hz using 14 mm reflective markers attached to the fingertip, and a ten-camera (MX-T040) motion capture system (Vicon Motion Systems, Lake Forest, CA). Computer-generated TTL pulses and a recording of the auditory pacing tones synchronized the two data streams via analog inputs to the Vicon system.

In both experiments, we presented trials in a pseudorandomized order, repeating each condition once per block, and repeating blocks to derive within-subject performance measures. The two experimental protocols are summarized in Fig. 1 by an illustration of the time series of stimulus and response events.

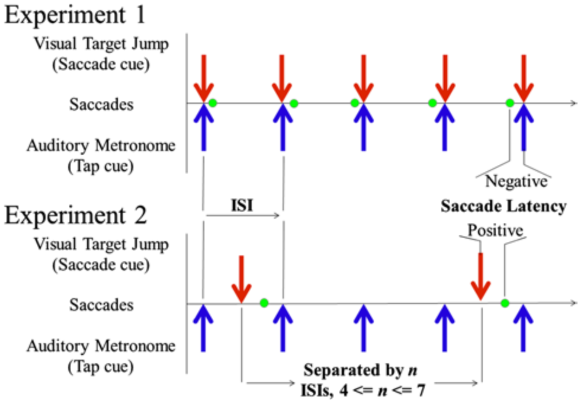

Fig. 1 Experimental protocol: typical series of stimulus and response events for Experiments 1 and 2. *Blue arrows* indicate the onset of auditory metronome cues. The separation between arrows represents the inter-stimulus interval (ISI), which was varied between 500, 750, and 1,000 ms. As shown in the figure, the tapping portion of Experiments 1 and 2 tasks was identical. The timing of visual target jumps is represented by the red arrows, each of which cues a saccade that is represented as a *green dot*. Although it is not discernible from the figure, successive saccades in both experiments are made in alternating directions between the two target locations. In Experiment 1, each visual target jump is synchronized with a metronome beep and tap. Over the first few intervals, participants synchronize their saccades to the metronome stimulus, resulting in reactive saccades that quickly transition to predictive saccades characterized by negative response latencies. In Experiment 2, the visual target jumps are at irregular times, and without a periodic timekeeping goal, the saccades are reactive. These reactive saccades are characterized by positive response latencies. Since the timing of visual target jumps in Experiment 2 was adjusted for the expected reaction time (~200 ms), saccades in both experiments occurred at approximately the same relative time in the tap-to-tap cycle

Behavioral task—Experiment 1

Participants ($N = 10$) performed unimanual finger tapping in synchrony with horizontal saccades. In separate trials, unimanual finger tapping was executed with the left or right index finger in time with auditory metronomic pacing tones (50 ms duration, 1 kHz pitch sinus wave, 5 ms volume envelope at onset). Participants also made alternating leftward and rightward saccades to track periodic visual stimuli on the display screen, in time with every tap. This saccade target (5 mm diameter, red in color) jumped between two locations separated by 20° of visual angle (±10° with respect to subject's centered gaze). The timing of visual pacing was synchronized with auditory tones, and in separate trials, we varied the pacing rate between fast (500 ms), medium (750 ms), and slow (1,000 ms) inter-stimulus intervals (ISI). Each trial consisted of a series of 26 intervals. We also included a control condition wherein finger tapping was repeated with the auditory metronome while participants fixated gaze on a stationary target centered on the display screen. Tapping in this control condition was included to establish the lateral deviation of finger trajectories without accompanying saccades. In total, twelve trial conditions (3 × ISI, 2 × HAND, 2 × EYE-TASK) were presented twice over two blocks of trials. Since timed saccades are generally predictive of their temporal goal, we anticipated that most saccades would occur while the finger was off the table immediately prior to each tap.

Behavioral task—Experiment 2

Finger tapping and saccading were cued separately so their execution occurred at the same instant, but in response to different events. In replication of the manual component of Experiment 1, we instructed participants ($N = 9$) to synchronize only finger tapping with the auditory pacing metronome. Unimanual finger tapping was again executed using either the left or right index finger, at 500, 750, and 1,000 ms ISIs. While the tapping task was repeated, the saccading cues were modified to produce reactive—not predictive, nor rhythmic—visual tracking. In Experiment 2, we cued reactive saccades with alternating visual targets that jumped at unpredictable and pseudorandomized times, once every 4th–7th tapping interval. The precise timing of these target jumps relative to the auditory tapping cues was structured so that saccades would likely occur between taps. In contrast to the negative latency of predictive saccades in Experiment 1, here we expected that saccade latency would be positive due to normal reaction time. The illustration in Fig. 1 contrasts the timing structure of auditory and visual stimuli, saccades, and taps between experiments.

Because of the unpredictable timing of these visual stimuli, reactive saccades do not require a discrete and predictable temporal goal specified in advance by motor planning networks. Unlike Experiment 1, in Experiment 2, there is no aspect of the task that encourages an overlapping representation of saccades and tapping movements by planning-related control networks.

Each trial was terminated when 10 saccades had been executed in each direction, which was a variable duration since saccades were spaced at pseudorandom intervals (i.e., coinciding with every 4th–7th tapping movement). This totaled in six task conditions (3 × ISI, 2 × HAND) that were all repeated over six blocks of trials.

Data analysis

The gaze and finger trajectory data were imported into MATLAB® (Mathworks Inc., Natick, MA), temporally aligned, and analyzed using scripts developed in our laboratory. We smoothed the finger trajectory data with a 5-sample equally weighted moving average filter (bidirectional), with successive windows advanced by one sample. The coordinate system defined positive displacement in the rightward direction of the horizontal axis and upward on the vertical axis. Each tapping event was detected by examining the vertical component of the finger trajectory to determine the moment at which the fingertip speed fell below 15 mm/s after its peak downward acceleration. The times when the finger was in mid-flight were determined by finding peak upward acceleration, then looking recursively for the first preceding sample where the speed was below 15 mm/s.

We used a single measure to quantify spatial interference in the finger trajectory, which was the series of values describing the horizontal fingertip translation between successive taps. To compute this measure, we recorded the Euclidean coordinates where each tap contacted the table and took the difference between the landing positions of successive taps to determine the tap-to-tap fingertip translation. Examining motion in the horizontal axis was our variable of interest because it is parallel to the primary axis of the saccades. Consequently, we expected that any aspect of saccadic planning or execution that was encoded with directional specificity would cause the finger trajectory to deviate in the horizontal axis.

In Experiment 1, we analyzed the series of horizontal finger displacements using the unbiased estimate of lag-1 autocovariance between successive finger taps. Since alternating left–right saccades were executed in-phase with successive taps, this first analysis examined whether a similar left–right trend was expressed in the landing position of successive finger taps. Significantly, negative autocovariance values would indicate that the translation vector between two taps was generally directed opposite to the preceding tap. The magnitude of the autocovariance function is then proportional to the size of alternating back and forth displacements. As illustrated in Fig. 1, the saccading in Experiment 2 was not executed synchronously with each tap. For this reason, the lag-1 autocovariance measure would not objectively characterize tapping behavior in Experiment 2. While it would be possible to assemble a series of tap-to-tap displacement values extracted from the responses that did have an accompanying saccade, the following analyses better characterize the statistics of individual responses.

The autocovariance measure in Experiment 1 is our first analysis, and thus helps to determine the proper conditioning of the data for the subsequent steps of analyses for both experiments. To explain this logic, consider that our hypotheses predicted that the horizontal component of the finger trajectory would be biased in the direction of the accompanying saccade. It is later discussed in the results section of our manuscript that we confirmed lag-1 autocovariance returned a significantly negative value. This implies that when making saccades—but not when maintaining fixation—the finger is indeed entrained to a left–right alternating pattern that can be observed in the landing positions of successive taps. However, an implicit caveat is that the autocovariance function is unable to determine whether the back and forth trend in fingertip positions is positively correlated with the direction of the accompanying saccade. The autocovariance analysis lends support for a tap-to-tap alternating trend in the series of fingertip displacements between taps. In other words, determining whether this displacement is directionally congruent with saccades requires analyses of our data at the level of individual taps. The next analyses discussed below must account for the direction of finger displacement as it relates to the direction of the accompanying saccade.

To determine whether mean displacement was significant in the direction of the accompanying saccade, we derived the SACCADE DIRECTION factor by grouping the lateral fingertip deviation from taps associated only with saccades in one direction or the other. In both experiments, displacement values associated with each tap were pooled together for calculating the mean with respect to the factors of HAND (2 levels: left and right), PACING RATE (3 levels: 500, 750, and 1,000 ms), and SACCADE DIRECTION (2 levels: leftward and rightward). For comparisons of data acquired within each experiment, we used repeated measures analysis of variance (ANOVA) to identify significant main effects and interactions involving the relevant factors.

We must also consider that the autocovariance analysis in Experiment 1 indicated the fingertip moved in opposite directions between successive taps. To test the hypothesis that fingertip displacement depends on the direction of the accompanying saccade, we must invert the sign of the displacement values for only the taps corresponding to saccades in one direction. Since our motion capture system defined positive horizontal motion toward the participants' right, we inverted the sign of the displacement data collected when accompanying saccades were directed toward the left. Consequently, when positive displacement values are observed with either the *left* or *right* level of the SACCADE DIRECTION factor, the interpretation is that positive values represent fingertip displacement in the same horizontal direction as the accompanying saccade, and negative values suggest the finger moved opposite to the saccade's direction. ANOVA significance was set to a threshold of $p < 0.05$, and significant main effects were corrected for multiple comparisons using Bonferroni's criterion. We also performed additional post hoc one-sample *t* tests on the null hypothesis that any of the observed motion in the fingertip was significant in magnitude whatsoever. Here, one-sample *t* tests against a test value of 0 mm determined whether fingertip translation was different from the null hypothesis that no horizontal fingertip displacement occurred.

To analyze data related to our hypotheses, we must constrain our analysis to taps that are associated with specific instances of saccading behavior. While these constraints were applied identically to the repeated measures analysis of data from both experiments, the following criteria were irrelevant for the autocovariance analysis as it required an uncut series of finger tap responses. Firstly, the most important factor to control for is that overflow-related effects from saccades occurred within the time window when they could theoretically interfere with finger-related motor commands. For this reason, we only analyzed tapping movements where the accompanying saccade was initiated and terminated while the finger was in motion, that is, at no point was the finger in contact with the table during the saccade. These inclusion criteria were important because any oculomanual interference that might occur due to overflow naturally requires that there are in fact motor commands descending to the finger that may be affected by the saccadic command. To implement these criteria, we used gaze data to determine when a saccade occurred: onset threshold >30°/s and 5,000°/s^2, offset <30°/s.

It was also important that our analyses avoided oculomanual interference from eye movements unrelated to the primary saccading task. When saccades considerably overshoot a visual target, the oculomotor system performs *secondary corrective saccades* immediately following and in the direction opposite to the primary saccade. Naturally, as our methods intend only to model the interference effects related to the execution of reactive saccades, and planning and execution of voluntary timed saccades, any interference from secondary movements must be avoided. Accordingly, we included the fingertip displacement associated with a given tap when no secondary saccades occurred before the finger landed on the table. Lastly, displacement data were not included from taps when the accompanying saccade amplitude was more than ±5° in error from the target. This last exclusionary criterion was instated because typical saccading behavior falls within this range, and larger errors may indicate the saccade was initiated toward some distracting stimuli.

We also analyzed our data for statistics that were descriptive of general ocular and manual behavior. Our analyses are all contingent on the accurate classification of saccades in Experiment 1 as predictive and timed, which is different than the expected reactive behavior in Experiment 2. Every saccade was analyzed for its temporal asynchrony with respect to the timing of the associated visual target jump. Asynchrony was measured in milliseconds and was negative when a saccade's onset preceded the target jump and positive when saccade onset followed the target jump. Moreover, we quantified subjects' general proficiency for tapping in all conditions and in both experiments by measuring the mean and variance of inter-response intervals (IRI).

Averaged trajectories of the fingertip paths plotted in Fig. 2 were computed by extracting fingertip position time series when the fingertip was not in contact with the table. Each in-flight trajectory was computed from each tap made by each subject, time-normalized by upsampling the number of points in each tap's trajectory to the length of the tap with the most data points. From these data, we computed a grand average 2D trajectory as well as the confidence interval by deriving the standard error of the mean—the sample standard deviation divided by the root of the number of samples. Since the mean and confidence were computed from the pooled data from within and between subjects, the error range is representative of cumulative variability in the expression of the interference effect at both levels.

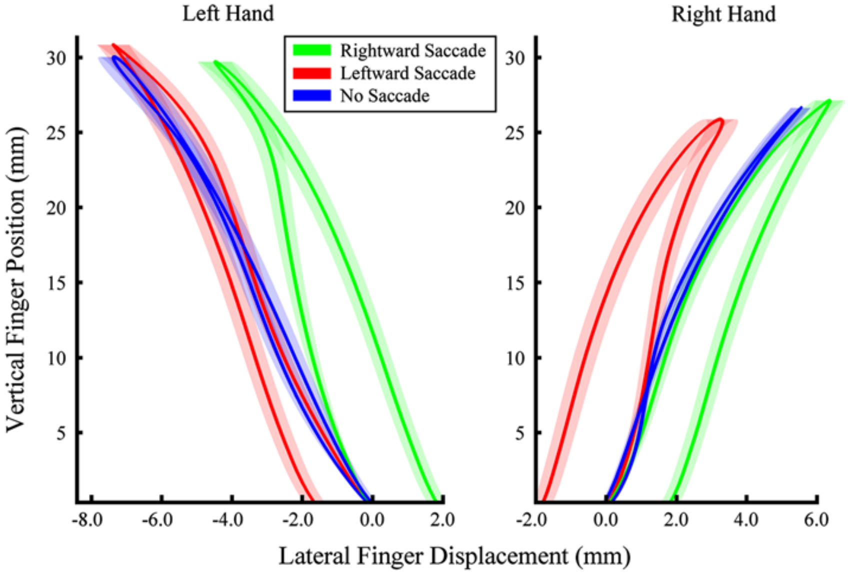

Fig. 2 Finger trajectories from Experiment 1: averaged finger trajectories from 500 ms ISI trials in Experiment 1 when subjects saccaded rightward (*green*), leftward (*red*), or maintained fixation (*blue*). *Left hand* responses are plotted in the *left panel*, and *right hand* responses in the *right panel.* The fingertip paths were derived from the time-normalized trajectory of all taps grouped over all participants (see "Materials and methods"). Importantly, the shaded area represents the standard error in the horizontal dimension computed across individual taps for all subjects. The start positions were normalized to lift from the origin (0 mm) on the *horizontal axis* to enable comparison across subjects. Negative values correspond to leftward fingertip displacement. From this illustration, it is evident that in control tapping (*blue*) when no saccade is made, the finger returns to the *horizontal axis* (lands on the table) in nearly the same place from where it was lifted. Saccading while tapping (*red* and *green*) caused the finger to land at some horizontal distance away from where it began the upward phase, in the direction of the concomitant saccade

Results

Saccading—temporal analysis

Our two experiments differed in the type of saccading behavior associated with each tracking paradigm, and so we must first examine whether subjects performed saccades as we anticipated. In Experiment 1, visual stimuli alternated periodically requiring that short-interval timekeeping was engaged to reproduce predictive saccades at accurate times. We computed the mean latency of saccades relative to the synchronized audiovisual stimuli in Experiment 1 ($M = -80.87$ ms, SD = 74.23). From this negative latency, or any latency values <80 ms—,that is, the shortest time required to evoke a saccade in response to an external visual cue (Wenban-Smith and Findlay 1991)—one can infer that the saccades must have been encoded by predictive motor plans.

In Experiment 2, saccade timing was unpredictable and each saccade temporally followed the presentation of the visual cues. We expected that saccading behavior would be reactive and initiated after the visual target jumped. The saccade latency data ($M = 211.02$ ms, SD = 39.82) confirmed that saccades were reactive in Experiment 2.

Finger tapping—temporal analysis

Our protocol was constructed so that the only change between Experiment 1 and 2 was the method we used to cue saccades. To confirm that only the saccading task changed, we must demonstrate that subjects performed the tapping component of the tasks similarly in both experiments. To quantify tapping accuracy, we measured the mean inter-response interval (IRI) and mean within-trial IRI variance (varIRI). From these data, we performed repeated measures ANOVA with factors HAND × PACING RATE. Only the main effect of PACING RATE reached significance for Experiment 1 ($F(2,18) = 16{,}154.99$, $p < 0.001$) and Experiment 2 ($F(2,16) = 196{,}704.12$, $p < 0.001$). We also found a significant main effect for PACING RATE in varIRI for Experiment 1 ($F(2,18) = 14.08$, $p < 0.001$) and Experiment 2 ($F(2,16) = 13.31$, $p < 0.001$).

We then used independent samples t tests to determine whether the tapping behavior was similar between experiments, at each level of the PACING RATE factor. At 500 ms pacing, IRI ($M_{\text{Exp1}} = 500.67$ ms, SD = 8.22; $M_{\text{Exp2}} = 504.72$ ms, SD = 1.41) was not significantly different between experiments. We did observe a significant between-experiment difference in IRI at 750 ms pacing

($t(17) = -6.11$, $p < 0.001$; $M_{\text{Exp1}} = 746.65$ ms, SD = 3.75; $M_{\text{Exp2}} = 755.31$ ms, SD = 2.09), and also at 1,000 ms pacing ($t(17) = -2.69$, $p = 0.016$; $M_{\text{Exp1}} = 998.10$ ms, SD = 9.18; $M_{\text{Exp2}} = 1{,}006.53$ ms, SD = 2.08). There were no significant differences in varIRI between experiments. While these statistics show that subjects produced tapping intervals with a slightly longer duration in Experiment 2, the difference is very small (~8 ms or 1 % of the interval duration) and unlikely to indicate that any pertinent differences in the tapping strategy between experiments to confound our primary investigation of spatial interference.

Inclusion/exclusion of individual finger taps

We recorded the number of finger taps from each trial used in deriving the mean displacement values for each subject and in each condition. In Experiment 1, on average, 27.98 taps (SD = 9.00) were used to compute within-condition mean displacement of the fingertip position from multiple trials. Based on the total number of cues presented (26 per trial multiplied by two trial blocks, 52 total), this means that approximately 53.8 % of taps were paired with saccades that were acceptable for inclusion in our analyses. In Experiment 2, on average, 46.11 taps (SD = 11.13) were used to calculate the mean displacement values in Experiment 2 analyses, which is approximately equivalent to 88.7 % of recorded taps.

The difference in these numbers between experiments can be explained by the methods of cueing saccades. The high percentage of taps included for Experiment 2 analysis is likely because we optimized the presentation schedule of the visual stimuli. Reactive saccade cues were structured so that saccades would likely occur when the finger was in mid-flight, and we accounted for typical reaction time in our calculations. In Experiment 1, we cannot explicitly optimize the timing of saccades, as they are instead initiated as a function of each participant's ability to make accurately timed eye movements. Moreover, there is cycle-to-cycle variability in any motor timekeeping task. Because we cannot otherwise control the task to account for this normal range of responses, it is a natural consequence that fewer responses occur in the specific time window that is pertinent in which to examine spatial interference according to our current protocol.

Experiment 1: Periodic saccading and tapping

When saccades and taps were planned and executed together in the synchronous timing task, the finger's path was attracted in the direction of the accompanying saccade. To help visualize this interference effect, Fig. 2 illustrates the data for a HAND × SACCADE DIRECTION interaction using averaged finger trajectories from the 500 ms pacing condition, wherein we observed the most robust interference. The following statistics demonstrate the strength of spatial interference was equivocal when saccading in either direction, when tapping with the left or right hand, and that interference was strongest for faster pacing intervals.

An ANOVA of lag-1 autocovariance in series of fingertip translations revealed the finger was entrained to an alternating tap-left then tap-right trend. This pattern was significantly stronger ($F(1,9) = 10.83$, $p = 0.009$) when saccading ($M = -5.67$ mm^2, SD = 4.56) than in control tapping ($M = -1.07$ mm^2, SD = 0.69). This was our first line of evidence that periodic saccades interfered with finger trajectory formation.

Next, repeated measures ANOVA determined whether horizontal deviations between taps were affected by the HAND, SACCADE DIRECTION, and PACING RATE factors. In all conditions, the fingertip displacement is reported in the context that positive values signify displacement in the direction of the accompanying saccade. A significant main effect of PACING RATE ($F(2,18) = 6.63$, $p = 0.007$) demonstrated that spatial interference scaled such that saccading caused the largest interference effects at faster pacing intervals. This effect is illustrated in Fig. 3 and presented with additional statistics in Table 1. The data showed no significant main effects or interactions involving the SACCADE DIRECTION or HAND, confirming the strength of spatial interference was similar when saccading in either direction and when tapping with either the left or right hand.

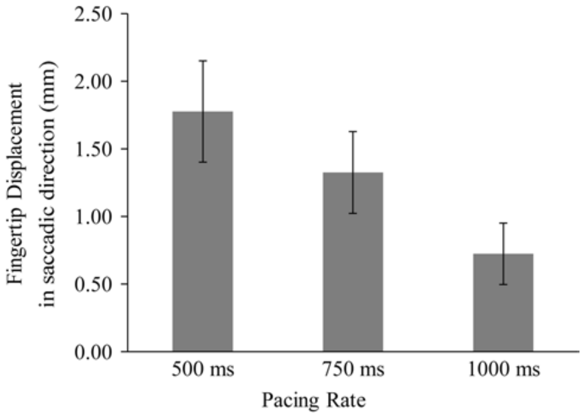

Fig. 3 Effect of pacing rate on horizontal fingertip displacements. The effect of PACING RATE is shown with error bars representing the standard error of the mean. At the faster 500 ms pacing rate (interstimulus intervals or ISI), the fingertip is more strongly attracted in the direction of the accompanying saccade, as compared with the slower 750 and 1,000 ms ISI. In addition to the data plotted in this figure, see Table 1 for the results of one-sample *t* tests showing that fingertip displacement in the direction of the concurrent saccade was significantly different from zero at all levels of the PACING RATE factor

Table 1 Descriptive statistics and *t* test scores from fingertip displacement

Experiment	Responding hand	Saccade direction	ISI	M	SD	*p* value	One-sample *t* score versus 0	d.o.f.
1	Both[a]	Both[a]	500	1.46	0.72	<0.001	6.440	9
			750	1.28	1.42	0.019	2.858	9
			1,000	1.09	1.13	0.014	3.037	9
2	Left	Left	All[a]	0.40	0.37	0.012	3.259	8
		Right		0.08	0.53	0.665	0.483	8
	Right	Left		0.08	0.25	0.337	1.022	8
		Right		0.50	0.25	<0.001	6.053	8

[a] Marginal means calculated after collapsing across the associated factor

While the interaction between the SACCADE DIRECTION × HAND factors did not reach significance, below we determine that the analogous interaction is of interest in characterizing behavior in Experiment 2. Consequently, Fig. 4a plots this interaction for Experiment 1, with which an intuitive visual contrast can be made to the analogous interaction in Experiment 2 results, Fig. 4b.

Our analyses have compared fingertip displacement between different experimental conditions, but we have not yet established whether we observed significant magnitude of displacement—indicative of *significant* spatial interference in the fingertip—in any direction. We must test the null hypothesis that no significant displacement occurred whatsoever, which is a separate task than using ANOVA to demonstrate how interference changed as a function comparing data within our nested model. As is standard practice with factors that do not meet statistical significance, we collapsed across the HAND and SACCADE DIRECTION factors and computed within-subject means. One-sample *t* tests against a test value of zero displacement indicated that at all remaining levels of PACING RATE, significant horizontal displacement of the finger did in fact occur, rejecting the null hypothesis that no significant displacement was observed (see Table 1). Familywise corrections for three comparisons maintain these results are significant at an experiment-wide error rate of $p < 0.0559$. In summary, we observed a significant spatial interference effect where the fingertip was attracted in the direction of accompanying horizontal saccades. Further, we determined that eye-to-hand spatial interference was significant at all pacing rates, and that the interference was significantly stronger at faster pacing intervals.

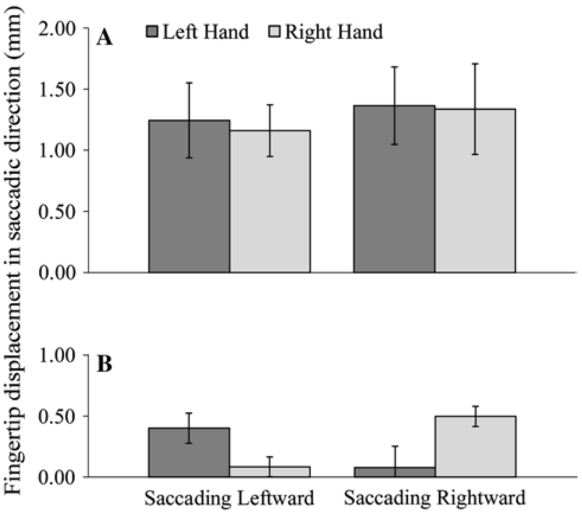

Fig. 4 SACCADE DIRECTION × HAND interaction plot, Experiments 1 (**panel a**) & 2 (**panel b**). This interaction reached significance for Experiment 2 but not for Experiment 1. An illustration is useful to clarify the importance of the one-sample *t* tests (Table 1). As it is easy to see in this **panel b**, some instances of saccading in Experiment 2 failed to cause fingertip deviation that was significantly different from zero (Table 1, *bottom*). This an important contrast to make against Experiment 1, where the fingertip was always significantly attracted in the direction of the accompanying saccade (**panel a**, see also Fig. 3 and Table 1)

Experiment 2: Periodic tapping and reactive saccades

In contrast to the above results, eye–hand interactions in this experiment were different and the finger exhibited weaker attractions to reactive saccades. Similar to the analyses used in Experiment 1, we tested for effects or interactions involving HAND, PACING RATE, and SACCADING DIRECTION factors in the mean displacement of the fingertip in the direction of the accompanying saccade. Overall, no significant effects or interactions involving these factors were observed at $\alpha = 0.05$. In Experiment 2, the test for an effect of PACING RATE did not reach significance ($F(2,16) = 1.442$, $p = 0.266$). Consequently, in the case of Experiment 2, there is no significant scaling of the extent of interference at different inter-stimulus intervals of tapping.

It is also important to discuss the significant interaction between SACCADE DIRECTION and HAND in Experiment 2 ($F(1,8) = 5.820$, $p < 0.05$). In a visual inspection of the decomposed two-by-two interaction plot (Fig. 4b), we noted that the interference in Experiment 2 data tended to be stronger when the responding hand was that in the hemispace in which the accompanying saccade was directed.

As discussed in the results section for Experiment 1, the ANOVA does not indicate whether the measured displacement was significantly different from zero, in any direction. Instead, one-sample t tests are used again in Experiment 2 to make this inference. Shown in Table 1, the only significant finger deviations observed in Experiment 2 occurred when saccading to the right caused the right finger to move rightward and saccading to the left caused the left finger to move leftward (see Table 1). These results remained significant after correcting for the familywise error rate across the four comparisons in Experiment 2 (i.e., corrected p's < 0.0125). The null hypothesis was not rejected and we cannot provide statistical support to significantly separate 0 mm of interference from the distribution of responses when saccading to the right and tapping with the left hand, or saccading to the left and tapping with the right hand.

Discussion

In the present study, we questioned whether a novel oculomanual paradigm could dissociate motor interference arising during motor planning and execution. The degree to which the brain recruited overlapping networks for controlling finger and eye movements was manipulated by the method of cueing saccades relative to a periodic finger tapping task. Our approach was motivated by evidence that timed, but not reactive saccades imposed demands on motor timekeeping networks (Joiner and Shelhamer 2006; Shelhamer and Joiner 2003). Moreover, timed saccades are voluntary and in comparison with reactive saccades involve different neural implementation (Mort et al. 2003; Müri and Nyffeler 2008).

Finger kinematics from both experiments demonstrated significant spatial interference. This was important for validating our task as a means to evoke unintentional eye-to-hand coupling. Since spatial interference in the finger trajectory was observed as lateral deviations toward the direction of a concurrent saccade, this coherence is perhaps best labeled as an eye-to-hand magnet effect due to its similarity to the interference observed in bimanual interactions (Franz et al. 1991; Franz and Ramachandran 1998). Another noteworthy characteristic of our timekeeping task is that visuomotor transformations were not required for tapping one's finger and thereby limited our focus to motoric interactions.

In order to attribute changes in eye–hand coupling dynamics to the modulation and effector-specific recruitment of motor planning, two points must be considered. First, varying the ISI of pacing cues in Experiment 1 led to a significant effect in scaling the interference strength. By changing the time between successive responses, we are potentially manipulating the time available to plan each movement. If we may draw conservative parallels with the bimanual control literature, it is noteworthy that Heuer et al. (1998a, b), albeit in a discrete and goal-directed task, also demonstrated a period-dependent modulation of bimanual coupling. In both our experiment and those of Heuer et al., an increase in preparation time for simultaneous actions led to a reduction in interference. Determining whether the same neural mechanisms are responsible for these similar effects is beyond the scope of this study, but would be an interesting query for future investigations. Nonetheless, in our task, the temporal goal was the only variable constraining the coordination of eye and hand movements. Varying the timing of this temporal goal directly modulated the spatial interactions when joint motor planning was a possibility in Experiment 1. However, whether the modulation of interference manifests as a function of limiting the time to decouple two jointly planned actions is not certain. Determining this would require other experimental conditions to control for motor planning time with various types of voluntary saccades, perhaps using delayed movements in a memory-guided oculomotor task.

We can, however, infer that the scaling of spatial interference with changing ISI in Experiment 1 is related to motor planning in some way. Potential confounds are perhaps that ISI causes interference scaling by passive effects, such as biomechanical constraints that change with the speed of finger movements, or by modulating the control networks in ways unrelated to motor planning. For example, one may argue that changing the ISI leads to changing the movement speed. By extension, faster movements are perhaps less controlled (*c.f.* Elliott et al. 2001) and could be influenced more strongly by a similar source of interference. However, should this have been the case, it would also be expected that finger trajectory interference should be modulated by pacing rate in both experiments, which it was not. Moreover, we provided data that tapping was otherwise performed identically in both experiments. The tapping task was purposefully kept identical between the two experiments and the inter-response interval (IRI) data reasonably equated the timing accuracy of finger tapping at all levels of ISI in both experiments. Trajectory formation of finger movements in both experiments should thus be comparable as the kinematic profile is known to emerge as a function of the accuracy of the response with respect to the timekeeping goal (Balasubramaniam et al. 2004; Torre and Balasubramaniam 2009). This provides reasonable support for inferring that the scaling of interference with changing pacing rate is an effect related to the interaction of the timekeeping goal with motor planning-dependent interference processes.

The next step is to characterize the interference that emerged as a function of online motor overflow. In the first experiment, saccades in either direction caused significant deviations in the finger trajectory when tapping with either hand. This contrasted results from the second experiment where saccades only attracted the finger of the responding hand located in the hemifield toward which saccades were directed. These results demonstrated that associative motor overflow accounted for an interference pattern that was weaker and lateralized.

The difference in coupling patterns is particularly interesting when one considers the neurophysiology of the related motor areas. Each hand is controlled primarily by the contralateral motor cortex and saccades by the oculomotor networks in the hemisphere contraversive to their horizontal direction. The lateralized interference effects we observed in Experiment 2 suggested that reactive saccades influenced only the motor coding of finger movements controlled by the same hemisphere. Conversely, in Experiment 1, the bilateral spatial interference was characterized by a widespread divergence of saccadic coding to manual motor networks in both hemispheres. This is an intriguing result considering the temporal goal that synchronized the execution of saccades and taps in Experiment 1 did not impose any spatial constraints, yet we observed different spatial interference patterns between experiments.

One possible explanation for the generalized planning interference is the observation that bimanual goals encoded in motor planning can induce widespread modulation of cortical motor interconnectivity, often in a generalized manner, and with distributed effects (Bestmann et al. 2008; Grefkes et al. 2008; Tallet et al. 2010). Our results might suggest that oculomanual planning is accomplished through a more generalized set of brain networks that are together less specifically associated with the control of the eyes *or* the limbs. In addition to demonstrating the generalization of motor planning-related interference to the trajectory of either hand, our results also suggest a broad spatiotemporal representation at a higher level of goal specification. A noteworthy finding in our experiments is that we observed spatial interference when the common goal for eye and hand movements was specified in the temporal domain. In this case of generalized recruitment, the brain areas related to planning the temporal goal also related to the parameterization of spatial variables in the same task. It is also possible that the brain areas related to planning spatial and temporal parameters are separate, but instead that their recruitment occurs in a generalized fashion regardless whether the coordinated variable is specified in the temporal or spatial domain.

Future investigations may seek to explain how planning modulates the state of oculomanual networks. For example, we cannot infer whether the bilateral form of coupling was due to co-parameterization of both actions in a single motor planning stream that later diverges, or instead whether planning-related networks exerted top–down modulation on the functional state of interhemispheric cross-effector networks. These are two distinct cases of a theoretical model of planning-related crosstalk. The former would mean coupled parameters were programmed *then* propagated via diverging cortical pathways to effector-specific networks (e.g., Akam and Kullmann 2010), while the latter would indicate the functional state of hardwired brain networks was modulated by top–down control. The latter of these has already been described in bimanual coordination as the transcallosal facilitation and transfer of inhibition models (c.f. Hoy et al. 2004). Extending these models to oculomanual coordination would be an interesting avenue for future research.

It would also be prudent to consider the influence of attentional shifts. According to the premotor theory of attention, motor actions, and covert attentional shifts are closely related (Rizzolatti et al. 1987); however, we suggest an explanation based only on attentional shifts is unlikely. We make this claim because ocular tracking tasks similar to those used in our study have shown that attention seems to be simultaneously co-allocated to multiple target areas as opposed to periodically alternating (Baldauf and Deubel 2008). This could be construed as evidence that our study implicitly dissociated the influence of attentional shifts from the effects of executing saccades.

One could also raise the possibility of somatosensory feedback processes contributing to the eye–hand interference patterns, as in the case of a well-known model of bimanual coordination (Mechsner et al. 2001). However, the metrics of movements in both experiments were similar, and one could extend this to inferring the feedback is also similar, thus if feedback plays a role it would be in the way it is used. Further, a potential caveat in our design is that inadvertent head movements might have contributed to the interference effect. While we did not measure head movements, in primate research, it is only common for saccades *greater than* 20° in visual angle to have associated head movements (Tomlinson and Bahra 1986). Saccades in our experiments were cued to exactly 20° in visual angle, and we again draw attention to the fact that these metrics were consistent between experiments. Consequently, any factors that might validly explain the interference must also demonstrate a similar change in their presentation between experiments to explain the observed modulation in the strength and specificity of the spatial interference.

In sum, the hands and eyes have very different physical structure, musculature, inertial properties, and neural correlates of sensorimotor control. By designing this novel oculomanual control paradigm, we have demonstrated that planning and execution are separate levels in the sensorimotor control hierarchy from where the independent sources of eye–hand interference can emerge. Our study has provided well-formed evidence that oculomanual control is mediated by distributed brain networks, and that the cause of interference between eye and hand movements depends on the overlap in networks recruited for the task at hand—and at eye. The susceptibility of oculomanual actions to spatial interference in planning was apparent only when we introduced a cooperative temporal goal and varied its pacing rate. Additionally, associated movements of the finger arising from saccade-related motor overflow also led to significant spatial interference and were dissociated from the crosstalk in motor planning. We speculate that further investigations of this eye-to-hand magnet effect with neuroimaging at macroscopic and microscopic scales, or that introduce other novel variations of our current task could provide unique insights into the neural mechanisms that mediate the task-dependent flow of oculomanual coding throughout the human brain.

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Chapter 5

Controlling for attention-related effects and visuomotor rotations in the eye-to-hand magnet effect

5.1 Citation & Author Contributions

This project was completed in full capacity by the primary author BA, and contributed to in a supervisory and senior role by JL.

Richardson BA, & Lyons J, (in prep, July 2013) Controlling for attention-related effects and spatial topological rotations in the eye-to-hand magnet effect.

5.2 Abstract

In a recent series of two experiments (Richardson, Cluff, Lyons, & Balasubramaniam, 2013), we reported results from a novel eye-hand coordination task that distinguished between two modes of coupling. Saccades caused slightly different patterns of spatially congruent attractions in the finger trajectory as a function of predictive or reactive tracking. In part, the current work extends this to determine whether interference in either of these cases resides completely in a motoric framework. The alternative sources from which we must dissociate coupling effects are the spatially-coupled covert shifts in the focus of attention. Accordingly, our current study is in part conducted to account for the possibility that shifts in the spatial allocation of attention can evoke an independent and separable interference with the coding of concomitant hand actions. Herein we also test whether coupling from vertical saccades sources a relevant form of interference. The inclusion of vertical tracking imparts, based on our previous results, a prediction that unlike horizontal *reactive* saccades, those made vertically will not show compatibility effects with a responding hand since their bilateral footprint in neural correlates is unlike the unilateral representation of horizontal saccades. Lastly, we include visuomotor rotations of the task to determine if the interference is reproducible using both parallel and perpendicular axes of primary motion for the respective saccadic and manual actions. The current results support the conclusion that shifts in attention are not alone adequate to drive the observed oculomanual interference effects, and that coupling consequent to vertical saccades is only evident in a hand-selective case of making downward reactive saccades. These results and those related to another partial visuomotor rotation of the task are interpreted and discussed toward revealing properties of overlapping representation at different levels of sensorimotor organization.

5.3 Introduction

It is no surprise that many sensorimotor processes are collectively involved in the production of meaningful actions and interactions within and with our peripersonal environment. The control of human movement is largely organized into functional subunits wherein specific sensory, motor, or psychophysical parameters of a task are correlated to distinct neural activity in distinct regions of the brain (Bassett & Bullmore, 2006). Exactly how specific regions are determined to exhibit a task-related sensorimotor or psychophysical process depends on the mode of investigation.

Whole-brain imaging studies can use fMRI to show that the posterior parietal cortex (PPC) is implicated in goal-direct actions such as saccadic eye movements and manual aiming to a visible target (Levy, Schluppeck, Heeger, & Glimcher, 2007). A general conclusion is that this area is involved in visuomotor integration for goal-direct actions. Investigations with electrophysiological and other low-level modalities further distinguish sets of neurons within the surrounding area that code for this visuomotor integration separately for the parametrization of saccades and reaches (Levy et al., 2007; Pesaran, Nelson, & Andersen, 2010). Sensorimotor processes in this area relate the coding of visual integration with respect to attention, planning, and intention (Snyder, Batista, & Andersen, 1997, 1998). While the coding for these variables spans a range of purposes, a common basis they share seems to be that their spatial context is specified in an eye-centric framework (Cohen & Andersen, 2002).

In regard to a visually-guided mode of coordinated tracking, the constituent eye and hand movements have very different physical plants with which to exert motion. For this reason the motor commands destined for the upper limb must be appropriately oriented and scaled for its respective contribution to the task while the saccadic eye movements to shift gaze to a congruent location must also be programmed and executed in parallel. A gaze-centric coordinate system in the encoded visuospatial networks of the PPC is convenient for mapping directly into the parametrization of saccades. Nonetheless, toward the formation of oculomotor commands the PPC's functions are not entirely specialized. Several other brain regions, such as the bilateral supplemental (SEF) and frontal eye fields (FEF) and subcortical structures like the superior colliculus are those which translate the visual information into appropriate response, thus comprising the oculomotor system (Pierrot-deseilligny, Milea, & Mu, 2004; Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998; Sparks, 2002).

The encoding process of manual actions must account for the different spatial frame of reference within which to locate targets execute actions. One region where the encoded actions are represented in limb-centric coordinates is the premotor cortex (PM). The PM receives and integrates information from a variety of regions, including the PPC, and is specialized for exerting modulations over the primary motor cortex (M1) and the spinal cord (Chouinard & Paus, 2006), not saccades. Even though the PM is predominantly associated with the independent and coordinated control of actions made with our upper and lower limbs (Carson & Kelso, 2004; Carson, 2005; Cincotta & Ziemann, 2008), it also exhibits coding representative of gaze position (Pesaran et al., 2010). The integration of gaze position is undoubtedly useful for updating manual actions to operate despite ongoing gaze changes. Since the retinotopic localization of a target changes during gaze shifts, but the target's physical location in the environment does not, eye-hand interactions in the PM seem to be conducive for mediating action in cases of coupling and decoupling (Donkelaar, Lee, & Drew, 2002).

The PPC and PM are just two examples of many regions that together from the entire set that contributes the internal representation of a given task. Depending on the behavioural task at hand, the type of information that needs to be shared and the degree to which it gets shared and integrated between upper limb and oculomotor control networks might vary considerably. Thus effective gating and, or selective routing of gaze- and limb-centric information within the stream of sensorimotor processes must control the flexible ways in which the two systems come together to mediate performance according to specific task demands (Akam & Kullmann, 2010; Bestmann et al., 2008; Kasess et al., 2008).

In a recent study (Richardson et al., 2013) we questioned whether cross-effector integration might be incompletely shunted in certain cases, resulting in the expression spatial interference between eye and hand actions. Using spatial topological constraints to manipulate the relative directions of concurrent finger tapping and saccadic tracking movements we observed two modes of coordination wherein saccades attracted the finger trajectory in congruent directions. In response to making reactive saccades in a horizontal plane while reproducing series of tabletop finger tapping responses in time with a periodic auditory metronome, the trajectory of the fingertip deviated toward the direction of a concurrent saccade, but only in accordance with their spatial compatibility. Reactive saccades caused only a discernible and correlated interference in the hand ipsiversive to their direction. In other words, rightward saccades caused the fingertip of the right hand to drift to the right, and the symmetric condition was true for leftward saccades causing a deviation to the left only in left hand responses.

When a fully synchronous timing goal was imposed on both the reciprocal saccading and finger tapping responses, the compatibility effect disappeared as there was no interaction reaching significance between the responding hand and the direction of a concurrent saccade. In the case of the voluntary predictive saccades that were entrained to reproduce temporal intervals in synchrony with the finger tapping, saccades made in either the left or right direction caused a significant interference in either hand.

The implications of contrasting different modes of interference consequent to these two variations of saccadic tracking is related to inferring the various levels in the control hierarchy wherein the coded actions of one effector interfere with those intended for another. Voluntary and involuntary saccades are correlated to functions of different brain regions (Mort, 2003), of which the former class of saccade is associated with predictive saccading at regular temporal intervals. Observing a different pattern of spatial interference consequent to engaging motor planning yields an implication that interference manifests differently depending on the task-set and internal representation.

In the current study we examined other variations of the tapping and saccading task to infer what other parameters of task representation might clarify the mechanisms of previously observed trends in the eye-to-hand interference effect, and perhaps predict new patterns under novel constraints. One question we addressed was if the observed fingertip interference was actually motoric in nature, and not a latent result of a related but underlying process. Our approach of parsing the sources of cross-effector interference is, in general terms, a reductionist approach by means of making series of dissociations to account for the whole set of observed trends in interference. By extension, to make a valid and defended claim that the observed effects are related to *motoric* processes, we must account for the covert shifts in the spatial allocation of attention that operate in advance of, and in parallel to saccades.

While it is possible to dissociate one's spatial allocation of attention from the current central gaze angle during visual fixation (Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007), the process of preparing a saccade is not similarly independent from shifting one's focus of attention (Hoffman & Subramaniam, 1995). The neural correlates of covert and overt shifts of attention are overlapping in some respects (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001), and dissociable in others (Juan et al., 2008; Neggers et al., 2007). Regardless of the degree of co-representation of saccades and attention, both are known to modulate the state of the motor system (Bédard, Thangavel, & Sanes, 2008; Johansen-Berg & Matthews, 2002). It is thus possible that simply shifting one's spatial focus of attention without a requisite saccade might cause tangible interference in the fingertip trajectory similar to that expected from saccades. To determine whether reciprocal covert shifts of attention might cause interference, we included complimentary variations of the task for contrasting the effects of making either reciprocal predictive saccades, or covertly tracking a reciprocally moving target in the peripheral space while maintaining visual fixation.

This attention-control task condition was implemented with timed reciprocal visual tracking tasks, either covert or overt, but not in combination with a reactive saccading protocol. An attention-control condition in reactive saccading would impart a change in paradigm that does away with the reciprocal tracking. In lieu of including such a manipulation to our task that would permit the investigation of attention separately in regards to reactive saccading, we've instead retained the reciprocal tracking nature and tested some predicted effects within other visuospatial rotations of the task. Further overview of the factors confounding the investigation of attention as it relates to reactive saccades is included in the discussion section.

In the eye-to-hand interference effect, the task is performed with perpendicular primary axes of saccadic and tapping motion. The observed interference was previously demonstrated (Richardson et al., 2013) such that horizontal saccades caused horizontal deviations in the finger trajectory. This perpendicular configuration can be maintained throughout a rotation of the task to examine whether vertical saccades cause a vertical interference effect on the fingertip trajectory when the tapping on a sagittal surface, such as with a palms-in orientation as one would use when grasping a box on either side between both hands.

Rotating the orientation of the task becomes an intriguing manipulation when one considers that the sensorimotor representation of vertical saccades is much different than horizontal saccades. For this reason, specific predictions can be made regarding the expected patterns of interference, should any arise consequent to vertical saccades. The compatibility effect hand and saccade direction which emerges consequent to reactive, but not predictive visual tracking is perhaps the result of an overflow of spatially coded saccadic parameters to hand-related motor areas within, but not between hemispheres. This suggestion is extrapolated from the lateralized encoding for horizontal saccades only in the hemisphere contraversive to their direction (McDowell, Dyckman, Austin, & Clementz, 2008) in conjunction with the contralateral control of the upper limbs (Cincotta & Ziemann, 2008).

Vertical saccades are, however, represented by an excitatory footprint in both hemispheres (Schlag, Dassonville, & Schlag-Rey, 1998; A. Tzelepi, Laskaris, Amditis, & Kapoula, 2010). Consequently, should any spatially congruent influence from vertical reactive saccades emerge in the finger trajectory, we hypothesized the result would be a loss in the aforementioned compatibility effect between hand and saccade direction as otherwise observed with horizontal reactive saccading. Also of interest is whether a *predictive* vertical saccading task would modify the relative expression of interference. In comparing cases of predictive and reactive vertical saccades, there seems to be a trend of lower latency execution for upwards rather than downward saccades. This facilitation relates to the an advantage in the upward target's sensory representation, and not to consequent motor representation. Conversely, saccade but not cue-related activity was larger for downward saccades (a. Tzelepi, Yang, & Kapoula, 2005). These results make predictions of an outcome difficult, but support the possibility that the various factors influencing the asymmetry of vertical tracking might carry over to the expression of any interference they may cause in the concurrently emerging finger trajectory.

A final line of enquiry in our current study related to the difference in the typical magnitude of interference expressed in reactive versus predictive responses. Spatial interference from predictive saccades was previously (Richardson et al., 2013) found to be larger in scale than compared with that caused by reactive saccades. One explanation is that the two sources of interference from motor planning and from an underlying source of motor overflow from the oculomotor to primary motor networks are implemented in a layered fashion with the effects from one acting to supplement those of the another. In other words, it is not so much that the interference from motor planning is stronger, simply that it is larger because it is additive with the effects related to the underlying overflow.

It could alternatively be the case wherein interference related to motor planning implements a larger scale interference effect if saccades imposed their corruption of manual motor encoding by means of biasing the goal of the finger movement at a stage in planning earlier than that which translates the goal into the finger's motor commands. Said differently, if the interference effect of predictive saccades is implemented by introducing a bias to the representation of the target location prior to its inverse translation into appropriate motor commands, then it stands to reason the saccade could cause a larger scale interference effect when implemented into larger scale movements as a function of amplifying the spatial bias. Such an explanation might be congruent if planning-dependent interference biases an effector-independent representation near a top level of a hierarchical model of movement encoding (Grafton & Hamilton, 2007).

There is no hidden fact that saccades and reaches demonstrate evidence of a common motor planning substrate (Snyder, Calton, Dickinson, & Lawrence, 2002; Lünenburger, Kutz, & Hoffmann, 2000; Tipper, Howard, & Paul, 2001; Kattoulas et al., 2008). Yet these examples are situated in the context of coordinated goal-directed action. The saccading and tapping task model used here is different in comparison to goal-direction aiming. The tapping component of our coordinated eye-hand task imposes no explicit spatial goal by instead implementing a temporal goal for discrete tapping. Spatially-directed manual aiming (D. Elliott, Carson, Goodman, & Chua, 1991) is a distinct class of action, and as compared with finger tapping (Balasubramaniam, 2006; Balasubramaniam, Wing, & Daffertshofer, 2004; M. T. Elliott, Welchman, & Wing, 2009) the two demonstrate evidence that their trajectory emerges by optimizing performance with respect to the type of control variable that defines their task, either a spatial location for aiming or a temporal expectation of contact-time for tapping.

To test whether saccades might interfere with the hand in a manner that scales with the kinetics of the manual action, we repeated the experiments with a partial rotation of the task. We included conditions of tapping and saccading wherein the reciprocal tracking of saccades was oriented such that eye movements occurred parallel or anti-parallel to the axis of tapping. In the case of making vertical saccades while tapping on the tabletop, we predicted that downward or upward saccades would cause a respective facilitation or decrement in the peak velocity as the finger accelerates toward the tapping surface. This effect would also be expected to demonstrate contingency on the relative congruence of the vector of either action.

Extending these hypotheses, when making left or right saccades the predicted modulation of peak tapping velocity from saccades oriented in a parallel axis would then be dependent on either hand. Since the palms faced each other toward the mid-sagittal plane when holding a box and tapping on its sides, the left hand executed rightward tapping motion toward the response surface. This configuration was expected to produce faster peak velocity in combination with rightward saccades, and slower velocity with leftward saccades. Conversely, the right hand produced tapping with leftward motion and we expected saccades in either direction to have an opposite effect in facilitating or slowing peak velocity of the manual responses.

5.4 Materials, methodology and procedure

In accordance with permission from the McMaster Ethics Research Board, eleven (N = 11) healthy and typically-developed participants (4 female) consented to the current experiments. In two session, each lasting approximately one hour in duration, research participants performed an oculo-manual motor task in response to cues presented visually on a 21” wide-screen LCD monitor, and auditory cues presented by desktop computer speakers.

5.4.1 Apparatus

Participants were seated comfortably at a desk with their hands placed on its surface, and approximately 75 cm from a screen that was centred with respect to horizontal and vertical neutral gaze. With a PC workstation running Microsoft Windows XP operating system task stimuli was constructed and displayed to participants on a 21” widescreen LCD monitor using Experiment Builder presentation software that is packaged with the EyeLink II head-mounted gaze tracker from SR Research (Osgoode, ON, Canada). Gaze direction was sampled and mapped onto the screen’s coordinates for quantitative analysis at a rate of 250 Hz. Auditory cues were presented on basic desktop computer speakers.

Using TTL signals for time-synchronization, a second PC workstation recorded the motion of that participant’s hands with the Vicon Nexus software and eight MX-40 cameras. Retro-reflective motion-capture markers 9 mm in diameter were fitted to the tip of the participants’ index fingers on the dorsal aspect over top of the distal end of the second metacarpal, and at the radial and ulnar sides of the wrist.

5.4.2 Experimental task

Following a participant’s arrival to our lab and calibration of the data acquisition equipment, a brief familiarization session demonstrated the expected responses in accordance with examples of all variations and combinations of task conditions. In short, participants tapped their finger on one of two working surfaces to an auditory metronome while also visually tracking to two target locations on the display screen.

The purpose of our task was to present stimuli that evoked saccades and finger tapping responses concomitantly to examine the degree to which a saccade caused spatial interference in the finger's trajectory. Table 1 shows all combination so of the following task variations that were applied in our current study. Herein the term *tracking* refers to the visual responses whether comprised of saccading or covert shifts in attention, and implies no tracking related to the manual tapping.

Table 5.1

Included combination of experimental manipulations

Description:	Visual tracking behaviour	Visual stimulus timing	Visual tracking mode	Visual tracking plane	Tapping plane	Pacing rate
Factor:	---	VisTime	VisTrack	TrackPlane	FinPlane	ISI
	Predictive	Periodic (P)	Covert (Cov)	Horizontal (H)	Perpendicular (PDR)	750ms 1000ms
					Parallel (PRL)	750ms 1000ms
				Vertical (V)	Perpendicular (PDR)	750ms 1000ms
					Parallel (PRL)	750ms 1000ms
			Saccades (Sac)	Horizontal (H)	Perpendicular (PDR)	750ms 1000ms
					Parallel (PRL)	750ms 1000ms
				Vertical (V)	Perpendicular (PDR)	750ms 1000ms
					Parallel (PRL)	750ms 1000ms
	Reactive	Non-periodic (R)	Saccades (Sac)	Horizontal (H)	Perpendicular (PDR)	750ms
					Parallel (PRL)	750ms
				Vertical (V)	Perpendicular (PDR)	750ms
					Parallel (PRL)	750ms

Spatial manipulations

Within each trial-run, participants performed series of finger tapping responses to a periodic auditory stimulus (1000 Hz beep, 150 ms in duration) at the same time as tracking a visual stimulus (red-filled, LED-like circle). Unimanual tapping responses were performed, and our experiment included responses with either the left (Hand-L) or right (Hand-R) index finger.

The visual target was presented reciprocally between two locations, with its visibility alternating back and forth to queue reciprocal saccades. By manipulating the tracking plane in which visual cues are aligned, TrackPlane-H trials used horizontally separated stimuli 7.5°to the left and right of the central gaze (15°total amplitude), whereas TrackPlane-V had vertical target locations the same relative distance up and down from central gaze.

Another experimental manipulation to the manual component of this task required that finger tapping be reproduced in both the horizontal and vertical plane. When tapping in the vertical plane —*i.e.* the primary axis of fingertip motion that was directed either away from and toward the tapping surface —this replicated common tabletop finger tapping tasks by tapping with the index finger and the palms face down on the surface of the table. For horizontal tapping, we placed a cardboard box between the hands of participants and instructed them to orient their hands in the sagittal plane (palms facing inward) to tap on either side surface of the box. To capture the congruency between the relative directions of the eye and the hand actions, the FinPlane factor is expressed in terms of the possible orthogonality with respect to the visual tracking plane. As such, FinPlane-PRL captures the case of *parallel* motion between ocular and manual actions, including horizontal tracking with horizontal finger tapping on the box, or vertical saccades with vertical tapping on the tabletop. These trials contrasted the FinPlane-PDR condition when the tapping was *perpendicular* to the orientation of the visual cues, as observed with horizontal tracking and vertical tabletop tapping, or vertical tracking and horizontal tapping on the box.

Timing manipulations

While the Hand, TrackPlane, and FinPlane factors captured the variation of spatial relationships of the task responses, the VisTime factor encompassed changing the timing of the presentation of visual stimulus trains. Through an experimental manipulation of the periodicity and regularity of the alternating back-and-forth target jumps across the screen, predictive saccades that were elicited when tracking a target that moved at regular periodic (VisTime-P) intervals, while reactive saccades (VisTime-R) were made in response to irregular intervals.

The VisTime-P trial-runs involved programming the visual stimulus to alternate, or jump, between the two target locations in synchrony with every metronome beep. The resulting behaviour is tapping and saccading on the beat, every beat for the duration of the trial. Two pacing rates of inter-stimulus intervals (ISI) were used, a fast 750 ms interval condition (ISI-750ms) and a slower 1000 ms interval condition (ISI-1000ms).

In VisTime-R trials there were no ways to apply the ISI factor and adjust pacing rate of visual cue timing, as it must inherently be timed at irregular intervals to elicit reactive saccades. For that purpose, we programmed target jumps to occur with a uniform probability once every 4th to 7th tapping interval. Tapping-rate during

VisTime-R trials was repeated only at 750 ms intervals.

Covert & overt tracking

Saccades are overt modes of tracking visual targets, and to account for the possible interference effects from independent non-motoric process of *covertly* shifting one's attention. These attention shifts often occur shortly preceding or in parallel to saccades, so a task that evokes tracking in a covert manner with only one's peripheral attention must be included. All VisTime-P trial conditions were permuted in two contexts manipulated according to the VisTrack factor. Overt tracking was engaged with saccading (VisTrack-Sac), and a second condition was included where participants maintained central gaze fixation while only covertly shifting their attention (VisTrack-Cov) to target motion.

In the VisTrack-Cov condition, an incentive was necessary for participants to attend to the alternating target locations, and not to some extraneous stimulus or to digress from the task due to general inattention. For this purpose we introduced a visual discrimination task at a random time within the trial-run. The discrimination task was implemented so that an alphanumeric character was displayed at a target location in lieu of the alternating target. The displayed character, a numeric '**3**' or an alphabetic '**E**' was displayed with uniform probability between the 26th and 36th tapping interval, and only for a brief 200 ms duration before it was masked and the trial was terminated. Both the brevity of displaying the target, and that the timing of the discrimination stimulus was aligned with the beat of the expected upcoming target jump are conducive to engaging the participant congruent shifts in attention. Following the display of the discrimination target, but not before, the participant was allowed to make a reflexive saccade to its location quickly, and make an attempt at discriminating the character with a verbal report.

5.4.3 Task presentation protocol

A particular testing session consisted of completing the entire collection of either VisTime-P trials, or VisTime-R trials on separate days. In each session, a number of trial-runs of series of saccadic and tapping responses were collected, with no fewer than 26 saccades per trial. The combination of manipulations implemented in successive trial-runs was pseudo-randomized in their order of presentation. A block of trials consisted of a single presentation of each trial condition, of which the VisTime-P session included 32 trial conditions (2-VisTrack × 2-Hand × 2-TrackPlane × 2-FinPlane × 2-ISI) and the VisTime-R included 8 conditions (2-Hand × 2-TrackPlane × 2-FinPlane). Successive trial-runs were pseudo-randomized in their order of presentation, with one iteration of each condition in each block of trial runs.

The series of stimuli in each VisTime-P trial cued 26 responses. Two blocks of trials were performed for the analysis of 52 total responses, which led to 26 responses each in either of the opposite directions in the reciprocal task, and for each task condition. In VisTime-R trials, saccades were cued less frequently. To avoid excessively long trial-runs, fewer visual responses were executed within each trial, which was balanced by collecting 5 blocks of trial recordings. On average 7 saccades were made in each direction of the reciprocal task in each trial, totalling in approximately 70 responses, 35 in either direction. A slightly larger number of responses were required for collection in the VisTime-R trials to account for a higher variability in the reaction times, and by extension the probability for the saccade to successfully overlap with the mid-flight phase of the finger tapping trajectory.

5.4.4 Data analysis

Using the respective eye and motion tracking host system's software for rendering and exporting gaze and hand motion data to plain-text files, the MATLAB software package from MathWorks (Natick, MA, USA) was used to design analysis scripts for examining the data time-series.

Dependent measures

FinPlane-PDR When finger tapping and saccading movements were performed in perpendicular primary axes of motion, as in FinPlane-PDR trials, the expected presentation of spatial interference in the finger trajectory was measured by comparing the location from tap to tap where the finger contacted the tapping surface. When tapping on the tabletop and tracking horizontal targets (TrackPlane-H), or when tapping on the sagittal box surface and tracking vertical targets (TrackPlane-V), the displacement in the fingertip position in the axis congruent with orientation of the visual targets was measured between successive tap responses.

The measure of deviation associated with each visual response was pooled together into one of two groups representing opposite directions of saccading in each trial, whether the response was paired with leftward, or rightward target motion, or upward or downward target motion, and was represented in our statistical model as the TrackDir factor. Means were calculated within trials for preserving this directional grouping, and also between trial repetitions across blocks of trial presentations. The respective TrackDir-UR and TrackDir-DL conditions captured the effects anticipated from statistical effects relating to opposite directions of saccading, with the former representing up and downward tracking whereas the latter encapsulated downward and leftward visual tracking. It is thus a disambiguating interaction between TrackDir and TrackPlane wherein one would obtain the objective comparisons of up versus down, and left versus right saccadic responses.

The raw measurements of deviation in fingertip position were naturally reported as a vector. In separate axes, the coordinate system was calibrated and recorded was configured with positively directed motion in the upwards and rightwards directions. To configure our analysis such that positive displacement numbers indicated a displacement that was congruent with saccade, taking the negative of the displacement vector was required for responses that were made concurrent to tracking downward and leftward target motion.

FinPlane-PRL In the case of a parallel orientation of tapping and saccading motion, our hypotheses stipulated that interference should manifest congruent with the saccades. While fingertip position in the primary axis was continually changing as a function of the tapping motion, we measured the peak velocity of the finger as it accelerated toward the tapping surface. The units of fingertip velocity were recorded in millimetres per second.

Means were pooled according to the TrackDir factor, but this factor required a slight modification in contrast to FinPlane-PDR trials. The UR and DL levels of the TrackDir factor were only labelled as such for FinPlane-PDR condition, wherein there was symmetry in considering that all combinations of TrackDir and TrackPlane were rotated 90° relative to one another. However, in the FinPlane-PRL condition the permutations of combining TrackPlane and TrackDir resulted in visual tracking directions that were either parallel (0°) or anti-parallel (180°) with respect to the finger tapping action. In this case the TrackDir factor was expressed as either TrackDir-0 or TrackDir-180 for these two orientations, respectively.

As an implicit step in representing this TrackDir-0 and -180 factors intuitively, the raw data recording of finger tapping was directed in opposite vectors to contact the sagittal box surface with either the left hand (finger accelerates rightward) and right hand (finger accelerates leftward) consequent to the palms-in orientation. Corrections for either hand were not required for tapping on the tabletop surface since both hands shared the same allocentric configuration for producing negatively directed (downward) velocities as they accelerated toward the tapping surface. So taking the negative vector of the left hand tapping in FinPlane-PRL trials was all that was required to produce similarly aligned velocity measures in all conditions. This results in congruent measures whereby TrackDir-0 responses in any condition might be expected to produce faster, *i.e.* comparatively more negative velocities if our predictions confirm a congruent facilitation effect from parallel visual tracking and manual responses.

Statistical models

In analyzing the subject means of our dependent measures, an important consideration in planning our analysis was the inclusion of two types of statistical tests. A standard repeated measures ANOVA was best for gaining insight into the way that task conditions modulate the degree of interference as one task variation was compared with another, in either the FinPlane-PDR or FinPlane-PRL conditions. However, for testing the overarching hypothesis that significant interference congruent with concurrent visual tracking exists whatsoever in FinPlane-PDR, the magnitude of the observed trends was itself of considerable importance as an absolute measure. An ANOVA was applied to the fingertip velocity measures with no a priori expectation for an expected velocity value relative to which the saccading task might modulate its expression. Thus our the ANOVA provided the most objective comparisons of velocity data as it is modulated by our experimental manipulations and represented by repeated measures. However, an additional consideration was given to the interpretation of the absolute positional displacement between taps in FinPlane-PDR trials.

Inferences regarding the magnitude of positional displacement between taps were best made using one-sample t-tests, which determined whether it was significantly probable to reject the null hypothesis that no displacement, or more precisely 0 mm of displacement in the direction of concurrent visual tracking was observed. An ANOVA, however, would consider the variance for both sets of groups being compared against one another in a pairwise manner. This would lead to a slightly different sensitivity than do one-sample t-tests. In the case of t-tests, only the within-subject variance of the group-mean is considered in each statistical comparison with a single vale, in this case 0 mm which has no implicit variance.

The consequent effect that is of statistical importance arising from this difference between these tests manifests in their interpretation as follows. Considering a hypothetical control condition exists wherein it is fact that no significant and congruent interference from concurrent visual tracking occurs, there still exists variability in the distribution of the responses about that 0 mm value that is unrelated to the actual factor of spatial interference. If one then considers that a complimentary hypothetical experimental condition exists wherein it is known as fact that visual tracking causes a slight spatial interference, determining the truthful significance of this small-magnitude effect that is related to the experimental task is more sensitively resolved with one-sample *t*-tests. Conversely, an ANOVA might obfuscate this truth, since an inherent variable in its application for this purpose is the incorrect assumption that the case of 0 mm of interference is best represented by a control task that has no inherent interference effects. A consequence of this is that the general variability in task performance unrelated to interference obfuscates the objective representation of the null-hypothesis —that no-interference exist —with variance about the mean despite factual known absence of interference.

In consideration of the contrasting purposes for applying either statistical test, our analyses used both to identify important behaviours and changes in their expression according to task conditions. Importantly, the use of one did not preclude the other. The ANOVA was useful for identifying trends in the expression of interference between task conditions, but not for identifying whether a given condition exhibited a significant magnitude of interference whatsoever. Because of the aforementioned sensitivity of *t*-tests for this purpose, even trends that were only reaching significance in the ANOVA were justifiably decomposed and investigated with one-sample *t*-tests. The combination of statistical tests yielded structure to a method for identifying trends to which neither one is conducive on its own. Put as simply as possible, this resulted in a hybrid application of the two tests for comparing the different sets of task conditions with one another to determine in what contexts significant interference occurred, and when it did occur, how it was modulated by task context.

Both cases of FinPlane-PDR and FinPlane-PRL data reported ANOVA main effects with Bonferroni corrected significance to $p < 0.05$. The decomposition of interactions were done with post-hoc pairwise t-tests whilst noting in the relevant sections what corrections were made for multiple comparisons according to the breadth of the interaction being decomposed.

5.5 Results

5.5.1 Descriptive statistics of task performance

Saccade onset latency

It is imperative to the validity of our investigations that saccades were in fact performed in accordance with expectations for different task conditions. A preliminary step was to contrast that saccades were in fact predictive in the timed tracking VisTime-P conditions, and reactive to non-periodic stimuli in the VisTime-R conditions. This contrast was not concerned with the differences in saccadic latency between ISI-750ms or ISI-1000ms trial conditions, as both should elicit predictive tracking. Within-subject means were calculated to collapse the pacing rate of the VisTime-P trials. The statistical advantage inherent in doing so was to contrast saccade latency between VisTime-R and VisTime-P with an omnibus repeated measures ANOVA in a fully factorial design.

A 5-factor ANOVA (VisTime, Hand, TrackPlane, FinPlane, TrackDir) reached significance in two cases. Confirming our general expectation that predictive and reactive tracking modes were observed in the latency of tracking VisTime-P ($M = -164.31, SD = 128.74$) and VisTime-R stimuli ($M = 199.89, SD = 25.18$), the

VisTime factor reached significance $F_{1,10} = 98.214$, $p < 0.001$, $\eta_p^2 = 0.908$.

An additional interaction reached significance between the VisTime, TrackPlane, FinPlane, and TrackDir factors $F_{1,10} = 6.801$, $p = 0.026$, $\eta_p^2 = 0.405$. Decomposing this interaction was not as daunting at task as one might have first expected of a 4-way interaction. Indeed the distinction of reactive and predictive tracking was consistent in all instances of breaking down this interaction for VisTime-R, and VisTime-P conditions, respectively. Within the VisTime-P condition, all means were similar and did not show any significant trends in their pairwise comparisons. Similarly in the VisTime-R trials all the mean latency measures encompassed within horizontal saccading conditions were similar. However, the latency values of vertical reactive saccades varied on a larger scale and post-hoc tests were needed to decompose the interaction between FinPlane and TrackDir factors.

Since one might expect that, compared to downwards saccades those that were directed upwards had the propensity for a faster latency (A. Tzelepi et al., 2010), the remaining two factors were best framed in their modulation of this expected trend. In the parallel vertical tapping and reactive saccading FinPlane-PRL condition, the onset of upward saccades ($M = 163.25, SD = 72.51$) was significantly $t_{10} = -2.35$, $p = 0.041$ faster than downward saccades ($M = 258.76, SD = 258.76$). In the case of perpendicularly-directed responses, the respective upward ($M = 191.70, SD = 35.40$) and downward ($M = 237.04, SD = 77.56$) means showed the same trends, but were not significantly different $t_{10} = -1.631$, $p = 0.134$.

The narrowing of this mean difference score was partly attributed to a significant reduction in the latency of downward saccades wherein the horizontal orientation of the hands —palms facing inward —in the FinPlane-PRL showed slower reactions $t_{10} =$

3.269, $p = 0.008$ than did downward saccades paired with a vertical hand orientation —palms on the tabletop. It was only this test that also survived corrections for multiple comparisons at $p < 0.0125$ in this post-hoc set. Additionally, in respect to upwards saccades there was a nearly significant $t_{10} = -2.136$, $p = 0.058$ trend wherein those made in the FinPlane-PDR hand orientation condition had a slightly longer mean latency than those produced in the FinPlane-PRL condition. In summary, this latency data showed a trend that the delay of downward (upward) reactive saccades was ameliorated (deteriorated) by the influence of hand orientation in the case of a palms-in (palms-down) forearm posture and consequent horizontal (vertical) axis of motion for finger tapping.

Overall, the latency data supported the distinction of predictive and reactive saccades in the appropriate VisTime conditions. This supported the inherent quality that predictive saccades were initiated by means of engaging motor planning, whereas reactive saccades were mediated by means of exogenous stimulation that was not anticipated nor planned for. The implications of the differences outlined in the post-hoc tests of the 4-way interaction were relevant to understanding the way in which the action plane of the hand might influence the readiness state of the oculomotor system or allocation of attention. Otherwise, this interaction did not contribute to explaining the role of interpreting the mechanisms by which the spatial coding of saccade parameters might have influenced concurrent trajectory evolution of the manual actions.

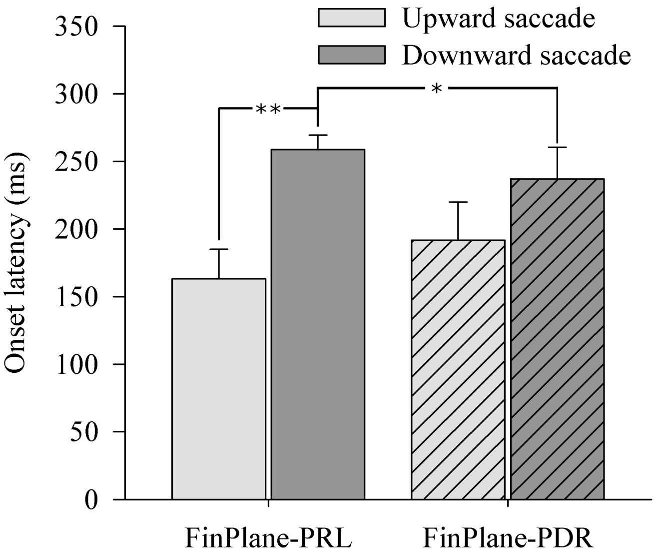


Figure 5.1: Saccade latency from VisTiming-R trials presented according to their relevant post-hoc comparisons. The illustration includes the effects of relative hand orientation, either parallel or perpendicular on the latency of upward and downward saccades. In a parallel tapping and saccading orientation, upward saccades were significantly lower in onset latency with respect to downward saccades. When tapping in a horizontal plane with a perpendicular relationship to vertical reactive saccades, downward saccades were significantly faster than compared to cases when the hand was tapping in a parallel vertical orientation. Diagonal shading is applied to FinPlane-PDR trials only, and a * denotes significance, while ** is included for comparisons surviving corrections for multiple comparsions.

5.5.2 Spatial eye-to-hand interference

It is important to underscore the use of two distinct dependent measures in the following results. In the case where saccades (or covert attention shifts) were directed in a plane perpendicular to the axis of finger tapping, as in FinPlane-PDR trials, spatial interference was expected to present in the finger trajectory as positional deviations between successive tap location that would be congruent with the visual tracking motion.

The line of reasoning in the following sections examines the interference in this context as we have already validated the use of this measure of interference in previous studies (Richardson et al., 2013). However, the results from complimentary saccading and tapping conditions in the context of parallel orientation between the primary axis of saccades and taps in FinPlane-PRL trials are reported in different units of measurement. In this latter case, we expected interference from concurrent saccades to manifest as modulations in the peak velocity of the fingertip following its acceleration toward the tapping surface. For this reason, an ANOVA inclusive of this factor was not appropriate. Each subsection of results in a given task condition include its own division for reporting those relating to FinPlane-PDR and FinPlane-PRL conditions.

Predictive visual tracking

FinPlane-PDR The first step was a planned comparison with a 5-way ANOVA between VisTrack, TrackPlane, ISI, Hand, and TrackDir to determine whether covert tracking in VisTrack-Cov trials caused any significant interference effects whatsoever. We aimed to answer this question because a case of no significant interference produced by tracking attention cues could more parsimoniously examine the other factors without the inclusion of modelling the variance of a null behavioural effect.

The interpretation began with a main effect of VisTrack $F_{1,10} = 6.479$, $p = 0.029$, $\eta_p^2 = 0.393$, where attention cues ($M = 0.25, SD = 0.42$) caused significantly less drift in the fingertip trajectory than that observed with saccade cues ($M = 0.58, SD = 0.49$). As illustrated in Figure 5.2a, testing these values against 0 mm reveals there was no identifiable interference when tracking attention cues $t_{10} = 1.932$, $p = 0.082$. There was, however, significant interference which rejects the null case of 0 mm when tracking saccadic cues $t_{10} = 3.927$, $p = 0.003$, which also survived corrections for multiple comparisons at $p < 0.025$.

The interaction between VisTrack × Hand also reached significance $F_{1,10} = 5.218$, $p = 0.045$, $\eta_p^2 = 0.343$ (Figure 5.2b). These findings implied that when tracking attention cues in conjunction with responses of either hand there was no difference between the interference observed in the left ($M = 0.19, SD = 0.36$) and right ($M = 0.30, SD = 0.54$) hands $t_{10} = -1.028$, $p = 0.328$, and that neither was significantly different from 0 mm $t_{10} = 1.710$, $p = 0.118$ and $t_{10} = 1.860$, $p = 0.093$. When tracking saccade targets, the left hand ($M = 0.22, SD = 0.32$) was only weakly attracted to the saccade, as compared with the right hand ($M = 0.94, SD = 0.91$). While the mean displacement was significantly greater for the right hand $t_{10} = -2.553$, $p = 0.029$, both the left $t_{10} = 2.289$, $p = 0.045$ and right $t_{10} = 3.456$, $p = 0.006$ hands were significant in rejecting the null hypothesis of 0 mm of displacement although only the right hand survived corrections multiple comparisons within this decomposition at $p < 0.0125$. Despite there being no difference in the Hand factor in attention-only control trials, the bias for stronger interference in the right ($M = 0.62, SD = 0.63$) rather than left ($M = 0.205, SD = 0.29$) hand was observed with a significant main effect of Hand $F_{1,10} = 6.098$, $p = 0.033$, $\eta_p^2 = 0.379$. Thus far, evidence has accrued to substantiate the case that tracking attention cues did not produce a significant interference effect in any condition.

Lastly with respect to VisTrack, the 3-way interaction with ISI × TrackDir also reached significance $F_{1,10} = 13.497$, $p = 0.004$, $\eta_p^2 = 0.574$. Since there was no main effect of ISI or other significant interactions of it in combination with VisTrack, or with other factors for that matter, we first examined whether significant differences existed between ISI-750ms and ISI-1000ms conditions of the 4 combinations of VisTrack and TrackDir factors. By first decomposing the ISI factor we also preserved the variations in the spatial manipulations of the task, in this case TrackDir which was, in contrast to ISI, of more direct relevance to our hypotheses regarding the spatial presentation of interference.

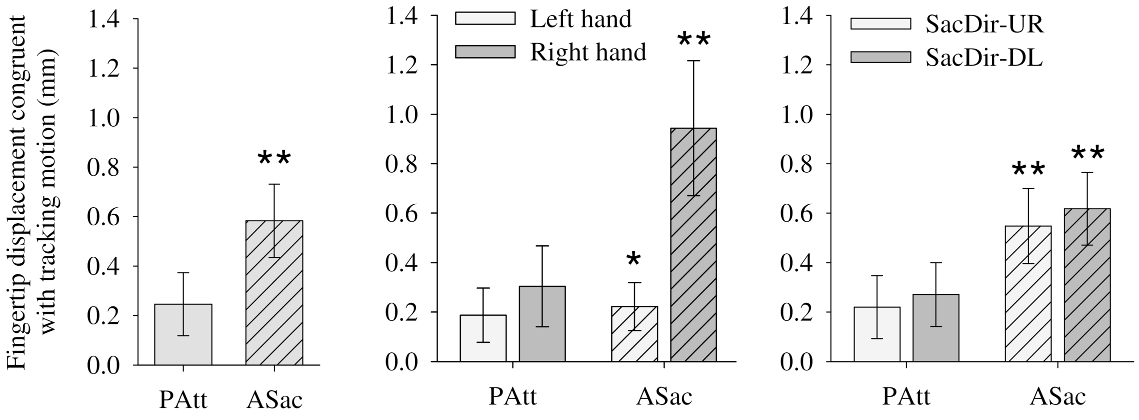
In these VisTrack-Cov trials, when tracking motion toward either the upward or rightward extent specified in the TrackDir-UR condition is compared from the ISI-750ms ($M = 0.33, SD = 0.75$) condition against that in the ISI-1000ms condition ($M = 0.11, SD = 0.25$), there was no significant difference $t_{10} = 1.033$, $p = 0.326$. Additionally, this was also the case for tracking downward or leftward targets in the TrackDir-DL condition, where ISI-750ms trials ($M = 0.39, SD = 0.80$) showed no differences in interference as compared to ISI-1000ms trials ($M = 0.16, SD = 0.23$) $t_{10} = 0.957$, $p = 0.361$.

In VisTrack-Sac trials, when saccading in TrackDir-UR directions there were also no significant differences observed between ISI-750ms ($M = 0.62, SD = 0.68$) and ISI-1000ms ($M = 0.48, SD = 0.66$) trials $t_{10} = 0.511$, $p = 0.621$. Finally, there were no differences when contrasting interference consequent to saccading in the TrackDir-DL condition between ISI-750ms ($M = 0.63, SD = 0.65$) and ISI-1000ms ($M = 0.61, SD = 0.65$) conditions $t_{10} = 0.077$, $p = 0.940$.

Subsequent to these post-hoc comparisons, it seemed easiest to decompose the role of VisTrack as it related to TrackDir without respect to the ISI factor, and to instead examine the marginal means after averaging the 750ms and 1000ms conditions, as shown in Figure 5.2c. The remaining data comparing the trends according to VisTrack × TrackDir is plotted in Figure 5.3. Of the remaining data, neither the TrackDir-UR ($M = 0.22, SD = 0.42$) or TrackDir-DL ($M = 0.27, SD = 0.43$) case of VisTrack-Cov were significantly different from 0 mm. Contrasting this, in VisTrack-Sac trials, both TrackDir-UR ($M = 0.55, SD = 0.50$) and TrackDir-DL ($M = 0.62, SD = 0.49$) were significantly different from 0 mm, respectively at $t_{10} = 3.614$, $p = 0.005$ and $t_{10} = 4.208$, $p = 0.002$.

The results of examining the VisTrack factor in this cursory ANOVA provided consistent evidence that covert tracking did not cause a discernible interference effect in the fingertip trajectory as measured by its perpendicular drift. The next step is removing the VisTrack factor from the analysis model to examine the remaining effects related only to saccading in VisTrack-Sac trials. Effects and interactions related to a 4-way ANOVA between the TrackPlane, ISI, Hand, and TrackDir factors for VisTrack-Sac data only was more clearly investigated in its own model as it pruned the variability related to VisTrack-Cov trials that we have reasonably concluded is unrelated to spatial interference effects.

This ANOVA was inclusive only of saccading conditions and a planned comparison



(a) VisTrack (b) VisTrack×Hand (c) VisTrack×TrackDir

Figure 5.2: The above plots are included to demonstrate the consistent trend at all significant levels of statistical representation that covertly tracking the motion of attention cues in the VisTrack-Cov condition do not result in any significant interference effects that rejects null case of 0 mm of fingertip displacement. Significance in one-sample t-tests versus 0 mm is denoted by single '*' when the test is significant at p <0.05, and '**' when significant after correcting for multiple comparisons: (a) p <0.025, (b) & (c) p <0.0125. Diagonal shading over the columns of overt saccading tracking in -Sac trials is included to make an easy visual comparison with respect to clear bars used for covert visual tracking in VisTrack-Cov trials.

was whether our TrackPlane manipulation contributed to any significant effects or interactions. We found a significant interaction between TrackPlane and TrackDir $F_{1,10} = 5.625$, $p = 0.039$, $\eta_p^2 = 0.360$, indicating there might have been a difference in the expression of interference when saccading in opposite directions relative to the saccading task being oriented in the horizontal or vertical plane. This interaction was decomposed in 5.3, showing that when making left $(M = 0.95, SD = 1.03)$ and right $(M = 0.95, SD = 1.03)$ saccades there was significant interference in both cases, $t_{10} = 3.058$, $p = 0.012$ and $t_{10} = 3.070$, $p = 0.012$ respectively. These both survived corrections for multiple comparisons at p <0.0125. However neither case of upwards $(M = 0.15, SD = 0.55)$ or downward $(M = 0.29, SD = 0.57)$ saccading caused significant interference, at $p = 0.125$ and $p = 0.401$. This effect was somewhat echoed by main effects of TrackDir $F_{1,10} = 4.898$, $p = 0.051$, $\eta_p^2 = 0.329$ and TrackPlane $F_{1,10} = 3.397$, $p = 0.095$, $\eta_p^2 = 0.254$ factors nearly reaching significance.

Also observed was a significant main effect of Hand $F_{1,10} = 6.517$, $p = 0.029$, $\eta_p^2 = 0.395$. It was apparent that the left hand responses $(M = 0.22, SD = 0.32)$ were influenced significantly less than those produced with the right hand $(M = 0.94, SD = 0.91)$. Both, however, were significantly different from 0 mm $t_{10} = 2.289$, $p = 0.045$ and $t_{10} = 3.456$, $p = 0.006$, with only the latter test of data from right hand responses surviving corrections for two comparisons at p <0.025. In this portion of the experiment, there was an apparent larger bias of interference that manifested in the right hand, even though a significant interference was observed in both hands.

Another significant interaction was found between TrackDir × Pacing factors

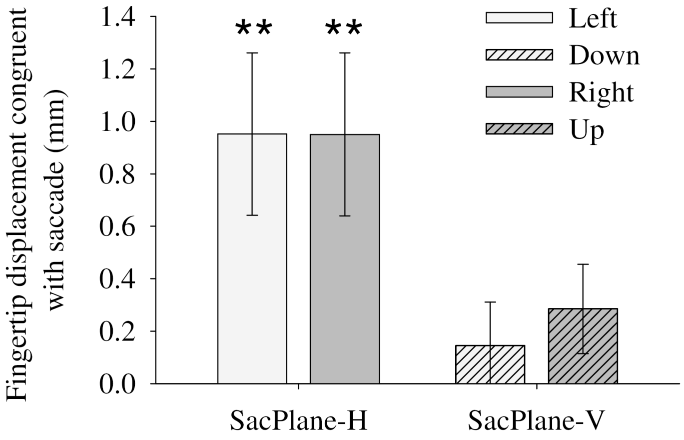


Figure 5.3: Using responses from VisTime-P trials, this figure illustrates the overall fact that we observed a significant interference effect from horizontal, but not vertical (diagonal shading) saccades. Significant indicated by '**' survives corrections for multiple comparison at p <0.0125.

$F_{1,10} = 19.507$, $p = .001$, $\eta_p^2 = 0.661$. In all cases of this decomposition, both instances of saccading either to the right or upward at ISI-750ms ($M = 0.62, SD = 0.68$) $t_{10} = 3.024$, $p = 0.013$ and ISI-1000ms ($M = 0.48, SD = 0.66$) $t_{10} = 2.435$, $p = 0.035$ were significantly different from 0 mm, although not surviving when applying a corrected p <0.0125. Saccades either to the left or downward were also significantly different from 0 mm at ISI-750ms ($M_{DL-750} = 0.63, SD = 0.65$) $t_{10} = 3.202$, $p = 0.009$ and ISI-1000ms ($M_{DL-1000} = 0.61, SD = 0.65$) $t_{10} = 3.115$, $p = 0.011$, even when correcting for multiple comparisons. A series of post-hoc pairwise t tests identified the source of the interaction as significantly smaller for the TrackDir-UR ISI-1000ms condition. While it was anticipated that interference would scale down with increasing interval duration, this was only apparent in this one condition. So the interaction was not surprising because of the smaller mean interference in this condition, rather it was the fact that TrackDir-DL-ISI-1000ms was not also significantly lower which we had not anticipated.

FinPlane-PRL In the case of measuring peak velocity in the condition of saccades and taps performed in a parallel or anti-parallel axes, we were not concerned with the magnitude of the velocity being different from any one-sample value, as we were otherwise interested in differentiating 0 mm of finger displacement in the FinPlane-PDR trials. Thus our only approach for FinPlane-PRL trials was in making pairwise comparisons between variations of our task. One-sample t-tests were not used here for decomposing relevant effects. Simply we examined our data for modulations of the peak velocity according to the experimental condition.

It is worthy of mentioning that we found two significant main effects that were related to the configuration of the task in ways that were not relevant to the FinPlane-PDR conditions. First it was relevant that we found a main effect of ISI $F_{1,10} = 6.452$, $p = 0.029$, $\eta_p^2 = 0.392$ where the peak velocity was faster at quicker tapping intervals ($M_{750ms} = -838.54, SD = 295.78$) than at longer tapping intervals ($M_{1000ms} = -821.51, SD = 290.20$). Accordingly this described the natural emergence where faster paced movements must be performed at a slightly faster speed.

Additionally, we observed a significant effect of TrackPlane $F_{1,10} = 28.047$, $p < 0.001$, $\eta_p^2 = 0.737$. While this condition is named according to the orientation of saccading, by extension in the FinPlane-PRL condition only this specifies the tapping surface, either on the sides of a box's sagittal surface with a palms-in orientation in TrackPlane-H trials, or on the tabletop in TrackPlane-V trials. With horizontal axis of tapping (and saccading) the peak velocity of the fingertip ($M = -752.40, SD = 300.53$) was much slower than compared to vertical tapping (and saccading) ($M = -907.65, SD = 293.04$). One may expect this effect simply because there was the contribution of gravity assisting the motion of tapping on the tabletop in the TrackPlane-V condition. Conversely, stiffness in the hand posture when maintaining a palms-in configuration on the box might have led to higher joint-stiffness and slower tapping. Irrespective of the exact reason, this main effect, or that of ISI was not related to the changing parameters of saccades as they did not involve an interaction wherein the parameters of saccading were manipulated.

For the case of describing interference as it manifested in the FinPlane-PRL variations of the task, the TrackDir factor was of primary importance. In this instance TrackDir-0 and TrackDir-180 describe parallel and anti-parallel saccades. It was in this respect and interaction with the TrackDir factor that the reciprocal nature of the task should lend support to any saccade direction-contingent effects.

The interaction between VisTrack × TrackDir $F_{1,10} = 6.26$, $p = 0.031$, $\eta_p^2 = 0.385$ was significant. When covert visual tracking was performed in VisTrack-Cov trials, post-hoc tests determined there was no significant modulation of peak velocity according to the TrackDir-0 ($M = -832.96, SD = 292.84$) and TrackDir-180 ($M = -833.98, SD = 296.56$) configurations of saccades with respect to taps. In conjunction with overt saccadic tracking, the case of peak velocity in TrackDir-0 condition was very similar ($M = -830.27, SD = 291.51$), whereas in the TrackDir-180 ($M = -822.91, SD = 293.67$) the peak velocity was slightly lower. While this trend suggested that when making saccades that are anti-parallel with respect to the tapping the peak velocity is slightly slower, this failed to reach significance compared to parallel saccading as the test only approached significance $t_{10} = 1.761$, $p = 0.109$. Consequently, there seemed to be no evidence that either concurrent overt or covert visual tracking modulated the peak velocity of finger tapping contingent on the tracking direction.

Reactive visual tracking

FinPlane-PDR All responses in the context of VisTime-R were overt saccades as there was no permutation of reactive tracking conditions with an attention-only target for covert tracking. There was also only the single 750 ms pacing rate, and so ISI was not an included factor. A 3-way ANOVA between TrackDir, TrackPlane, and Hand measured the changes in positional displacement in the finger trajectory that were congruent with the direction of concurrent reactive saccades in a plane perpendicular to the primary axis of tapping.

While a main effect of TrackDir narrowly missed significance $F_{1,10} = 4.627$, $p = 0.057$, $\eta_p^2 = 0.316$, its 2-way interaction with Hand $F_{1,10} = 5.362$, $p = 0.043$, $\eta_p^2 = 0.349$ was significant. Moreover, the interaction between TrackDir × TrackPlane also reached significance $F_{1,10} = 7.388$, $p = 0.022$, $\eta_p^2 = 0.425$ as well as a 3-way interaction between all TrackDir × TrackPlane × Hand factors $F_{1,10} = 15.358$, $p = 0.003$, $\eta_p^2 = 0.606$. Conveniently, with each level of interaction the model gained further explained variance as the η_p^2 became progressively larger.

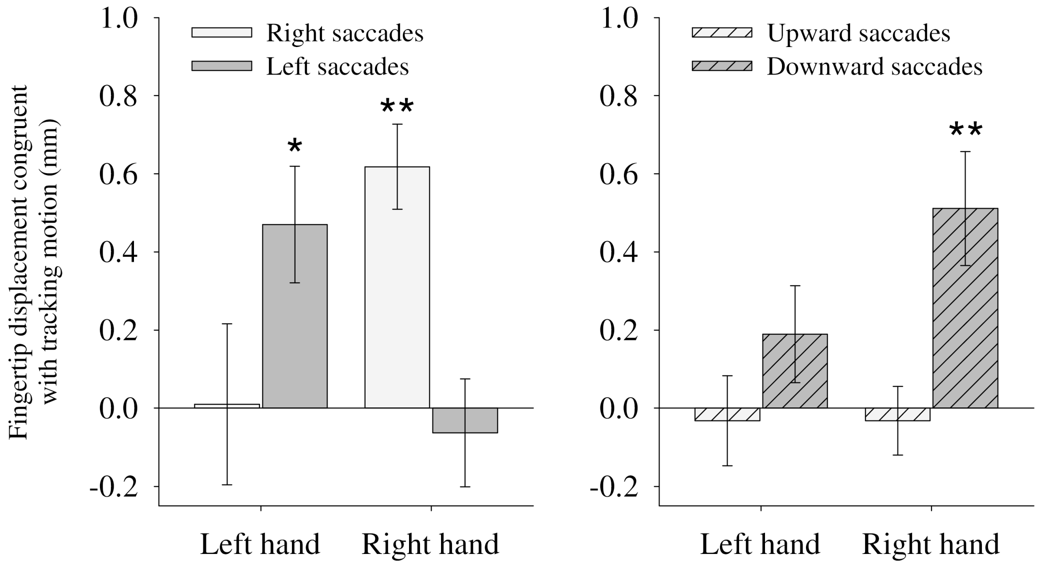
As in our previous experiment (Richardson et al., 2013), there was a compatibility effect observed within the context of horizontal reactive saccades. The planned comparison in this context showed that the right hand was significantly attracted in the direction of rightward saccades $t_{10} = 5.646$, $p < 0.001$, and the left hand to leftward saccades $t_{10} = 3.146$, $p = 0.010$. Within this context of the 4 possible permutations of conditions of horizontal saccading, significance was conserved to the extent of applying corrections for multiple comparisons to p <0.0125.

Vertical reactive saccades produced a significant deviation in the fingertip trajectory of the right hand, but only in combination with downward saccades ($M = 0.51, SD = 0.49$) $t_{10} = 3.495$, $p = 0.006$.

FinPlane-PRL In this case, the only task condition that modulated peak velocity of tapping was the main effect of TrackPlane $F_{1,10} = 20.432$, $p = 0.001$, $\eta_p^2 = 0.671$. As in the case of FinPlane-PRL responses in the predictive visual tracking condition, there was a slower peak velocity when tapping on the sagittal surface of the box during TrackPlane-H trials ($M = -692.81, SD = 220.63$) as compared with tapping on the tabletop in TrackPlane-V trials ($M = -842.50, SD = 236.79$).

5.6 Discussion

The current study investigated eye-hand coupling in the specific context of concurrent saccading (or covert visual tracking) and finger tapping. In previous work with this novel task paradigm (Richardson et al., 2013) we identified that different modes of visual tracking, either predictive or reactive saccading caused different modes of spatial interference in the finger trajectory. The advantage of contrasting the interference-causing effects of these two types of saccades was that only predictive saccades implicated a dependence on motor planning. For this reason we examined the degree to which interference emerged as a function of compartmentalized effects either relating to motor planning or to other mechanisms specific to oculomotor execution or reactive saccading.



(a) TrackPlane-H (b) TrackPlane-V

Figure 5.4: These figures show the degree to which either the left or right hands were attracted to concurrent reactive saccades in the VisTrack-R conditions. In the case of making left and right reactive saccades, subplot 5.4b illustrates a compatibility effect between the responding hand and the direction of concurrent saccades. Only rightward reactive saccades attract the right hand to the right, and similarly a significant and symmetric trend in the left hand consequent to leftward saccades. Post-hoc comparisons reveal no relative difference in their means. The subplot 5.4b has diagonal shading to indicate the TrackPlane-V condition. In this case, downward saccades caused a congruent interference only in the right hand, and no other combination of saccade direction or responding hand resulted in identifiable interference effects.

It is first important to demonstrate a general replication of our previous results. Following a cursory saccade latency analysis to confirm saccades were predictive in all variations of VisTime-P and reactive in all VisTime-R trials, corroboration with our previous methods is derived from the isolated decomposition of our current data to examine the effect of horizontal saccades in the FinPlane-PDR condition with tabletop tapping responses. In the case of FinPlane-PDR trials, the interference effect was measured as the positional displacement in the fingertip from one tap to the next, with positive values indicating a congruent attraction to the visual tracking direction. Until FinPlane-PRL trials are discussed, interference is herein implied as being represented by means of this tap to tap positional drift.

We replicated trends in the pattern of observed interference relative to both VisTime-P and VisTime-R conditions as they were combined with TrackPlane-H and FinPlane-PDR. The interference from reactive horizontal saccades again showed a clear compatibility effect between the saccade direction and the responding hand. Only rightward reactive saccades caused significant rightward deviation in right hand tapping responses, with a complimentary pattern for leftward saccades and the left hand. In replication of VisTime-P trials, we observed that horizontal predictive saccades caused significant interference in either hand, regardless of the direction of the saccade. Replicating the Hand × TrackDir interaction in VisTime-R, as well as noting its absence in VisTime-P trials is important to corroborate the two distinct coupling modes consequent to the selective recruitment of motor planning.

In the current results, however, we observed a few differences in comparison to our previous study. Firstly, we did not replicate an effect whereby the strength of interference scaled with the pacing interval. We had anticipated stronger interference in the ISI-750ms condition, as compared to ISI-1000ms. Failing to reproduce this effect is not completely surprising, because our current set of conditions only included two levels of ISI, whereas an even faster rate of ISI-500ms was included previously. Despite participants performing relatively well in these fastest trials, they often remarked it was difficult to maintain precision in their responses. Since the current study needed to investigate many factors, we only included two ISI levels and thus perhaps lacked the statistical power to replicate this distinction. Nonetheless, the remainder of the study was well represented as many VisTime-P results reached significance in expressing interference effects when marginal means were computed and analyzed irrespective of ISI.

Another novel effect to consider from the present study was that the observed interference from horizontal saccading expressed itself with a distinct preference for stronger effects in the right hand. Our previous investigation did not reveal a hand-centric lateralization in the expression of the interference in the VisTime-P condition. Since this study derived its goals for the purpose of assessing asymmetries in representation and different neural correlates with respect to saccading in different contexts, we had not initially considered taking an inventory of handedness. Consequently, one might argue that our selection of participants happened to be comprised of those who are predominantly right handed, which by extension might be reason to suggest the dominant hand has a stronger propensity to become coupled with the eyes. While this may be, a counter-argument that our data is not consistent with that explanation is a logical response since we did not also see a similar down-scaling of the magnitude of interference expressed in the left hand consequent to leftward reactive saccades. In other words, this right-handedness bias did not present with a similar modulation of the replicated effects in the VisTime-R conditions.

Resolving the issue of handedness as it relates to the relative expression of interference with reactive and predictive behaviours is one which is obviously important, but having only introduced this motor paradigm recently has thus far precluded the option for testing it. The breadth of investigations required to make inferences regarding the influence handedness also concedes the requirement of controlling for the possibility of reciprocal lateralization effects in the expression from the source of the interference, perhaps related to ocular-dominance. Factors such as asymmetries in the correlated functions of bilateral oculomotor regions should be considered in such investigations. In fact, there is evidence of a weaker representation of motor planning in the right, rather than the left supplementary eye field (SEF) (Donkelaar, Lin, & Hewlett, 2009). Yet it stands that the current study is not optimally configured for making an inference on this matter.

Although a few possible explanations exist for stronger interference in the right hand, it is important to underscore that the main effect of the hand factor in VisTime-P trials did not alter the interpretation of, nor detract from confirming the expected trends when making the important comparisons against VisTime-R trials. The expected contrast wherein a significant saccade-direction and hand compatibility interaction exists in VisTime-R but not VisTime-P trials is replicated despite the main effect of hand. This still permitted the identification of separate modes of interference consequent to predictive or reactive of visual tracking. In fact, it is consistency in this comparison between reactive and predictive behaviours that lends support to validating our previous study, and the suggestion that interference which emerges as a function of overlapping oculomanual demands on motor planning is imparted on the trajectory of either hand, whereas that which emerges as a function of overflow from the reactive saccadic network affects only the hand located in the hemispace wherein the saccade is directed.

Subsequent to the replication of previous results, a preliminary step in our analyses was determining whether an identifiable interference effect was expressed when covertly tracking reciprocal targets. This condition, in effect, was included as a control task for determining whether the interference effects from saccading are actually attributed to the preparation and execution of a saccadic command, and not instead to covert shifts in the spatial focus of attention. All the significant statistical tests involving the VisTrack factor were decomposed (Figure 5.2) and consistently failed to show that covertly tracking reciprocal targets in one's periphery resulted in any identifiable deviation congruent to the target motion.

Within these results our current study provided evidence that the source of interference between saccades and taps related to the motor coding of the saccadic action, and not to the covert shift in attention between spatial locations. It is certainly feasible to distinguish the separate coding of spatial shifts in attention from that which encodes parameters related to a saccade (Neggers et al., 2007; Juan et al., 2008). In this context, we support current views that a premotor theory of attention —*i.e.* that saccades and covert attention shifts are effectively different expressions derived from a common fronto-parietal substrate (Rizzolatti, Riggio, Dascola, & Umiltá, 1987) —is not relevant for explaining the dissociation between predictive saccades and attention shifts in many other regards (Smith & Schenk, 2012), of which we showed evidence in favour of our own dissociation.

It would be beneficial for a future investigation to corroborate the role of attention in the case of reactive saccades, as they are recognized as being more tightly coupled to a reflexive mode of attention orientation (Smith & Schenk, 2012). In the case of exogenous cues to which reflexive saccades are made without any prior element of expectation, there is a more significant overlap with attention than that shared by any form of voluntary saccade. Consequently, we may hypothesize that attention shifts may play a more relevant role with regard to the patterns of interference expressed in VisTime-R conditions than in the VisTime-P conditions we tested here.

In our specific procedure for evoking reactive saccades tracking behaviour was certainly reactive in nature, but fell short of being fully qualified as reflexive saccades. This was because our current task involved reciprocal targets and the location of upcoming cues was not unknown despite being temporally unpredictable. Since it is known that the focus of attention can deviate from central gaze when maintaining static fixation (Horowitz et al., 2007), it was likely that participants in our VisTime-R study had already shifted attention to the expected location of the next cue by the time the reactive saccade was initiated. In this case, the unmasking of the cue at that next location would not have been expected to evoke a shift in the spatial focus of attention as the focus of attention was perhaps already there. For this reason, by means of the nuances in the design of our reactive saccading paradigm our results were somewhat robust in refuting the capacity for attention to evoke any tangible effects under these constraints.

In follow up studies, a hypothetical task designed for resolving the respective roles of attention and saccades as it relates to reflexive orientation might use a centre-out tracking paradigm with left, right, up, and down targets presented in randomized series. If done properly this would account for a fully reflexive saccadic mode of tracking. However one must consider the additional complexity introduced when separating attention from concurrent motor-related representations. Often times a dissociation between these two factors leads to the necessity of introducing the element of response inhibition in a go, no-go task from which other confounding effects emerge (Bremmer, Kubischik, Hoffmann, & Krekelberg, 2009). Nonetheless, we provided evidence that covert tracking contributed no significant interference effects to the task.

Another major grouping of the trial manipulations imposed in the current study required vertical saccades, in TrackPlane-V trials. We had initially made specific predictions that, should interference emerge when making saccades in a vertical plane, the compatibility effect from horizontal reactive saccades would be lost. These followed from reasoning that a more bilateral representation of vertical reactive saccades could couple more evenly with either hand, as compared with the interference from lateralized representations of horizontal saccades in the hemispheres contraversive to their direction (Schlag et al., 1998). Unfortunately, our results identified no significant interference from predictive vertical saccades (Figure 5.3). Moreover, the trend in interference from reactive vertical saccades did not conform to any a priori expectations (Figure 5.4b).

The only case that a vertical saccade caused an identifiable interference in the fingertip trajectory was when downward saccades caused a significant downward deviation only in right hand responses. Here we openly speculate on a possible explanation that would most certainly require future testing to corroborate, yet is founded in a deliberate logic. As mentioned above, it is recognized that a premotor theory of attention is valid for the case of tracking exogenous cues (Smith & Schenk, 2012). There are known asymmetries in the division of the upper and lower hemifields in regard to their modulation of task factors relating to attention and motor processing, including the distinction of greater magnitude downward versus upward saccade-related activity in task-relevant brain regions (Zhou & King, 2002; a. Tzelepi et al., 2005; A. Tzelepi et al., 2010). It is also known that motor processing for manual actions in the lower visual field have privileged implementation of visuomotor processing (Goodale & Danckert, 2001). In this respect, a preferential interference effect of downward saccades is not aberrant to the extent that supporting theories would be difficult to construct and test. Indeed a future study may explore this in combination with the similarly biased onset latency, whereby only the plane of manual action facilitated the execution of downward saccades.

A last point of discussion is that of the partial rotation of our task into the FinPlane-PRL condition, where saccades were directed either parallel or anti-parallel with respect to the action of the hand as the fingertip accelerated toward the tapping surface. The purpose of including this task variation was not so much the fact that it applied yet another spatial rotation in its configuration, but rather that it tested the hypothesis that saccade-congruent interference can manifest in the modulation of a different kinematic measure. When saccades were initiated in the same direction as the fingertip does as it moved toward the tapping surface, we anticipated a congruent representation of the saccade would enhance the peak velocity of the fingertip. In some respects, this prediction is a reciprocal variation of the known fact that congruent arm movements enhance saccadic velocity (Snyder et al., 2002). We anticipated observations that saccading in an opposite direction to that of the fingertip would result in a slower velocity.

Contrary to our predictions, none of our task variations in the FinPlane-PRL conditions resulted in significant modulations of peak fingertip velocity. This consistent lack of relative saccade orientation in modulating velocity was conserved in both predictive and reactive saccding conditions. At first, this might seem to be an underwhelming result and a null finding. Yet we can interpret the lack of any modulation itself as perhaps revealing of important properties about the way in which saccades *did* cause interference in the case of perpendicular orientation between the eye and hand movements. There are a few relevant factors to consider, the first of which is that in the FinPlane-PDR configuration the magnitude of interference as it was expressed by tap-to-tap deviations was itself very small. Responses made in the FinPlane-PDR condition were conducive to a better resolution for measuring these small effects because there was no large scale variability expected within this axis of motion. Conversely, velocity signals recorded in FinPlane-PRL were much larger in scale and inherently more variable.

Our FinPlane-PRL results indicated that any signal representing the cross-integration of the saccade parameters into the motor command of the fingertip was obfuscated by the larger variability inherent in measuring the finger trajectory in its primary axis of motion. However, one must consider that many studies suggest there is a common goal representation in motor planning for coordinated eye-hand actions (Tipper et al., 2001; Kattoulas et al., 2008; Lünenburger et al., 2000; Snyder et al., 2002). Evidence suggests that in coordinated eye-hand aiming, there is a goal representation in planning from which motor commands for the eye and arm can be derived. Specifically, the two seem to share a common planning substrate because the degree to which the velocity of a saccade is facilitated by a congruent arm movement is modulated by the impending kinetic requirement of the arm. This scaling effect occurs in the saccade even prior to the initiation of the arm movement, and is accordingly determined to be a function of an overlap in representing the pre-programmed arm kinetics. It would seem that the faster saccade velocity is results from a bias introduced in the saccadic goal, as there is no execution-related arm reaching signal to bias the saccade velocity. And as mentioned above, our current and previous (Richardson et al., 2013) results in FinPlane-PDR conditions contrast VisTrack-P and VisTrack-R responses to demonstrate distinct motor planning-related interference effects.

So it is then logical ask why we failed to observe a similar effect whereby the goal of the fingertip action might have scaled as a function of the saccade congruency? In such terms, we may not expect the small effect of saccading would become lost in the larger variability of the primary tapping axis. Instead, if the motor commands for saccades and taps are derived from an inverse translation of an effector-unspecific goal representation, then one would expect the interference introduced to the encoded goal from concurrent saccade preparation might scale according to the magnitude of the finger's motor commands. We failed to observe this trend, which by extension could mean that the motor planning-related effects we observed in our VisTrack-P task and FinPlane-PDR configuration emerged as a function of mechanisms other than those biasing an effector-unspecific goal representation.

The first explanation we offer as to why this did not happen is simply that our task was perhaps designed so this did not happen. Earlier in the discussion and in the introduction sections we reviewed evidence that the respective trajectory formation in manual aiming movements is representative of a control strategy that is optimized by a spatial goal (D. Elliott, Helsen, & Chua, 2001). Conversely, the trajectory of the fingertip during paced tapping is a function of optimizing the temporal goal by means of error in the contact time of the fingertip with respect to the pacing goal (M. T. Elliott et al., 2009; Balasubramaniam et al., 2004). For this reason, the nature of the finger tapping in our current experiment was categorically different from the manual component of aiming tasks, in that tapping was a timing task with no explicit spatial goal specified by which to constrain its execution. While a common spatial goal representation for eye-hand aiming might lead to correlated kinematics, the absence of overtly controlling for a spatial goal specified for finger tapping might be the reason the action was immune to spatial interference effects that scaled with the fingertip velocity in its primary axis.

Importantly, this line of reasoning does not change the conclusion that the interference we did observe in VisTrack-P FinPlane-PDR trials was correlated to the involvement of motor planning. Yet it does warrant a revised hypothesis about its related mechanism by which interference was actually implemented. Accordingly, it could be the case that the observed interference related to motor planning implements its effects not as an interference on the actual goal representation, but rather by means of causing a generalized decrease in the effective gating, and increase in overflow of effector-coded signals between oculomotor and the upper limb's motor system. To confirm this hypothesis, future work would need to investigate variations of the task using an exogenously imposed incentive to control for spatial accuracy in the tapping responses. This might be accomplished by means of placing a tactile goal on the tapping surface.

In summary, the current results replicated and extended the findings of our previous study that investigated eye-hand coupling by means of a novel saccading and tapping motor paradigm. This task was used as a tool to investigate the organization of concurrent eye and hand movements within an alternative context from the common model of coordinated eye and hand aiming. This provided a unique insight into the sensorimotor control processes for determining how the task constraints manipulated the internal representation of the task and consequently affect the expressed modes of coordination. Interference observed in fingertip trajectory consequent to executing concurrent saccades, but not covert tracking supported the notion of a motoric framework for eye-hand coupling in this context, specifically one that does not appear to be compatible with a premotor theory of attention. Vertical predictive saccades did not show any generalized or specific interference causing effects as we had predicted, but downward reactive saccades did evoke congruent spatial deviations in the fingertip of the right hand. The current results provided a basis for further enquiry into what degree the distinction is relevant between reactive saccades from those which are fully reflexive in regards to their effects on coupling. Overall, our results support the distinction that motor planning exerts eye-hand coupling effects by different means than does execution-dependent processes, while providing the framework for testable predictions in future studies.

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Chapter 6

General discussion

6.1 Online saccadic corrections

A long series of literature has developed a number of claims regarding the control theory of goal-directed upper-limb actions (Elliott, Helsen, & Chua, 2001). More recently, work examining saccadic trajectories has extended some of these claims to explaining the operation of online spatial corrections in saccades. Leading into the formulation of the current studies, one recent parallel drawn between the behaviour of manual aiming (Heath, Westwood, & Binsted, 2004) and saccading (West, Welsh, & Pratt, 2009) was that feedback-based corrections for either movement operated more efficiently in visually-guided responses than in memory-guided responses. A reasonable inference from these observations stands to conclude that spatial working memory (SWM) is the culprit for exerting the deteriorating effects in online corrections.

While this is true, the simple fact that SWM itself implicates a broad neural footprint (Brignani, Bortoletto, Miniussi, & Maioli, 2010; Ungerleider, Courtney, & Haxby, 1998) implies that stating *anything* is a function of SWM bears an inherent imprecision within a reductionist framework. Accordingly, studies in Chapter 2 and 3 have refined the precision to which a model defines the mechanisms that contribute to modulating the efficiency of online saccadic corrections. Chapter 2 resolved the distinction that a SWM-related deterioration of corrections in delayed memory-guided (dmgSac) saccades was avoided in the case of predictive saccades. Since predictive saccades also derived their metrics from a representation in SWM, we concluded that the contribution of SWM to trajectory formation in saccades was modulated by other concurrent task factors. These results leave open the question whether the correction-diminishing effect of SWM on dmgSac responses was avoided in predictive saccades due to the additional encoding of saccades in motor planning, or if the otherwise inefficient operation of SWM was enhanced or habituated as a function the serial reproduction of reciprocal responses.

Future research should indeed seek to confirm if one of these suggested mechanisms explains why predictive saccades are conducive to efficient online corrections, a topic alluded to in the discussion sections of Chapters 2 and 3. However, Chapter 3 did not progress incrementally to answer these question as its formation precluded the results of Chapter 2. Whereas Chapter 2 aimed to resolve whether the recruitment of SWM induced a mandatory cost in the operation of online corrections, Chapter 3 aimed to dissociate why SWM can exert a deteriorating influence on dmgSac responses as it has been shown to in isolated responses (West et al., 2009).

A preliminary hypothesis tested the theory that spatial uncertainty in the encoded saccade and target metrics could explain both the degraded performance from SWM in dmgSac responses, and that consequent to anti-saccades (Heath, Dunham, Binsted, & Godbolt, 2010; Heath, Weiler, Marriott, & Welsh, 2011). We used Gaussian blob targets to induce varying degrees of perceptual uncertainty in their spatial localization. We observed a modulation of onset latency and total amplitude in the corresponding saccade metrics, which indicated the range of blurring applied in our stimuli did modulated their perceptual representation in a graded manner as we had intended. Despite these behavioural modulations, no trends in the variability and regression of trajectory kinematics supported any diminished operation of online corrections. We failed to corroborate an explanation of deteriorated dmgSac and antSac responses from perceptual spatial uncertainty.

Interestingly, other results from Chapter 3 confirmed a modified version of our initial predictions. We hypothesized that SWM exerted its effect in deteriorating the performance of dmgSac responses as a function of its correlates that coincide with the ventral visual processing stream. Engaging the contribution of ventral stream operations for encoding saccade metrics was accomplished by means of illusory M*ü*ller-Lyer targets. Indeed we observed a modulation of the evidence for online corrections in saccades to illusory targets relative to control targets, but the modulation effect revealed a trend that was opposite to what we had initially predicted.

As opposed to the predicted consequence of diminished corrections when saccading to illusory targets, we observed that larger corrections were implemented in these responses. We explained these observations, but not as a function of enhanced operations of online corrections since this is rather unlikely. Instead, we argued that kinematic evidence for larger scale corrections results from correcting for larger errors in trajectory by means of online corrections that are implemented with a normal efficiency as compared with those typically observed in visually-guided saccades to control targets. In line with this, we also contended that a greater degree of intervention from corrective mechanisms is perhaps required to resolve the increased conflict in the encoded metrics from discrepant representations in the dorsal and ventral stream.

Our interpretations posit separate sensorimotor operations encode different the target by means of different parameters in dorsal and ventral streams. Importantly, the preceding research sections have supported a modularized view of functional-anatomical segregation with many referenced examples of shifting patterns of neurophysiological correlates. It is often the case that differences in neural activation patterns between and intermediate to the superior parietal lobules (SPL) and inferotemporal cortices (IT) are associated with the varying psychophysical nature of the task. So our findings are independent of the current debates regarding the postulated dissociation of perception and action with ventral and dorsal anatomy.

Additionally, our interpretations of the neuropsychological consequences imparted by the range of variation of task psychophysics are not mutually exclusive with either perspective in the debate for or against the claim whether dorsal and ventral processing reflects direct and indirect means of motor parametrization in its most literal sense. While a number of our experiments have derived empirically testable hypotheses from duplex vision theory, our findings are not by inherently susceptible to all the same criticisms. For example, it is not debated that sensorimotor operations associated with the ventral stream are relevant to encoding allocentric target properties related to inducing perceptual and motoric illusions. Instead, criticisms are often directed at the claim that the illusory motor effect increases as a dorsal representation decays (V. H. Franz, Hesse, & Kollath, 2009). In this respect, our studies provide continuing support for the evolving view that visuomotor integration is an integrative process of modularized function without making claims regarding the overall validity of duplex vision theory (Milner & Goodale, 2008; Goodale, 2011; Westwood & Goodale, 2011) or of its contenders (Schenk, 2010; Schenk, Franz, &

Bruno, 2011; Bruno & Franz, 2009; V. Franz & Gegenfurtner, 2000; V. H. Franz et al., 2009).

The most significant contributions of our studies to the overall understanding of factors that influence the efficient and inefficient implementation of online saccadic corrections are revealed when considering the collective results from the full range of studies on this topic. An emerging trend that our current studies confirm is consistent across the entire set of these works reveals that efficient corrections are evident in all cases of visually-guided responses whether it is directed to a control, illusory, or blurred target. In the case of dmgSac responses, we reasoned the most refined explanation for their diminished online corrections is then more precisely claimed to be a consequence not only as a function of their encoded responses being contributed to by ventral stream visual processes. Rather it is because dmgSac responses are exclusively dependent on that representation.

Research in the general investigation of online saccadic corrections has made quick progress in adapting control theory and analysis techniques from the study of trajectory formation in manual aiming. Despite the advancing investigations of trajectory formation in saccades, the precision in examining saccade trajectory and in modelling its control theory is comparatively coarse to that relating to manual aiming. To this effect and in extension of analogous studies in manual aiming (Elliott, Carson, Goodman, & Chua, 1991), the online corrections in saccadic trajectories have thus far been impervious to their distinction as being implemented in a continuous or discrete intervention strategy.

Future studies of oculomotor encoding, specifically those related to trajectory can certainly build incrementally on our current work to resolve the questions our current research studies have opened in the process of answering others. To this point, the current literature on the operation of online saccadic corrections has employed a range of visual stimuli and tracking protocols. Experimental manipulations in this form have been useful, but future directions should seek other forms of task variation to improve on the coarse precision of the current investigations. For example, while human studies cannot directly measure single-cellular neural dynamics, the results from non-human primates studies can be adapted to account for lower levels effects than those we can directly measures.

In line with this idea, one particular limitation of our methods in Chapter 3 is the use of Gaussian blobs to induce perceptual uncertainty. It is perhaps the case that spatial uncertainty in the perceptual representation is not paralleled in the uncertainty of the tuning of a consequent saccadic response. Should diminished online corrections function as a results of uncertainty in motor, but not perceptual encoding our methods remain insensitive to this distinctions. Future work might circumvent this limitation in the application of probabilistic models to the presentation paradigm of task stimuli and of the observed responses. This idea is based on the notion that even low level oculomotor structures like the superior colliculus (SC) represent target probability-contingent activations (Basso & Wurtz, 1998). So, future paradigms might infer more detailed properties about the processes contributing to the trajectory formation by testing more detailed models.

In summary, while no one study can include the necessary breadth to fully dissociate why and how online corrections in saccades become modulated by a range of task factors the results from Chapter 2 and 3 contributed significantly to this process.

6.2 Eye-hand coupling

Bimanual interactions are one instance of coupling wherein the distinction of different sensorimotor processes is relatively clear as they separately contribute to the observed behaviour. There is a wealth of evidence to demonstrate that the interaction of homologous limb movements is a special case related to a number of functions that implicate motor planning (E. A. Franz & Ramachandran, 1998; E. A. Franz, Zelaznik, Swinnen, & Walter, 2001; Heuer, Kleinsorge, Spijkers, & Steglich, 2001; Heuer, Spijkers, Kleinsorge, Loo, & Steglich, 1998), execution-dependent interactions (Carson & Kelso, 2004; Carson, 2005), and perceptual integration (Mechsner, Kerzel, Knoblich, & Prinz, 2001). A number of studies have also demonstrated the correlation of performance measures between oculomotor and manual motor responses in coordinated goal-directed tasks (Donkelaar, 1997; Donkelaar, Siu, & Walterschied, 2004; Snyder, Calton, Dickinson, & Lawrence, 2002; Gueugneau, Crognier, & Papaxanthis, 2008; Cohen & Rosenbaum, 2007; Lünenburger, Kutz, & Hoffmann, 2000; Kattoulas et al., 2008). Evidence from these tasks suggest the interactions of eye and hand responses is encoded at least in part in preparatory motor planning, but provide little insight in resolving whether these coupling effects emerge as an exclusive function of spatial coordination.

We examined fingertip trajectory from tapping responses in a tabletop motor timekeeping task while saccacdes were performed concurrently either in synchrony with the tapping or at random intervals in reaction to unpredictable timing. In either variation of the saccading task, the fingertip trajectory demonstrated spatial attractions congruent to the direction of the concurrent saccade. From this preliminary finding, our studies made the novel distinction that preconceived spatial coordination is not a necessary requirement for spatial interference between eye and hand actions.

In Chapter 4, we demonstrated spatial interference in the fingertip presented with different patterns from predictive and reactive saccades. Reactive saccades exhibited a limited interaction with the hands, wherein the rightward saccades only attracted the trajectory of the right hand fingertip responses to the right. A mirrored compatibility effect was consistent in left hand responses consequent to leftward saccades. Despite the specificity of spatial interference from reactive saccades, predictive saccades that were executed in fully synchronous series of responses with finger tapping induced a spatial interference effect that was not selective of the compatibility between the responding hand and saccade direction.

These results reveal new perspectives that spatial coupling between eye and hand movements is not contingent on any explicit intention for their coordination. Perhaps the most intriguing result we ascertained from this work was that motor planning-dependent spatial coupling effects emerged as a function of an overlap in planning eye and hand movements irrespective of motor planning being engaged to implement their coordination in form of a spatial or temporal goal.

An extension of these results in Chapter 5 revealed no significant spatial interference effects from covert visual tracking of the target motion. This particular finding led us to reject the alternative explanation that the shifts in the spatial allocation of one's attention are responsible for a subordinate source of the interference observed from saccades. On this bases, we concluded that an explanation for the eye-hand interference effects we observed was best modelled in a motoric framework that claims the coupling emerges as a results of encoding the eye and hand responses and not other perceptual factors that were otherwise inherent to our initial paradigm.

We attempted to compare the relative presentation of spatial interference from horizontal saccades with that from vertical saccades. This investigation followed our predictions that reactive vertical saccades would interfere equally with the trajectory formation of tapping responses in either hand because of their bilateral cortical representation (Gaymard, Ploner, Rivaud, Vermersch, & Pierrot-Deseilligny, 1998; Schlag, Dassonville, & Schlag-Rey, 1998), unlike the hand specificity demonstrated in the implementation of interference from horizontal reactive saccades. However, the absence of consistent patterns of interference from vertical saccades in any instances of our task precluded and prevented us from confirming these predictions. The only case of significant interference from vertical saccades was found in downward reactive saccades causing a significant downward deviation in right hand responses. The mechanism of this effect was unclear, and future investigations might query its replication and explanation in a context that considers handedness and the bias for enhanced attention and visuomotor integration in the lower visual hemifield (Previc, 1990).

In fact, we tested another prediction that aimed to reveal the mechanism of motor planning-dependent spatial interference. We hypothesized that the specific case of interference from saccades which was contingent on motor planning was an effect that integrated its interference by means of biasing the encoded metrics of manual responses in planning. This theory contended that evidence to support this mechanism would demonstrate that spatial interference from saccades would scale with the magnitude of the encoded metrics. Specifically, we predicted that small scale interference from saccades directed perpendicular to tapping was in fact small in scale because it had biased the encoding of the finger tapping metrics in planning, for which the encoded metrics in any direction other than that of the primary tapping axis is a minimal component of its representation. This extended to predicting that interference which biased the encoded metrics of tapping in its primary axis would introduce a larger scale interference effect as a function of introducing spatial corruption of the metrics that encode a comparatively larger scale component of the action.

However, our current results did not demonstrate any significant modulation of tapping velocity as a function of saccading in a (anti-)parallel axis and provide no support that motor planning-dependent interference was implemented in the preparatory encoding of manual metrics. Contrary to the predicted mechanism of interference, the current results instead supported the contention that motor planning-dependent interference implements its effects by means of exerting a top-down modulation of overflow between the encoded eye and hand responses at a level that integrates lower in the control hierarchy than that which specifies movement metrics in planning. This explanation is consistent with evidence from bimanual studies that demonstrated the interactions between primary motor areas are mediated by the top-down influence from secondary motor areas (Bestmann et al., 2008; Grefkes, Eickhoff, Nowak, Dafotakis, & Fink, 2008). Here, and also in the discussion section of Chapter 5 we underscore these conclusions are specific to our task context. In the current task, finger tapping responses did not rely on any explicit form of spatial control. Future studies might introduce a novel manipulation to engage an explicit mode of spatial control in similar fingertip responses by means of introducing a tactile cue to define a spatial location on the tapping surface where to the fingertip responses should be directed. It stands to hypothesize such studies may reveal other mechanisms of spatial interference specific to the processes which mediate a constraint of spatial accuracy in manual responses that was otherwise not inherent to the responses produced in our current tasks.

In summary, the current research into the mechanisms by which oculomotor encoding interferes with the concurrent performance of a basic manual task contributed to a refined model of the functional organization of processes contributing to oculo-manual coordination. These works are, nonetheless, preliminary in their application of the novel oculo-manual task we designed for these studies. Future studies can certainly take advantage of this new motor task to examine the contribution of many other factors that may influence the operation and the mechanisms of eye-hand coupling. We underscore the value of our task paradigm for permitting the analysis of eye and hand coordination in a context that does not imply the requirement for their spatial coordination.

6.3 Future directions

The current research program derived its cohesive aims between studies in examining how the sensorimotor encoding of ocular control influenced the trajectory formation in its own subsequent motor responses, and those in coupled hand actions. Further research into these topics is undoubtedly important, but these incremental directions have already been presented in the sections specific to each study. Taking one step further, here we present a general plan for future research that is both complimentary to our current work and innovative in its design.

Chapter 4 and 5 work demonstrated the influence of oculomotor encoding on concurrent hand movements. In a complimentary approach, here we promote the reciprocal case wherein hand movements exert a modulation over concurrent oculomotor output. We have already provided a few examples of this case of coupling from studies that have demonstrated the correlated scaling of saccade metrics relative to manual responses in coordinated reaching and saccading tasks (Kattoulas et al., 2008; Donkelaar et al., 2004; Lünenburger et al., 2000). It is apparent these effects emerge from an overlapping representation for reaching and saccades in motor planning, but an attempt to reveal further mechanisms of hand-to-eye coupling is difficult in the case of goal-directed tasks since saccades and manual actions are executed on very different time scales.

The brevity of typical saccadic durations and their natural variability in the evolution of their trajectory are both limiting factor for investigating their trajectory formation as a function of any effects that occur on a slower time scale. While this fact introduces a technical challenge, it does not preclude the possibility that manual actions might influence ouculomotor output for other reasons than those previously ascribe to motor planning. In the case of isolated upper-limb actions, fast modes of feedback-based corrections contribute to their respective trajectory formation (Pruszynski et al., 2011). The efficient integration of proprioceptive feedback from the upper-limbs serves these corrections. In general, control policies serving a range of actions are mediated by the optimal integration of all the task-relevant information that is provided by the combination of our senses and our predictions (Wolpert, 2007; Ernst, Bulthoff, & Bülthoff, 2004). In extension, it stands to reason that a coordination dynamic between the eyes and hands emerges as a function of either action integrating any available feedback that describes the performance of the other.

Herein we include a brief report that provides cursory evidence that ascending somatosensory information from the limbs is integrated into the online control of saccades.

6.3.1 Pilot study: Saccadic control from upper-limb sensory feedback

We conducted a preliminary investigation to query whether saccade trajectory formation exhibited any evidence of integrating somatosensory feedback from concurrent upper-limb movements. In accordance with permission granted from the McMaster Research Ethics Board, and the Hamilton Integrated Research Ethics Board five research participants were recruited from local affiliate labs.

In this pilot study, we recorded gaze position to reconstruct the trajectory of saccadic eye movements when participants made horizontal responses in an eye-hand coordinated centre-out aiming task. Gaze position was recorded by means of a head-mounted eye tracker (EyeLink II, SR Research) and manual aiming was produced by controlling an on-screen cursor by means of a stylus-like manipulandum (Phantom Omni, SensAble Technologies) held in the right hand. The spatial configuration of the task and the relative posture of the participants was of primary importance to the purpose of the study. Right arm posture was constrained so that the forearm was placed on an arm-rest, with the right hand grasping the manipulandum. The rotation of the forearm was maintained at a midway point between supination and pronation, with the palm facing inward toward the body. With respect to the centre-out tracking task, in this configuration to move the cursor in a rightward direction participants aimed the manipulandum to the right by means of extension at the wrist. Conversely, leftward cursor motion was produced by aiming the manipulandum to the left with flexion at the wrist.

Every trial began with the presentation of a fixation target at the center of a computer display screen that was aligned with their central gaze. Participants were required to maintain steady gaze fixation on this target, and a neutral (0° of flexion/extension) wrist posture was calibrated so that the aiming cursor also maintained steady fixation on the central target. Subsequent to a brief period of maintaining stable oculo-manual fixation, a movement target appeared either to the left or the right of the central fixation target. Participants were instructed to saccade to the target location and to point to the same target with the aiming cursor.

Importantly, in catch trials our task applied a perturbation to the manual aiming responses. We used a single electromagnetic pulses from a transcranial magnetic stimulation (TMS) unit (Rapid^2, MagStim) to induce unexpected perturbations to the trajectory of aiming responses by directly inducing a brief muscular contraction in the forearm. In a pseudo-randomized presentation scheme, 20% of trials included TMS stimulation directly to the extensor or flexor muscle groups in different blocks of trials. In effect, the perturbations were applied in one of two ways, either causing a perturbation that was spatially congruent or opposite to the direction of the cued response.

The spatial congruency of the TMS-induced perturbations relative to the intended direction of the eye and hand response is the most important factor to consider. Whereas spatially congruent perturbations caused deviation in the arm's trajectory in the direction of the intended target, incongruent perturbations caused trajectory deviations away from the intended target. Since we stimulated two muscle groups in separate trials, this congruency emerged differently with respect to either flexor or extensor stimulation. Extensor stimulation always induced a muscle contraction that caused deviations in pointing toward the rightward direction, which was spatially congruent to rightward-directed responses, and incongruent to leftward-directed responses. The opposite relationship of congruency exists for flexor stimulation relative to the directional response targets.

We hypothesized that the trajectory of saccades might reflect the integration of the perturbation induced in the arm's trajectory. Since the saccades produced as a part of this task are very brief, to assure that the perturbation to arm trajectory was applied at an instant that overlapped with the saccade, the onset of the TMS pulse was explicitly triggered as a function of saccadic onset. In other words, following the presentation of the response target, at the instant the eye tracker detected the onset of the corresponding saccade ($>30°/\text{sec}$ and $5000°/\text{sec}^2$) a TTL pulse was triggered from the eye tracking system within 1 ms and sent to the TMS unit to evoke the stimulation pulse and consequent arm perturbation that it incurred. A total of 600 trials were collected, thus permitting the analysis of saccade trajectory in 120 saccades that were paired with TMS perturbations, 30 of which were in either the left or right direction and paired with either congruent or incongruent TMS.

As a function of either the spatially congruent or incongruent application of the perturbation with respect to the cued direction of the responses, we hypothesized that the saccade trajectory would demonstrate differences in its kinematics if its formation was at all contingent on integrating sensory feedback. The limited breath of our pilot study precluded the use of elaborate trajectory analysis using variability and regression techniques that were included in Chapter 2 and 3 studies. Instead, we examined trends in the mean way that our intervention modulate the deceleration time from the saccade's peak velocity to its offset. Despite the TMS perturbation being applied at the instant saccades are initiated, we anticipated that any modulations of saccade trajectory would necessarily occur in this late phase of its trajectory, consequent to the inherent transduction delay (approximately 20 ms) of the upper-limb afferent signals even for fast direct integration into subcortical networks. In respect this respect, deceleration time is an appropriate cursory indicator of changes in trajectory formation (Roy, Kalbfleisch, & Elliott, 1994).

To this effect, even with the small sample size of five participants, an ANOVA demonstrated a significant interaction between the Intervention (noTMS, TMS) × TMSCongruency (Congruent, Incongruent) factors $F_{1,4} = 13.448$, $p = 0.021$, $\eta_p^2 = 0.771$. Post-hoc comparisons revealed this interaction emerged as a function of a significant difference in the deceleration time of saccades when TMS was applied congruent to the response direction ($M = 54.41, SD = 14.80$) relative to incongruent perturbations ($M = 61.99, SD = 18.83$) $t_4 = 3.031$, $p = 0.039$. Additionally, there was no significant differences between the deceleration time measures from noTMS control conditions and TMS that was applied congruent to the response direction.

In summary, this pilot study has demonstrated that saccade trajectory was indeed influenced by the online integration of feedback from concurrent upper-limb movements. We observed a significant increase in the saccade deceleration time when a concurrent arm movement was perturbed to cause a deviation in the direction opposite to the current response. While we have provided preliminary evidence for fast sensorimotor integration in this manner, whether this effect reflects the operation of networks that mediate an explicit coupling dynamic is unclear. Future extensions of this work need to corroborate that the modulation we observed in deceleration time of saccades by other means, with more complex forms of trajectory analysis. Overall, results from this pilot study revealed new perspectives in oculo-manual control strategy that are important considerations in the grand scheme of characterizing mechanisms of eye hand coordination in future work.

6.4 Final words

The current dissertation studies have successfully made a number of inferences regarding the functional organization and sensorimotor representation of eye and hand movements. In addition to the contributions our current results for refining models of control theory related to specific instances of these actions, the general implication of our work is an obvious demonstration that the characterization of motor behaviour is a process that must be conducted with consideration to context-specific effects in regard to which motor behaviour emerges. Examples of this are provided in our studies wherein even subtle changes in the constraints imposed on the performance of a given action are often correlated to different control strategies. In turn, each control strategy engages a specific range of sensorimotor operations. To this effect, by means of comparing how motor behaviour changes in response to a range of task-specific constraints, our studies have provided new perspectives in dissociating separable sensorimotor processes as they contribute by independent and interactive means to trajectory formation in isolated saccades and oculo-manual coupling.

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