COORDINATING THE EYES AND HAND IN GOAL-DIRECTED MOVEMENT SEQUENCES

by

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Abstract

Coordinated gaze and hand movements predominate a number of our interactions in reachable space and yet few studies examine the potential contribution of tactile feedback in planning these actions. This thesis was designed to investigate eye and hand coordination during movement sequences when reaching out to interact with objects. We developed a virtual reality paradigm that allowed us to control visual, tactile, and in some cases, auditory feedback provided to participants. Participants reached and touched five objects in succession. We measured behaviour that resulted from removing one or more of the aforementioned sources of feedback – focusing on task accuracy, and the timing and dynamics of eye and hand movements. Our principle manipulations were to remove visual feedback of the hand, and/or to change the object response to contact. We also unexpectedly removed tactile feedback signaling contact. In Experiment 1, we examined gaze and hand movement timing relative to contact events. Gaze remained long enough to capture contact in central vision, but also followed a time course indicating that contact timing was predicted. In Experiment 2 we examined the influence of dynamic object consequences (i.e., motion). Gaze remained to monitor consequences that follow initial contact especially when the hand was invisible; with longer delays it became difficult to differentiate between predictive or reactive movements. In Experiment 3 we directly tested whether gaze would hold upon a site of action during prolonged manipulation. Here, gaze remained past contact time and instead its departure was associated with the completion of action. Our findings are congruent with the notion that visually guided reaches are controlled to facilitate directing the hand to viewed locations of action – without visual feedback of the hand accuracy diminished and hand approach changed across all experiments. However, we provide consistent evidence that gaze is also controlled to capture planned sensory consequences related to action at its viewed location. Monitoring these sites would facilitate comparing predicted sensory events with those that are actively measured and improve control throughout the movement sequence. Such a process also indicates the importance of considering tactile feedback when examining coordinated eye and hand movements.
Co-Authorship

My colleagues R.J. Flanagan and R.S. Johansson co-authored the manuscript “Eye-hand coordination in a sequential target contact task” submitted to the journal Experimental Brain Research and published in v195 (2009). This work comprises Chapter 3 of this dissertation.
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Chapter 1

Introduction

The past two decades have been a time of dramatic and prosperous growth for investigating the psychological and physiological mechanisms involved in calculating the body’s comportment. In particular, there has been a great deal of interest in examining how the Central Nervous System (CNS) uses available information from key events that define task progress to generate accurate and well-timed motor responses during complex movements. One potential means of organizing the manifold sensory information available in action has been submitted by my colleagues: action—and its consequences—is planned relative to key events in a task by establishing and updating correlations between involved sensory systems (Johansson, Westling, Backstrom, & Flanagan, 2001). These events are called control points by the nature of their purported role; they influence motor planning by providing task-critical sensory information – often in more than one sensory modality. Such simultaneous feedback might arise, for example, from a viewed point of contact between the hand and an object where somatosensory, visual, and auditory feedback may be associated. The information gleaned at control points can help furnish the CNS with a means of registering ongoing task progress and aid in preparing for future considerations in a task (Flanagan, Bowman, & Johansson, 2006; Johansson & Flanagan, 2007). When information assumed to contribute to planning is otherwise limited or removed, making use of control points may become especially important. The current studies examine this issue with regard to movements within sequenced eye-hand tasks.
Many investigations into the coordination of more than one action system have examined how gaze is positioned during hand action, and for good reason: we look to where we plan to act (Hortsmann & Hoffmann, 2005). Such predictive gaze placement emerges early in life when newborns move their arms to where they fixate and by way of experience the association between the eye and hand systems is gradually refined (von Hofsten, 2004). By adulthood, we engage in a multitude of predictive visually guided movements preceding manual responses without overtly attending them (Medendorp, Beurze, van Pelt, & van der Werf, 2008). Gaze behaviour has been documented in walking (Patla & Vickers, 2003), block manipulation (Ballard, 1992; Flanagan and Johansson 2003), driving (Land, 1993; Land, 1998), playing cricket (Land & Macleod, 2000), table tennis (Bootsma & Weiringen, 1990), and conducting daily routines (Land, Mennie & Rusted, 1999; Hayhoe, Shrivastava, Mruczek, & Pelz, 2003). In all these cases gaze placement is described as subserving manual action, often by leading intended action with the hand or object-in-hand.

Of course, the interplay between controlling gaze and the hand is not as simple as the eyes being a slave to desired hand action; each system has the potential to influence the other (Melcher & Colby, 2008; Thura, Hadj-Bouziane, Meunier, & Boussaoud, 2007). Yet many of the general control mechanisms allowing these two independent motor systems to be coordinated remain unclear. By registering sensory information related to key parameters in a task (e.g., the moment a hand contacts an object), control might be achieved for the current but also for future actions (Johansson et al., 2001; Flanagan et al., 2006). Thus, by studying gaze and hand behaviour relative
to control points—where task-critical sensory information is obtained—we stand to learn much about how these separable action systems can be coordinated.

The rich and contributory sensory information provided through tactile receptors in the hand can feasibly influence how action between the eye and hand systems is coordinated. Yet paradoxically many researchers specifically avoid tactile feedback while studying visually guided hand movements (see e.g., Beurze, van Pelt, & Medendorp, 2006; Batista, Buneo, Snyder, & Andersen 1999; Prablanc, Eschalier, Komilis, & Jeannerod, 1979; Prablanc, Pellison, & Goodale, 1986; Prado, Clavagnier, Otzenberger, Scheiber, Kennedy, & Perenin, 2005; Sober & Sabes 2003; Sober & Sabes 2005). These same papers have influenced the current conceptualization of how eye-hand movements are organized and executed without addressing the potential involvement of tactile feedback. The present research addresses this issue by investigating visual and tactile feedback arising from control points in a task—both of which may signal task success—to determine how each input influences planning and executing a visually guided sequenced manual task.

This dissertation was devised to manipulate the multisensory information that might contribute to planning and executing sequenced actions. A series of four experiments were conducted employing a virtual reality environment in which participants held a robot handle and were instructed to reach out to touch five objects in succession. Gaze movements and hand movements in the task were quantified and compared. In particular, the spatial and temporal association leading up to and moving away from the goal of contacting each object was examined. Behaviour was analyzed
with respect to the idea that feedback obtained from control points fundamentally determines how future action is executed.
Chapter 2

Literature Review

This program of research was comprised of four experiments designed to further investigate questions related to the contribution of control points in influencing visually guided manual action. In each experiment the available sensory information was changed as participants reached out to contact objects in a virtual reality. The manipulations influenced the available information relative to a purported control point in our task: object contact. To properly rationalize the current studies then, an examination of the literature related to planning visually directed hand movements—especially pertaining to control points—is in order.

2.1 Planning action relative to goals

The control of virtually all purposeful action depends on learning correlations, or mappings, between executed motor commands and the predicted sensory consequences of these commands (Wolpert & Flanagan 2001, Wolpert, Ghahramani, & Flanagan, 2001). To this end, action systems do not appear ready-made; the learned mappings are primarily determined by interactions with the environment that are shaped during development (von Hofsten, 2004). A critical facilitator of learning these mappings is through measured sensory input from key events—or control points—within a task (Johansson et al., 2001) that can inform the success of a component of a task (i.e., sub-goals) or that action’s relation to a larger goal (Johansson & Flanagan, 2007; Maravita, Spence, & Driver, 2003; Medendorp et al., 2008). Control points are task-specific, highly relevant events often characterized by providing sensory information in more than one
modality (Flanagan et al., 2006; Flanagan & Johansson, 2003; Johansson et al., 2001). Thus, key events are often the finite markers that define a task’s beginning and end (Binstead, Chua, Helsen, Elliot, 2001; Johansson et al., 2001; von Hofsten, 2004) such as the initial and final positions of an object moved from one location to the next. With sequences of actions, identifying key events may become less obvious. Reaching to a target while avoiding an obstacle might first require navigating around an obstacle (a sub-goal) and then reaching to the target (the final goal). By using rules and regularities that are learned through experience and thus influenced by feedback, the goals of action—whether simple or complex—can be predicted when planning how to move (von Hofsten, 2004).

Because the majority of action tends to be part of a larger set (i.e., related to a larger goal) it is prudent to study whether the availability of information from determinable sub-goals can influence subsequent movements related to a larger action goal. For example when controlling action, planning specific components of movements can be distinguished from planning how to achieve the final goal (Johansson & Flanagan, 2007; Medendorp et al., 2008; von Hofsten, 2004). We learn to identify goals early; infants attend to purpose over form when imitating and when generating novel movements (von Hofsten, 2004). The importance of identifying goals may have a neurological basis as well. When a macaque monkey observes a conspecific performing an action or generates the observed action, many of the same neurons show elevated activity; however, this common activation during observations only occurs when the goal of the action can be evinced (Umiltà, Kohler, Gallese, Fogassi, Fadiga, Keysers et al.,
Importantly then, understanding the goal of action is paramount to understanding how to plan and execute the movements needed to accomplish the goal.

Accounting for consequences of a planned action and its effect on the environment is a further requirement of action planning (Brown, Halpert, & Goodale, 2005; Goodale, Gonzalez, & Króliczak, 2008). Control points may be a critical component in determining these consequences (Flanagan et al., 2006); and may depend on the availability of—or ability to register—sensory feedback. Consider that many goal-based movements are executed while having to filter out irrelevant information in addition to selecting a given action from among several possible alternatives. Such complexity increases the computational requirements and cognitive resources used in determining action. As an example, the increased demand in planning reaches to multiple possible targets results in elevated BOLD activity in parietal and motor areas (Chapman, Pierno, Cunnington, Gavrilescu, Egan, & Castiello, 2007). Since most goal-related movements are not single unitary actions, action plans must update and account for each constituent component of a task (or sub-goals) with respect to the representation of the final goal (Flanagan et al., 2006). Sub-goals must also be determined relative to the final goal, lest compensations be required throughout the action set in order to properly achieve the desired final goal. One cannot reach to an object behind an obstacle without first accounting for how to avoid the obstacle.

Recent physiological evidence from Mushiake and colleagues (2006) has shown that preparatory neural activity occurs when planning action relative to a larger goal. When monkeys engage in a multi-step visually guided series of freely determined hand movements to a final goal, greater prefrontal cortex (PFC) activity precedes and follows
a sequenced movement than occurs during the movement series. This activation is independent of the motor activation related to executing individual movements in the task, and is instead thought to reflect the available means (i.e., ways of moving the hand) by which the final goal might be achieved and assessed. These authors speculate that PFC activity might result from monitoring the determination of the final goal independent of the potential intermediary movements (Mushiake, Saito, Sakamoto, Itoyama, & Tanji, 2006). Stated another way, action in this complex task was assessed relative to the final position that indicated task success (i.e., a control point). It is possible that in more complex action sequences, control points are useful for assessing sub-goals in direct relation to a larger goal.

2.2 Control Point Theory

Many parameters of control are determined with reference to the object to which future action is based (Brown et al., 2005) – the goal of action. While planning manual action, for instance, visual markers of position, orientation, and the properties of an object are continually updated such that planning motor responses to those objects can be facilitated (Brown et al., 2005; Milner & Goodale 1995). My colleagues’ research has also focused on planned goal-oriented behaviour and its sensory consequences (Flanagan & Johansson, 2003; Johansson et al., 2001; Sailer, Flanagan, & Johansson, 2003). Their findings suggest that sensorimotor correlations, necessary for retaining control during complex goal-based actions, are very likely maintained by registering feedback at key events or control points (Johansson et al., 2001; Sailer et al., 2005).

Control points in visually guided reaching tasks may facilitate planning and controlling complex movements by providing several key benefits to motor planning and
executing action (Flanagan et al., 2006). Control points might increase the probability of detecting task-sensitive sensory information because this information is signaled concomitantly in more than one sensory modality (Driver & Spence, 1998; Maravita et al., 2003; Stein, Jiang, Wallace, Stanford, 2001; Wallace, Merideth, & Stein, 1993; Wallace, Meredith, & Stein, 1998). Control points may also improve sensory estimates of the parameters needed to retain control during action and improve the precision of predicted future action and its consequences (Flanagan et al., 2006; Johansson & Flanagan, 2007). Control points might therefore facilitate: generating estimates used in controlling future actions (e.g. moving the hand between targets), as well as predictions of how to account for sensory consequences following interactions with the environment (e.g. preparing the hand to deal with the force borne out at contact with an object). As such, an investigation of behaviours relative to control points could benefit our understanding of how accommodating for the consequences of goals might change when new feedback becomes available or when expected information is removed.

2.2.1 Control points and improved sensory detection

Employing more than one sensory modality to identify an event increases the probability of detecting that event (Driver & Spence, 1998; Maravita et al., 2003; Stein et al., 2001; Wallace et al., 1993; Wallace et al., 1998). Indeed most actions produce consequences simultaneously in time and/or space, modifying detection thresholds and making it more likely that a stimulus is registered (Wallace et al., 1986; Wallace et al., 1998; Stein et al., 2001; Thura et al., 2007). As mentioned above, these associations can be learned through experience and then later relied upon (von Hofsten, 2004). The direct benefit of such a combination is that key sensory signals may be better registered and can then
more readily contribute to detecting and correcting errors (Doyle & Walker, 2002; Flanagan et al., 2006). Improved detection might also increase the accuracy of estimates that shape ongoing perceptual processes that may rely on integrating detected task-specific sensory information (Bresciani, Ernst, Drewing, Bouyer, Maury, & Kheddar, 2005; Bresciani, Dammier, & Ernst, 2006; Ernst & Banks, 2002; Gepshtein, Burge, Ernst, & Banks, 2005). Furthermore, by providing the system with more information, learning which signals to attend and which to filter out can be facilitated (Droll, Hayhoe, Triesch, & Sullivan, 2005; Ernst and Banks, 2002; Treisch, Ballard, Hayhoe, Sullivan, 2003). Perhaps by exploiting the associated sensory signals arising from a goal, a greater efficiency in comparing predicted and actual sensory outcomes may be achieved.

### 2.2.2 Control points improve estimations of task parameters

The second benefit of monitoring control points is that sensory estimations of the actor, relevant objects, and the remaining components of the task can be refined such that a greater control of the parameters necessary to complete a given task is made possible (Flanagan et al., 2006; Johansson & Flanagan, 2007). Such a benefit would be useful in determining how to grab a slippery object, for example. By comparing multiple sources of information related to predicted sensory outcomes the accuracy of the estimated control parameters can be improved (Wolpert & Ghahramani, 2000; Wolpert & Flanagan 2001). Gathering information from multiple sources allows the CNS to combine highly variable estimates across modalities, filling in information in one modality where it may be lacking in another (Gepshtein et al., 2005; Burge, Ernst & Banks, 2008). Of course increasing information does not by itself increase the precision of the estimates needed to retain
control since information could be superfluous. It is features related to the task that must be best determined – otherwise information load might become too great and the task computationally untenable. Indeed, the more task-irrelevant features that are attended, the more errors are made (Hodgson, Bajwa, Owen, & Kennard, 2000).

Combining spatially and temporally associated sensory signals may be a sensible approach to parameterize the necessary features of action in a task given that the senses have varying conduction times (Groh & Sparks, 1996; Joiner, Lee, Lasker, & Shelhamer, 2007; Stein et al., 2001) and can provide different aspects of information needed to retain control. When deficiencies in one modality arise, another contributory modality can compensate for this shortcoming (Diederich et al., 2003; but see also Gepshtein et al., 2005). Such a strategy might allow modifications to planned action when information is lacking in one modality such as when visual input is limited by darkness while tactile input can still inform the actor as to whether the slippery object is sufficiently grasped or when tactile information provides information used when grasping an object on surfaces that cannot be viewed. It is possible that combining otherwise weakened sensory estimates may allow sensory signals to be bolstered such that temporally and spatially robust parameterizations for controlling the components of movement can still be generated (Diederich et al., 2003). Similarly, if sensory signals are measured and combined in areas where precise estimates are most accurately generated (e.g., in front of an individual in comparison to an individual’s side), it follows that parameterized components of forthcoming action would be most accurate (Brown et al., 2005; Diederich et al., 2003). Combining multiple estimates can therefore result in greater precision than would be possible from one estimate.
2.2.3 Control points improve sensory prediction

Improved prediction is the final benefit bestowed from control points. Prediction allows the CNS to plan movements by taking into account expected sensorimotor consequences in a given phase of action so that the next phase might be launched before the current one is completed. Such overlap facilitates smooth transitions through component phases of an action rather than the erratic and intermittent movements that would result with reactively programming each phase (Flanagan et al., 2006; Johansson & Flanagan 2007). Especially in sequences of movements, planning adaptive behaviours depends on the ability to produce compensatory adjustments necessary to retain control of the task prior to the movement being made. However, when there is a mismatch between expected and predicted information, the motor system needs to be able to respond by generating appropriate compensatory adjustments. Generating these compensations requires that control mechanisms predict and react to sensory events with varying time sensitivities that partly owe to the different conduction times of the senses (Joiner et al., 2007). Stated differently, properly predicting consequences requires accounting for the various means in which sensory feedback might be generated following goal-based actions while still allowing reactions to discrepancies in predicted consequences when they arise.

Because the potential exists for the system to be overwhelmed with sensory information, a further task-protective component of predicting sensory consequences may be learning which irrelevant sensorimotor information can be filtered out (Droll et al., 2005; Triesch et al., 2003). While learning a task, predictions of expected feedback become more precise, leading to more efficient filtration of self-generated sensory
feedback (Mitra, Bhalarao, Summers, & Williams, 2005) in addition to better filtration of task-relevant information by predicting certain sensory information prior to movement (Angel & Malenka, 1982, Chapman & Beauchamp, 2006; Seki, Perlmutter, & Fetz, 2003). Such a strategy also allows measured sensory information to shape future performance because predicted motor outcomes are refined and adapted to incrementally produce smaller errors when compared to the actual feedback resulting from the movements (Harris & Wolpert, 1998; Wolpert & Ghahramani, 2000). When only certain components of an event are anticipated, or can be anticipated, the ability to accurately predict the expected outcomes of action will be diminished and the efficacy of planned action would presumably degrade. Effectively executing sequenced action may therefore require preparatory compensations in the ongoing action that hinge upon feedback at key events – that is, relative to control points.

2.3 Planning sequenced manual action

Prior to movement, preparatory compensations are made in the motor system that can affect perceptual processing. For example, receptive fields at a to-be-fixated location show marked increases in sensitivity prior to a saccadic movement (Duhamel, Colby & Goldberg, 1992; Sommer and Wurtz, 2000; Sommer and Wurtz, 2002). These predictive changes are not limited to the oculomotor system and have also been demonstrated in the supplementary motor area (Haggard & Whitford, 2004) and motor cortex (Chapman et al., 2007) preceding planned touch. Importantly, several studies have identified activity prior to planned movement even when the movement is not executed; it is the intention to act that brings about preparatory changes that normally precede action (Melcher and Colby, 2008). The presence of anticipatory preparations may indicate that the
sensorimotor system predicts the necessary compensations needed to retain control following goal completion (Johansson & Flanagan, 2007) particularly during movement sequences and that these compensations can span the involved sensory modalities of the action.

Registering feedback at control points might be a critical component of eliciting changes in predicted movements. Zorn and colleagues (2007) have argued that sensory feedback unrelated to movement can nevertheless instigate changes in a motor plan. In a task where participants followed a timed moving visual stimulus, those who first viewed the stimulus without moving their eyes on time with it showed faster learning than those who set about moving straight away. Here, movements were not necessary for learning so long as an error signal could otherwise be determined from sensory information (Zorn, Joiner, Lasker, Shelhamer, 2007). Thus future actions can be based upon predictions of sensory consequences relative to a goal, or control point (where several sources of information might be obtained), even when interactions with the object do not occur. This might explain why even when walking in darkness gaze leads trunk and feet to future points of predicted consequences (Patla & Greig, 2005). It is possible that control points are linked to a representation of where sensory consequences related to the goal of action might be expected to take place irrespective of whether that location can be seen.

When engaging in target-directed movements the predominant theory holds that planning is done relative to an occulocentric frame of reference (Batista et al., 1999; Buneo Jarvis, Batista, & Andersen, 2002; Buneo & Andersen, 2006; Crawford, Medendorp, Marotta, 2004). Gaze typically guides intended action by leading future
hand positions (Aivar, Hayhoe, Chizk, & Mruczek, 2005; Ballard, Hayhoe, Whitehead, 1992; Batista et al., 1999; Buneo et al., 2002; Buneo & Andersen, 2006; Epelboim, Steinman, Kowler, Edwards, Pizlo, Erkelens et al., 1995; Flanagan & Johansson, 2003; Hayhoe et al., 2003; Johansson et al., 2001; Land et al., 1999; Neggers & Bekkering, 2000; Neggers & Bekkering, 2001; Mennie, Hayhoe, & Sullivan, 2007; van Donkelaar, 1997). In doing so, efferent and/or afferent signals related to gaze position could help guide the hand – even when the hand cannot be seen (Prablanc, Desmurget, & Grea, 2003; Prablanc & Martin 1992; Prablanc et al., 1979; Prablanc et al., 1986). Moreover, with a stable gaze position, visual feedback of hand position can also be used to guide the hand toward a target (Paillard, 1996; Land et al., 1999; Carlton, 1981; Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995; Saunders & Knill, 2004; Sarlegna, Blouin, Vercher, Bresciani, Bourdin, & Gauthier, 2004). So long as the position of the fovea is maintained, reaches to this location are accurate (Prado et al., 2005), while moving gaze from this position when the hand cannot be seen systematically introduces error to a reach (Crawford et al., 2004; Prado et al., 2005).

Gaze often determines, and remains at, future sites of hand action until the hand achieves that position (Neggers & Bekkering, 2000). Maintaining gaze position upon a site to which action is directed might indicate that hand-based control parameters rely on signals related to that viewed location (i.e., a goal; Neggers & Bekkering, 2001). Indeed, gaze may be inextricably tied to how hand action is assessed and modified (Neggers & Bekkering, 2002) because both vision and somethesis can provide crucial information for the sensorimotor system in visually directed pointing tasks (Spence, 2002; Spence, Nicholls, & Driver, 2001; Medendorp et al., 2008). Vision plays an important role in
determining object shape and size, control parameters that will determine fingertip forces (Jenmalm & Johansson, 1997; Jenmalm, Goodwin, & Johansson, 1998; Flanagan & Beltzner, 2000). However, there are sometimes parameters that cannot be determined by gaze such as 3D shape, friction and hardness, and sometimes even object weight (Castiello, 2005; Klatzky & Lederman, 1995) As such, a focus on strict gaze-centered influences underlying action might underestimate the potential contributions of other sensory inputs needed when planning action.

There have been indications of the hands’ influence on eye movements, as when gaze movements are delayed during pointing tasks in order to monitor hand-based feedback relative to the goal. In Neggers and Bekkering’s (2000) work, participants were asked to direct gaze to a target and the hand toward another target. At variable times during the pointing motion, a new gaze target would appear. Upon its appearance participants were asked to fixate the new target as quickly as possible. Generally—when the hand and gaze target were spatially proximate—gaze movement to the new target was delayed until the hand reached the current target and when the targets were spatially disparate, the timing delay occurred less often (Neggers & Bekkering, 2000). Interestingly, gaze was even delayed when the hand could not be seen (Neggers & Bekkering, 2001). Gaze delays of this nature might indicate that completing and confirming coordinated gaze and hand movements is done relative to the final point for both effectors (Neggers and Bekkering 2000; 2001; 2002) – a shared goal. As mentioned above, planning done relative to a goal could reference all of the available sensory systems that may provide feedback as a result of the action.
It is possible that the above described goal-related evaluation and planning occurs in an internal reference frame influenced by, but not entirely constructed in visual coordinates (Burr, Morrone, & Ross, 2001, but see also Pouget, Ducom, Torri, & Bavelier, 2002). Such internal multisensory representations might help account for the consequences of achieving a goal beyond the goal’s visual position. For example, in estimating object properties, haptic (i.e., active touch) and visual feedback can be flexibly weighted to provide more accurate estimates than either mode will alone (Ernst & Banks, 2002). These estimations are a critical feature of planning movements to interact with an object (Bresciani et al., 2006; Ernst & Banks, 2002; Gepshtein et al., 2005) and action may be best planned relative to perceived or discernable components of object properties as well as with regard to where they are located in space.

When multimodal signals correspond in time and space—an indication of their potential contingency—they are most efficiently integrated (Gepshtein et al., 2005) and can best modify future actions. If action is planned relative to goals—or sensorimotor consequences arising from interactions therewith—then there may be a means of representing the workspace (i.e., the area in which action takes place) that would allow accounting for multisensory effects of a goal around which action is planned. In a recent example, Shore and colleagues (2005) showed that closely spaced tactile stimuli administered to the hands when near the body were more likely perceived as coming from the same source, whereas the same stimuli administered to the hands when far from the body were more readily discriminated. These authors contend that such an effect might plausibly be explained by a goal-based environmental representation of immediate reachable space rather than a somatotopic (body-based) representation
(Shore, Gray, Spry, & Spence, 2005). A body-based representation that contributes to planning might differently influence movements than visually-based representations.

Representations that incorporate spatially as well as temporally proximate features of the environment would be consistent with the notion of goal-based or externally referenced planning made possible through the use of control points. Shore and colleagues’ study is one of the few contributions showing that hand-based feedback may influence the representation of the immediate space in which action is planned, and as such a full understanding of hand-based feedback’s influence on visually guided pointing has yet to be established. Many studies have examined proprioceptive and visual integration during visually guided hand movements, but few have specifically examined how tactile information might be integrated in this process. Upon contacting a target, the available tactile information, might, for example, modify the precision of later estimates used in planning action toward that location.

Tactile influences are being better considered as potential influences in action planning, as previously influential theories claiming that future hand positions are encoded in gaze-centered coordinates (Buneo et al., 2002) have been revised to incorporate encoding future goal states using multisensory representations (e.g., that are influenced by hand signals; Buneo & Andersen, 2006). This is a profound adaptation because encoding and representing hand and target positions (i.e., goals) independent of viewed locations allows dynamic changes in the workspace arising from action to be accounted for when calculating the goal, and may allow somatosensory feedback to influence its representation. A direct benefit of such a strategy would, these authors contend, better provide the brain with a means of determining motor error – or the
difference between an intended action and what was executed (see Buneo & Andersen, 2006 for a review). As discussed above, this would require encoding action plans using more than just visual references to which action is directed. Using such a strategy might allow the motor system to address the myriad sensory consequences during planning, consequences that extend beyond the visual location of a goal.

Recent physiology studies have also supported the notion that hand position feedback related to a goal can influence how movements are planned. An increase in the activity in dorsal premotor cortex (PMd) previously thought to be associated with coordinated gaze and hand movements (Jouffrais & Boussaoud, 1999) has recently been shown to more likely be the product of gaze and hand movements referenced to a goal (Peseran et al., 2006). The increased PMd activity prior to action was associated with a reach goal, and may have been used to reconcile differences between resultant gaze and hand positions relative to this goal; the response fields of the PMd neurons showed the greatest activity when the target, hand, and eye position corresponded (Peseran, Neilson, & Andersen 2006). Recall that prior to the initiation of a motor command, the desired (i.e., predicted) outcomes must be estimated such that predicted feedback can be compared to the actual feedback (Wolpert & Ghahramani, 2000; Wolpert et al., 2001). It follows that for gaze and hand related movements that produce measurable consequences, predictions related to each associated sensory modalities would be required to best assess the just-completed action. Again, this issue is directly addressed by the modifications to Buneo & Andersen's (2006) theory; by accounting for multisensory consequences of action, a more complete assessment of action is possible, and errors can be more efficiently mitigated.
When it is task-related, hand-based feedback might affect such consequences as visually determined error. For example, during a mirror-drawing task, proprioception can facilitate the speed with which errors are detected, and improving visuospatial processing (i.e., sensory detection) of movements made to important spatial points (Balslev, Miall, & Cole, 2007) – or control points. Importantly, these authors contend that accuracy in such tasks is most influenced by improved visuomotor planning (from multiple senses) relative to key points rather than proprioceptive-visual mismatches between the seen and felt hand position at these locations (Miall & Cole, 2007). To be clear, such facilitation would require an integrated prediction of the consequences of action (i.e., here, hand position relative to key points in a task) using both modalities rather than comparisons between them. Their claim is well supported by the finding that TMS pulses to the contralateral somatosensory cortex can effectively interrupt this multisensory facilitation by blocking proprioceptive feedback (Balslev et al., 2007).

The potential for hand-based sensory information to influence the way in which action is planned and assessed in a task highlights why some researchers have speculated that visually guided pointing would be differently influenced by hand-based feedback than reaching-to-grasp movements – these actions might extract different information from the scene. Perhaps these different visuomotor control systems have distinct operating characteristics consistent with the function they were evolved to fulfill. After all, calculations involved in pointing need not account for how to wrest control of an object (Thompson & Westwood, 2007). Irrespective of teleological suppositions, it is important to distinguish that different gaze-directed movements might be variably
influenced by hand-based feedback. With such potential, it is important to isolate those movements most likely to be subject to tactile influences during planning.

2.4 Pointing and reaching

In the recent past several researchers have begun to investigate whether the way in which an eye-hand task is planned or represented changes when it involves a significant non-visual component (see Castiello, 2005). There are several reasons why this might be the case. Coordinated eye and hand movements have been well documented as reciprocally influencing one another (Snyder, 2000; Thura et al., 2007); and evidence is mounting to suggest that tactile inputs can specifically influence behaviour toward a goal. It has been known for some time that hand-based information can increase the speed and precision of gaze and hand movements when looking at and touching a sequence of targets compared to the same movements made with only the eyes (Epelboim et al., 1995; Epelboim, Steinman, Kowler, Edwards, Pizlo, & Erkelens, 1997). Moreover, tactile input derived from vibrations to the hand can increase the accuracy of saccadic movements to a common location (Amlot, Walker, Driver, & Spence, 2003; Arvind & Tharion, 2005), and increase the speed with which participants respond to a visual stimulus (Diederich, Colonius, Bockhorst, & Tabeling, 2003). When gaze and hand are directed to the same location, the hand moves more quickly than a hand movement alone (Snyder, Calton, Dickenson & Lawrence, 2002) but this effect seems to be limited to movements whereupon the effectors are directed to a shared goal (Snyder, 2000). Estimating the timing of the consequences of action might be facilitated through tactile feedback that may influence the representation of stimuli in the immediate reachable
space (Shore et al., 2005). Thus, hand-based feedback may more readily influence behaviours when this sensory information can meaningfully contribute to a task.

Associated gaze and hand movements also show well-correlated neural activity. Cortical activation increases in the parietal reach areas responsible for programming hand movement parameters concurrent to fixating a desired reach location (Buneo et al., 2002). This activity may signal the greater computational efforts required to represent the goal of action for the eyes and hand within a common reference (Buneo & Andersen, 2006). During a guided saccade task, activity in monkey frontal eye field (FEF) increases with a congruent hand position, irrespective of whether the hand can be seen. This is taken as evidence that a non-visual signal, related to the arm controller, is likely the impetus for the increased activity (Thura et al., 2007). Recall that increased activity in PMd was also observed as the goal of a movement relative to eye and hand positions was being planned (Mushiake et al., 2006; Pesaran et al., 2006). Moreover, increased activity in monkey PMd has been associated with activity in FEF that occurs prior to hand movements to a goal (Peseran et al., 2006).

Activity in PMd, as mentioned earlier, is strongly correlated with the goals of hand-based action (Mushiake et al., 2006). It is reasonable to extrapolate that hand and eye movements related to goals within reachable space have a special association as they are planned. Indeed, Iriki and colleagues (2001) have demonstrated one such effect with macaques when visual receptive fields, whose activity was defined by reachable space, adapted after training with a tool that increased reaching distances; the response fields expanded to include the now-reachable targets (Iriki, Tanaka, Obayashi & Tanaka, 2001). Not surprisingly, prior to complex grasping maneuvers in humans, activity in the
dorsal premotor cortex (dPMC) increases in the same way activity increases have been observed in the monkey homologue PMd (Castiello, 2005; Culham & Valyear, 2006). These homologous findings help instantiate the position that hand-based feedback related to a reachable goal can influence how the CNS plans to account for the consequences of action and that planning action requires more than simply determining where to move the hand.

One of the foremost reasons that hand-related feedback might change the way in which a task is conceptualized is that the hand often actively contributes to completing the task. Even when tactile information is not immediately available, to preserve the positional relationships among environmental features, the CNS must continually engage in spatial updating to account for changes made during a task (Medendorp et al., 2008). While it is generally believed that the putative extraretinal signal necessary for gaze-centered updating is a corollary discharge of a saccadic movement (Sommer and Wurtz, 2002, Wurtz & Sommer, 2003), it remains unclear whether such a signal would underlie spatial updating if the action involved a significant manual component (see Castiello, 2005 for a review) especially as not all manual control parameters can be visually discerned (e.g., grip locations, object weight). As a result of these differences, pointing and grasping movements are increasingly regarded as separable actions (Begliomini, Caria, Grod, Castiello, 2007; Castiello, 2005; Culham & Valyear, 2006).

If pointing and grasping movements are separable, tactile feedback might differently influence their planning. Consider that pointing indicates a target that will not necessarily be interacted with, whereas grasping motions necessarily involve contact, and often, subsequent manipulation. The differentiation is not a matter of semantics
since these movements elicit distinct activation as measured by fMRI imaging. Chapman and colleagues (2007) have indicated that activity in the somatosensory cortex increases when tactile feedback is expected to coincide with a pointing task. In addition, grasping movements—involving a complex interaction with an object and the hand—elicit activity localized to the intraparietal sulcus whereas pointing movements result in activation in the medial occipital-parietal junction (Castiello, 2005; Culham & Valyear, 2006). Expecting tactile input at a site of contact may not only change how the movement will be accounted for, but may even change how the movement is planned.

Perhaps the distinction between pointing and grasping lies in whether hand-relevant sensory information will be provided upon achieving an object. With pointing movements new information about an object may not result from the movement; in reaching, the hand registers and may be required to respond to features of an object during action (Smeets & Brenner, 1999). With manipulation a rich source of non-visual information following an initial contact can directly furnish the CNS with information. Cutaneous receptors in the fingertips provide information about grip and load forces (Jenmalm & Johansson 1997), information related to postural adjustments (Wing, Flanagan & Richardson, 1997) as well as textural information related to object identity (Klatzky & Lederman, 1995). Tactile information may change the approach of the hand relative to qualities that may be indeterminable using only vision (e.g., object weight; Flanagan & Beltzner, 2000). For example, Patchay and colleagues (2006) have shown that tactile distractors can specifically disrupt grasping movements when participants hold an object of one size in their left hand, resulting in incorrectly scaled grip aperture when reaching to grasp another differently-sized object with the right. Notably, these
authors point out that neither the visuospatial representations of the workspace, nor other movements within it are distorted; the error is isolated to the goal of grasping the object (Patchay, Haggard, & Castiello, 2006).

In sum, support is amassing to suggest that many actions are planned relative to a visually-determined, goal-centered representation to which the contribution of tactile feedback remains unclear. In achieving a goal, its location is preferentially attended to, since it is often the source of task-critical feedback. Control points proffer specific information related to the interaction between an object and the actor and likely provide information necessary for retaining control during movement sequences. Control points bestow three benefits that can impact motor control specific to the information arising from a planned action. Because there is sufficient evidence to warrant a stance that tactile information has the potential to influence movement planning, I am specifically interested in these potential influences with reference to control points. By exploring how movements change relative to control points in a task, their role in developing and preserving coordinated movements between the eyes and hand within the workspace might be elucidated. Since many sequenced movements depend on the success of recently completed actions, it will be interesting to determine whether earlier task feedback might influence later hand and eye movements.

2.5 The present experiments

This dissertation is comprised of four experiments designed to further investigate the contribution of visual and tactile feedback to generating continuous and accurate movements within a sequential motor task. Based on the review of the literature, it is clear that the eye and arm control systems can synergistically affect one another.
Specifically, because vision is known to extract information needed for controlling the hand, tactile feedback—when it is available—might also influence how gaze is used. Each chapter is designed to incrementally investigate the overarching question of what potential influence vision and touch have on eye-hand coordination in sequenced movements.

To test this question a novel virtual reality setup was used to control the timing and position of available visual and tactile feedback. The paradigm allowed visual and tactile information to be manipulated by removing the visual position of the hand and objects, and/or changing the dynamics between the hand and object resulting from contact. The sensory information we predicted to contribute to participants’ assessing their performance relative to goal states was limited or changed. Accuracy of contacts, the approach of the hand, and the timing of gaze movements were recorded and assessed in relation to the aforementioned manipulations.

I sought to answer three main questions regarding the availability of goal-related tactile and visual feedback. First: Will limitations in sensory feedback influence the accuracy of contacting the objects? Specifically, I hypothesized that removing sensory information expected at, or pertaining to, a control point would disrupt how the next phase of action is calculated and executed, thereby producing more errors in contact.

Second: Would changes in sensory feedback relative to a goal influence the control of the hand? Ergo, I measured hand control parameters as the objects were approached and contacted (i.e., as the goals of the task were completed). By comparing performance across different conditions I would be able to ascertain potentially critical sources of sensory information at, or following from, a goal of action and how they
influenced action. I hypothesized that when participants were less able to predict hand and object interactions, hand approach would be less well controlled. This would be demonstrated in adaptations to hand movements, as well as the measures associated with predicting the timing of the hand-object contact. Changes in gaze-hand coupling should also arise as participants adapt gaze movements to monitor changes relative to the goal of contacting the object.

Third: How can the nature of the signal governing the timing of gaze movements to and from objects be elucidated? Several outstanding possibilities remain as to how gaze is controlled in sequential tasks. While gaze is known to direct the position of the hand, it has also been suggested that gaze control is influenced by non-visual signals related to key events; perhaps tactile feedback has the potential to influence gaze movement timing. I hypothesized that tactile feedback signaling a successful interaction with an object could be used as a signal to influence gaze movement timing.

Chapter Three is a manuscript published in Experimental Brain Research with my colleagues J.R. Flanagan and R.S. Johansson. In it we examine the contribution of visual and tactile feedback in controlling directed action to reach and contact a series of stationary targets. Gaze shifts in this sequential task may have been predictive or reactive. In some cases we removed visual feedback of hand position. We also measured the consequences of unexpectedly removing tactile feedback at some contacts. We expected that tactile feedback might influence the organization of behaviour such that the timing of gaze and hand actions would continue to follow a time course indicating planning based on predicted events rather than reactions to them.
These predicted movements would be achieved using sensory information available at control points.

In *Chapter Four* I investigated how behaviour was organized when the goal exhibited a dynamic property. In *Experiment 1* I incorporated movable objects to determine whether object response mattered in how movements to and from purported goals were planned. Performance was assessed after manipulating visual feedback of the hand, and/or after adding a dynamic consequence to object contact. I expected that without vision of the hand participants might change their behaviour owing to the lack of sensory information, though I was unsure whether performance would differ on account of attempts to register information related to the goal (i.e., the consequences of contacting the objects) or because with an invisible hand, participants might have reactively triggered movements. In *Experiment 2*, after removing vision of the hand, I tested the extent to which feedback arising from contact might influence movements to the next object. To do this I introduced changes in the ways the objects responded to contact and measured how these changes (relative to the goal of contact) influenced subsequent movements and whether reactive movements emerged.

In *Chapter Five* I examined the role of visual and tactile input when object manipulation was required. With a manipulation component—involving pressing and then depressing a series of mechanical switches rather than just contacting the objects—the role of the hand increased whereas the role of gaze during manipulation may have been minimized. It was not immediately clear how changing the goal-requirements of contacting each object might have influenced the eye and hand controllers. For example, if gaze arrived early enough to guide the hand to the object, it
was unclear whether gaze would have maintained its position at that site or if gaze might have been free to move ahead and locate the next site of action. If action was planned relative to the location of a planned interaction, gaze might have continued on ahead of the hand; however if planning action was done relative to the consequences arising from a goal, gaze should have remained until the goal was completed. Put another way, it was not clear whether gaze was aligned with control points even when gaze-related signals may not have been required for guiding hand actions. Irrespective of the coordination between the two systems, with increased sensory information available from longer manipulations, I expected more adroit and accurate hand control in relation to the objects.
Chapter 3

Eye-hand coordination in a sequential target task.

This chapter is comprised of an article published in Experimental Brain Research v.195 in 2009 titled: Eye-hand coordination in a sequential target contact task. The authors on this manuscript were Miles C. Bowman, Roland S. Johansson, and J. Randall Flanagan.

3.1 Abstract

Most object manipulation tasks involve a series of actions demarcated by mechanical contact events and gaze is typically directed to the locations of these events as the task unfolds. Here we examined the timing of gaze shifts relative to hand movements in a task in which participants used a handle to contact sequentially five virtual objects located in a horizontal plane. This task was performed both with and without visual feedback of the handle position. We were primarily interested in whether gaze shifts, which in our task shifted from a given object to the next about 100 ms after contact, were predictive or triggered by tactile feedback related to contact. To examine this issue, we included occasional catch contacts where forces simulating contact between the handle and object were removed. In most cases, removing force did not alter the timing of gaze shifts irrespective of whether or not vision of handle position was present. However, in about 30 % of the catch contacts, gaze shifts were delayed. This percentage corresponded to the fraction of contacts with force feedback in which gaze shifted more than 130 ms after contact. We conclude that gaze shifts are predictively controlled but timed so that the hand actions around the time of contact are captured in central vision. Furthermore, a mismatch between expected and actual tactile information related to
contact can lead to a reorganization of gaze behaviour for gaze shifts executed greater than 130 ms after a contact event.

3.2 Introduction
When pointing or reaching to a single target, people usually direct their gaze to the target as they initiate their hand movement and maintain gaze on target until around the time that the hand arrives (Crawford et al. 2004; Desmurget et al. 1998; Gribble et al. 2002; Neggers and Bekkering 2000; Neggers and Bekkering 2001). This gaze behaviour can improve reach accuracy in at least two ways. Looking at the target allows effective use of visual feedback of hand position to guide the hand to the target (Paillard, 1996; Land, Mennie & Rusted 1999; Carlton, 1981; Berkinblit et al., 1995; Saunders & Knill, 2004; Sarlegna et al., 2004). In addition, efferent and/or afferent signals related to gaze position can be used to guide the hand even when the hand is not visible (Prablanc et al. 2003; Prablanc & Martin 1992; Prablanc et al. 1979; Prablanc et al. 1986).

Many manual tasks involve a series of actions directed towards different target objects (Johansson et al. 2001; Land et al. 1999). These phases are often bounded by mechanical contact events that represent sub-goals of the task. For example, when picking up a hammer to strike a nail, contact between the digits and handle marks the end of the reach phase, the breaking of contact between the hammer and support surface marks the end of the load phase (during which vertical lift forces are applied to overcome the weight of the object), and contact between the hammer head and nail marks the end of the movement phase. In such tasks, gaze is typically directed to successive contact locations as the action unfolds, arriving before the hand (or object in
hand) and departing around the time the sub-goal is completed (Ballard et al. 1992; Epelboim et al. 1995; Hayhoe and Ballard 2005; Johansson et al. 2001; Land et al. 1999; Flanagan and Johansson 2003). In addition to improving manual accuracy through visual feedback and the use of gaze related signals to guide the hand (or object in hand), directing gaze to contact locations may serve two further functions (Johansson et al. 2001; Flanagan et al. 2006). First, foveating a contact location at the time of contact may facilitate the comparison of predicted and actual visual consequences of action. By comparing predicted and actual sensory events related to contact (including visual, tactile, and auditory events), the motor system can monitor task progression and adjust subsequent motor commands if errors are detected. Second, by aligning gaze with contact events, the sensorimotor system may be able to establish and maintain correlations between retinal and extraretinal signals and other sensory signals—including those from tactile receptors—that arise from contact.

In manipulation tasks, a key question concerns how successive action phases are linked together. Specifically, is the execution of the next phase triggered by sensory information confirming that the goal of the current phase has been achieved, or is the next phase launched predictively, in advance of sensory goal confirmation? The answer to this question presumably depends on the particular task being performed, the behavioural context, and the certainty with which sensory outcomes can be accurately predicted. If the outcome of the current action phase can be predicted with confidence, then the next phase can be launched based on the predicted, as opposed to the sensed, goal completion. This strategy would allow for smoother and quicker phase transitions
and thus more dexterous actions as compared to a strategy based on sensory verification of goal completion. Both predictive and reactive sequential phase control can be observed in object manipulation tasks. For example, in precision grip lifting, the transition between the load phase and the subsequent lift phase demarcated by the instance of object lift-off is usually predictive. That is, people normally scale the rate of change of force output to the predicted weight of the object such that load force drive at lift-off, which accelerates the object, results in a natural, smooth and critically damped lifting motion (Johansson and Westling 1988). However, when people are uncertain about object weight they may employ a probing strategy whereby they keep increasing vertical force, intermittently, until lift-off occurs and only then terminate the load phase reactively (Gordon et al. 1991; Johansson and Westling 1988).

Because gaze is directed to successive movement goals in visually guided manipulation tasks, the degree to which action phases are linked reactively versus predictively can be posed at the level of gaze control. Given that eye movements are rapid, it is conceivable that gaze shifts from the current goal to the next could, in many situations, be delayed until sensory confirmation of goal completion is obtained. On the other hand, predictively shifting gaze to the next target, before completion of the current goal is confirmed, may facilitate performance by allowing earlier use of visual and gaze related signals linked to the next goal. Neggers and Bekkering (2000) examined the coupling between gaze and hand movement in a target pointing task in which a second “gaze” target could appear during the pointing movement. Although participants were instructed to look at the gaze target as quickly as possible—while continuing to point to the hand target—they were unable to do so until about 50 ms (on average) after the
fingertip contacted the target. This gaze anchoring, also seen when the hand was not visible (Neggers and Bekkering, 2001), confirms the important role played by gaze position signals in guiding the hand towards the target. However, the fact that gaze shifted so soon after contact suggests that commands specifying these shifts were initiated prior to sensory confirmation of the movement goal.

In the current study, we investigated the timing of gaze shifts in a task in which participants moved a handle, in a horizontal plane, to tap sequentially five virtual target objects. Simulated contact forces were applied to the handle and the targets were always visible. In different conditions, the position of the handle, during the movement, was either visible or invisible. Based on previous findings (Epelboim et al. 1995; Johansson et al. 2001) we predicted that, in the handle-visible condition, participants would typically shift their gaze proactively to the next target around the time of contact. In the handle-invisible condition, prediction of contact times in the visual modality may be less accurate and this could lead to more reactive gaze behaviour, with gaze shifts occurring well after contact. To determine whether tactile feedback related to contact might trigger or facilitate gaze shifts to the next target, in both conditions we occasionally removed the force that simulated contact between the handle and a target object. If triggered by tactile feedback, gaze shifts would be delayed in these catch contacts.

3.3 Methods

3.3.1 Participants

Eight participants (18-24 years old) with normal or corrected to normal vision performed the task with their dominant right hand. The experimental protocol was conducted in
accordance with local ethics procedures and took approximately one hour to complete. Prior to testing, participants provided written informed consent and were later compensated for their time.

3.3.2 Apparatus

While seated, participants moved the handle of a lightweight force-reflecting robotic device (Phantom Haptic Interface 3.0L, Sensable Technologies, Woburn MA) to contact a series of five visible virtual target objects located in a horizontal plane placed approximately 40 cm below the eyes (Fig. 1A, B). The handle was a vertically oriented cylinder (2 cm in diameter and 10 cm in height) mounted on an air sled that slid across a horizontal glass surface. The position of the handle was recorded at 1000 Hz with a spatial resolution of 0.1 mm. A projection system was used to visually display, in the same horizontal plane, the target objects (2 by 2 cm squares), a circle (2 cm diameter) representing the position of the handle, and a start position (2 cm diameter circle) for the handle. The start position was located 15 cm in front of the eyes in the midsagittal plane. The light gray boxes (4 by 4 cm) shown in Fig. 1B indicate the areas in which the centers of the five targets could be located on a given trial. The target locations were randomly selected from these areas, subject to the constraint that the distance between any two targets in the x direction was no less than 1 cm. The horizontal plane in which the targets and the handle and start positions were represented was aligned with the top of the handle and hence the location at which forces were imparted to the handle.

The robotic device provided force feedback to the hand by simulating contacts between the handle (i.e., the circle representing the handle) and the target objects. The
handle was defined as being in contact with a target whenever the perimeter of the circular handle overlapped with the perimeter of the square target. The target objects were modeled with slightly compliant sides linked to the center of the object via a damped spring with stiffness and viscosity of 1000 N/m and 0.00009 Ns/m, respectively. Because of the high stiffness of the target objects, the sides did not move appreciably during contact and we did not render target deformation visually. Images were displayed using an LCD projector (LC-XNB3S, Eiki Canada, Midland, ON) with a refresh rate of 60 Hz and a fixed (minimum) delay of 13 ms. Thus, in the handle-visible condition, there was an average delay of ~21 ms between the time the handle contacted an object (and contact forces were initiated) and the time the handle visually contacted the object.

An infrared video-based eye-tracking system (ETL 500 pupil/corneal tracking system, ISCAN Inc. Burlington, MA), mounted below a headband, recorded the gaze position of the left eye at 240 Hz. A bite-bar was used to help stabilize the head. Gaze was calibrated using a two step procedure: an initial 5-point calibration using ISCAN’s Line-of-Sight Plane Intersection Software followed by a 25-point calibration routine. Calibration points (4 mm diameter circles) were projected onto the horizontal plane where the targets were projected and distributed over a region that incorporated the hand start location and all possible target locations. The ISCAN calibration converted raw gaze signals into pixels from the line-of-sight camera and the 25-point calibration converted pixels (i.e., the output of the ISCAN calibration) into the coordinates of the Phantom in the horizontal plane. Gaze was calibrated at the start of the experiment and was checked following each block of trials (see below) so that, if necessary, gaze could be recalibrated before starting a new test block. The spatial resolution of gaze in the
Figure 1. Apparatus and task. A. While seated, participants held a handle attached to a lightweight manipulandum. The handle was mounted on air sleds and could be easily moved over a horizontal glass surface. An image was projected onto a screen via a 45° mirror and viewed by the participant in a mirror. This image appeared at the level of the top of the handle. The image contained the targets, the start position for the handle and gaze and, in some conditions, a circle representing the position of the handle. A video-based eye tracker was used to record the position of the left eye and a forehead strap and small bite-bar were used to stabilize the head. B. Top view of the gaze targets (dark gray squares) from a single trial in which visual feedback of hand position was provided. The large light gray squares represent the possible center locations of the gaze targets. The gray and black traces show the paths of the hand and gaze, respectively. The small open black circles represent gaze positions at the start of successive saccades between targets, and the large circles on the hand path represent the corresponding positions of the handle. The arrow indicates the initial direction of the hand at the start of the trial. In this trial, gaze shifted away from targets 1 and 2 before the target was contacted, and shifted away from targets 3–5 after contact. C. Contact force, gaze velocity and gaze and hand positions in x and z as a function of time. The horizontal lines in the lower two panels show the x and z positions of the Wve targets. Note that two saccades were used to bring gaze to the gaze target and single saccades were observed between targets.
horizontal plane of the hand, defined as the average standard deviation of all calibration fixations, was 0.36° visual angle. This corresponded to ~3 mm when gaze was directed to the center of the target zone for the middle (i.e., third) target.

3.3.3 Procedure
To initiate a trial, participants were required to maintain the handle and their gaze within 5 and 60 mm, respectively, of the center of the start position for 200 ms. A larger area was used for gaze because of the larger variability of the recorded gaze position. Vision of the handle position was provided during this initial phase of the trial. Five targets (dark gray boxes in Fig. 1B) then appeared and participants were asked to reach out and lightly contact, on the near surfaces, the targets from left to right before returning to the start positions. In the handle-invisible condition, vision of the handle was removed at the same time that the targets were displayed. At the end of each trial, text was displayed (30 cm distal to the start position in the horizontal plane) for 1 s providing feedback on movement speed and whether the targets had been contacted in the correct order. “Too Fast” or “Too Slow” were displayed if the average time interval between successive target contacts was less than 350 ms or greater than 750 ms, respectively, and “Wrong Order” was displayed if the targets were not contacted in the correct order. Otherwise, “Good” was displayed. Participants were not instructed where to look during the task.

All participants performed 60 training trials followed by two test blocks of 70 trials each. Visual feedback of the handle was provided in one test block (handle-visible condition) and removed in the other test block (handle-invisible condition). The order of these two blocks was counterbalanced across participants. Each test block of 70 trials
contained 9 randomly selected catch trials in which force feedback related to contact was removed for one of the middle three targets in the sequence (i.e., the 2nd, 3rd, or 4th target) with each of these targets used three times. Thus, out of the 350 contacts in a test block (70 trials x 5 targets), 9 (< 3%) were catches. We kept the catch rate low to guard against the possibility that catches would alter behaviour in the non-catch trials. When force feedback was removed, the handle could move through the target. Thus, in the hand visible condition, participants received both visual and tactile feedback about contact in standard trials and only visual feedback during catch trials. In the hand invisible condition, participants received tactile feedback related to contact in standard trials and no feedback during catch trials.

### 3.3.4 Analysis

Hand and gaze position in the horizontal plane where the targets were located and forces in the horizontal plane of hand movement were sampled at 1000 Hz. This involved oversampling the gaze data provided, at 240 Hz, by the ISCAN system. The ISCAN software applied a 10-point moving average to the gaze data (sampled at 240 Hz) resulting in an average delay of 20 ms. We therefore time advanced the gaze signal 20 ms so that the gaze data would be temporally aligned with the hand data. To detect saccades, we further smoothed the x and z gaze-position signals (see coordinate system shown in Fig. 1B) using a fourth order low pass Butterworth filter with a cutoff frequency of 6 Hz, double differentiated these signals to obtain x and y gaze accelerations, and computed the magnitude of the resultant gaze acceleration. When a saccade occurred, the resultant gaze acceleration featured two peaks and a saccade was deemed to occur if both peaks exceeded $5 \text{ m/s}^2$ and were less than 150 ms apart.
Once a saccade was identified, we used the gaze data provided by the ISCAN system to determine saccade start and end times. Saccade onset and offset times were defined as the times at which saccadic velocity first exceeded and dropped below 0.2 m/s, respectively. The x and z hand position signals were smoothed using a low pass fourth order Butterworth filter with a cutoff frequency of 14 Hz.

We focused our analysis around contact attempts coded into three categories: correct hits, misses, and mishits. A correct hit occurred when a target was contacted in the proper order and any part of the handle contacted the near surface. Of the 5145 contact-attempts analyzed, 4704 (91.4 %) were correct hits. Misses, in which the handle failed to make contact with the target, occurred 169 times (3.3 %) and mishits, where the cursor contacted the left, right, or backside of the target occurred 272 times (5.3 %). We excluded from analysis contact attempts that involved lost gaze signals, blinks, and errors in contact order. We also excluded contact attempts immediately following misses, mishits, or catch hits because these events might influence behaviour when contacting the subsequent target. Of the 6161 total recorded contact attempts, a total of 1016 (16.5%) were removed.

To characterize the timing of saccadic gaze shifts, we determined gaze arrival and exit times for each analyzed contact attempt. The gaze exit time was defined as the onset time of the saccade shifting gaze away from a target (to the next target), relative to the actual or estimated time at which the hand contacted the target (see below for details about estimated contact times in misses). The gaze arrival time was defined as the offset time of the saccade bringing gaze to a target, relative to the actual or estimated time at which the hand contacted the target.
To assess hand behaviour, we computed the hand path distance between successive target contacts as well as the hand movement duration between successive contacts. For each target, we also computed the hand approach angle and hand retraction angle based on the position of the hand at contact and the positions of the hand when entering and exiting a 3 cm perimeter around the hand contact position (see Results). Finally, we also determined the maximum contact force for each target contact. For all analyses, an alpha level of 0.05 was considered to be statistically significant.

### 3.4 Results

As illustrated in the single trial depicted in Figure 1, participants performed the task by generating curved hand movements between the successive target objects (Fig. 1B). Participants almost always fixated each of the 5 targets well before the handle arrived and shifted gaze to the next target around the time the handle contacted the current target. In this particular trial, gaze shifted away from targets 1 and 2 before contact but shifted away from targets 3 to 5 shortly after contact (Figs. 1B, C). Participants rarely directed their gaze to viewed position of the handle or any locations other than the target objects. Participants were quite accurate in shifting gaze to the targets and gaze shifts between targets were generally achieved with a single saccade (Fig. 1C). As a consequence, corrective saccades bringing gaze on target were infrequent.

#### 3.4.1 Hand and Gaze Accuracy

Figure 2A shows frequency distributions of the x position of the center of the handle at the time of target contact, or attempted contact, relative to the x position of the center of the target. For both the handle-visible and invisible conditions, separate distributions are
Figure 2. Hand and gaze movement accuracy. A. Cumulative distributions of hand x position at the time of contact, relative to the center of the target, when contacting targets with and without vision of the handle. Each curve represents the data from one of the eight participants. In each panel, the filled gray bar represents the width of the target. The region between the dashed vertical lines shows the range of handle positions that would enable a successful contact. The dashed curves in the lower panel show the three participants who most frequently missed or mishit targets when vision of the handle was not provided. B. The gray crosses show the locations of fixations, relative to the target (open black square), associated with correct hits for two participants in the handle-visible and invisible conditions. The intermixed black crosses show fixations associated with misses and mishits.

shown for each participant. Each distribution includes all hits, mishits and misses. For mishits and misses, we took the x position of the center of the handle when the surface of the handle crossed the z position of the near surface of the target (i.e., where the handle would have contacted the target had the target been wider). For misses where the handle did not reach this z position, we took that x position of the center of the handle at the maximum z position of the handle (closest to the target along the z axis). When the center of the handle was within ± 10 mm of the center of the target (gray region in Fig. 2A) a correct hit was registered provided the handle reached the target. When the center of the handle was outside ± 20 mm of the center of the target (dashed lines in Fig. 2A), a miss was registered. When the center of the handle was between 10 and 20 mm of the center of the target and contact occurred, either a correct hit or a mishit could be registered depending on the angle of handle approach (see Methods). In the handle-visible condition, participants successfully contacted the near surface of the target in 98 % of contact attempts. In the handle-invisible condition, correct hits were observed in 80 % of all contact attempts. Mishits and misses were observed in 12 and 8 % of attempts, respectively. Three participants accounted for most of these mishits.
and misses (see dashed curves in Figure 2A) and the distributions for two of these participants appeared to be more variable.

To quantify the effect of vision of the handle on reach accuracy, for each participant and condition, we computed both the median and the standard deviation of the \( x \) positions of the center of the handle, relative to the \( x \) position of the center of the target, at the time of contact (or attempted contact). Repeated measures ANOVAs did not reveal a significant difference between the handle-visible and handle-invisible conditions for either the median contact position, \( F(1, 7) = 1.12, p = 0.33 \), or the standard deviation of the contact positions, \( F(1, 7) = 0.63, p = 0.45 \). To test whether the variability in median contact positions across participants differed between conditions, we used the Levine test for homogeneity of variances. This test indicated that the inter-participant variability was greater in the hand invisible condition than in the hand visible condition, \( F(1, 14) = 12.94, p = .003 \). Thus, removing vision of the handle significantly increased contact location variability between participants but not within participants. Figure 2B shows two participants’ gaze fixation locations, relative to the target position (normalized across the five targets), in the handle-visible and handle-invisible conditions. Each cross represents the location of gaze at the end of a saccade bringing gaze to the target; fixations related to all contact attempts are shown. As illustrated by these two participants, no obvious differences were observed between fixation locations in successful hits (gray crosses) compared to mishits and misses (black crosses). Paired \( t \) tests, based on median values computed for each participant, failed to show a significant difference in either the \( x \) or \( z \) gaze positions between the handle-visible and handle-
invisible conditions ($p = 0.79$ and $p = 0.06$, respectively). These results suggest that the accuracy of gaze shifts to the targets was similar in the two conditions.

We also computed, for each participant and condition, the median peak contact force generated in correct hits. No reliable differences in peak contact force was observed between the handle-visible and handle-invisible conditions, $F(1, 7) = 0.56$, $p = 0.48$. This suggests that participants could quite accurately predict contact time in the handle-invisible condition. Had participants poorly predicted when contact would occur in the handle-invisible condition, we might have expected differences in contact force between the two conditions.

### 3.4.2 Hand trajectories

Figure 3A shows representative hand paths produced in the handle-visible and handle-invisible conditions by two participants. In the handle-invisible condition, the u-shape of the hand path between successive targets was more pronounced and the hand retracted further between targets, resulting in longer hand paths from target to target. A repeated measures ANOVA, based on the median hand path distance between successive correct hits computed for each participant and condition, confirmed that the distance between target contacts was greater, $F(1, 7) = 11.7$, $p = 0.011$, in the handle-invisible condition ($M = 13.17$ cm, $SD = 2.13$ cm) than in the handle-visible condition ($M = 10.97$ cm, $SD = 1.65$ cm). (Note that these means and standard deviations are based on the median values provided by each participant.) Similarly, the time interval between correct target contacts, also based on median values, was significantly greater, $F(1, 7) = 27.1$, $p$
< 0.001, in the handle-invisible condition (M = 483 ms, SD = 39 ms) than in the handle-visible condition (M = 429 ms, SD = 49 ms).

Consistent with the observation that the hand retracted further between hits in the handle-invisible condition, the hand tended to approach the near surface of the target at a more perpendicular angle in the handle-invisible condition. To examine the angle of approach, for every successful hit, we computed the angle of the vector from the center of the handle at contact to the center of the handle at the location where the displacement between the two center locations first decreased below 3 cm. Similarly, to examine the angle at which the hand retracted from the target, we computed the angle of the vector from the center of the handle at contact to the center of the handle at the location where the displacement between the two center locations first exceeded 3 cm.

The gray lines in Figure 3B illustrate the median approach and retraction angles for each participant in the handle-visible and invisible conditions. The thick black lines illustrate the mean approach and retraction angles averaged across participant medians. A repeated measures ANOVA revealed that the approach angles in the handle-visible and invisible conditions were significantly different, $F(1, 7) = 14.0, p = 0.007$. However, no significant difference was observed in the retraction angle, $F(1, 7) = 5.11, p = 0.058$.

Thus, participants approached the target at an angle more perpendicular to the contact surface in the handle-invisible condition compared to the handle-visible conditions. The more perpendicular approach used in the handle-invisible condition may be a compensatory strategy employed to increase the chances of contacting the object surface, given increased uncertainty in the position of the handle in the $x$ direction. A
similar suggestion related to approach angles has been made in the context of grasping (Smeets and Brenner 2001, 1999; Cuijpers et al. 2004; Kleinholdermann et al. 2007).

Figure 3. Hand paths. A. Top views of hand (gray traces) and gaze (black traces) paths from single trials with the handle-visible and invisible shown for two participants. The dark gray squares represent the locations of the five targets. B. Handle approach and retraction angles in the handle-visible and invisible conditions. In each panel, the top gray circle represents the position of the handle when first contacting the target. The bottom left circle shows the average location (based on participant medians) of the handle when the center of the handle approached within 3 cm of the center of the handle at the contact position. The bottom right circles shows the average location of the handle when the center of the handle retracted 3 cm from the center of the handle at the contact position. The thin gray lines show the approach and retraction angles for each participant (based on medians), and the thick black lines show the average approach and retraction angles. The arrows represent the direction of handle movement.
3.4.3 Temporal coordination of gaze and hand movements

Figure 4A shows cumulative frequency distributions of gaze arrival and exit times, relative to the instance the handle first contacted the target in both the handle-visible (top panel) and handle-invisible (bottom panel) conditions. Separate distributions are shown for each of the 5 targets where each distribution includes all correct hits from all participants. Repeated measures ANOVAs, based on participant medians, revealed significant effects of target on both gaze arrival and exit times in both the handle-visible and handle-invisible conditions ($p < 0.001$ in all four cases). Gaze arrived earliest at target 1 and exited latest from target 5 (see Fig. 4A). The early gaze arrival at target 1 was presumably related to the relatively large amplitude hand movement between the start position and the first target. After contacting the target 5, participants were required to bring the handle back to the vicinity of the start position but there was no time constraint imposed on this movement. This may explain the relatively late gaze exit from target 5. Figure 4A also suggests that gaze tended to arrive increasingly later from targets 2 to 5 and tended to exit increasingly later from targets 1 to 4.

To examine differences in the timing of gaze arrivals and exits across conditions, we focused on the middle three targets (and thus disregarded the early gaze arrivals and late gaze exits observed for targets 1 and 5, respectively). Figure 4B shows separate cumulative frequency distributions of gaze arrival and exit times for correct hits involving the middle three targets for each participant and condition. Repeated measures ANOVAs based on median gaze arrival and exit times computed for each participant failed to reveal a difference in gaze arrival times, $F(1, 7) = 2.56, p = 0.15$ between the handle-visible ($M = -208$ ms, $SE = 15$ ms) and handle-invisible ($M = -248$ ms, $SE = 20$ ms).
Figure 4. Gaze arrival and exit times. A. Cumulative distributions of gaze arrival and exit times, relative to contact, for each target and for the handle visible and invisible conditions. Each distribution combines data from all participants. B. Cumulative distributions of gaze arrival (gray curves) and exit (black curves) times for each participant and condition. Data from targets 2, 3 and 4 have been pooled together in these plots.
ms) conditions. However, gaze exits in the handle-visible condition (M = 106ms, SE = 7 ms) were slightly but significantly later, $F(1, 7) = 16.5$, $p = 0.005$ than in the handleinvisible condition (M = 87 ms, SE = 8 ms). As can be visually appreciated in Figure 4B, gaze arrival times varied considerably across participants (due to the fact that different participants moved their hand between successive targets at different speeds). In contrast, there was far less variability in gaze exit times across participants. This finding is consistent with our previous results showing that, in a block stacking task, changes in movement duration affect gaze arrival but not gaze exit times (Flanagan & Johansson, 2003).

### 3.4.4 Catch hits
To assess how haptic contact information influenced the timing of gaze shifts from one target to the next, we included occasional trials in which we removed force feedback when one of the middle three targets was contacted. If gaze shifts from one target to the next were reactively triggered, based on haptic contact cues, we would expect to see a delay in the gaze exit time referenced to the instance of contact. In our analysis of contact events not involving force feedback, we only included correct hits and will therefore refer to these events as catch hits (as only a handful of catch mishits and catch misses were observed, these attempts were not analyzed). Figure 5 shows, for both the handle-visible and handle-invisible conditions, cumulative frequency distributions of gaze arrival and exit times, relative to contact for correct hits and catch hits. The data for correct hits were taken from the middle three targets only so that they could be directly compared with the catch hits. Each distribution shows data from all participants.
In both the handle-visible and invisible conditions, the distributions of gaze exit times that occurred before 130 ms after contact were very similar for correct hits and catch hits (Figure 5; dashed vertical lines mark 130 ms after contact). This accounted for approximately 65 and 75 % of catch contacts in the handle-visible and invisible conditions, respectively. Thus, in the majority of catch hits, gaze exits were not delayed. However, gaze exits that occurred later than 130 ms after contact appeared to be delayed for catch hits in comparison to correct hits. In the hand visible condition, the median gaze exit times of gaze exits occurring > 130 ms after contact were 284 ms and 153 ms for catch hits and correct hits, respectively. In the hand invisible condition, late gaze exits in catch hits were even more delayed. The median gaze exit times of gaze exits occurring > 130 ms after contact were 632 ms and 160 ms for catch hits and correct hits, respectively. Kolmogorov-Smirnov tests verified significant differences between the distributions for correct hits and catch hits in both the handle-visible ($Z = 3.48$, $p < 0.001$) and handle-invisible ($Z = 1.63$, $p = 0.01$) conditions. (Note that the correspondence between late exit times in correct hits and delayed exits times in catch hits was clearly evident at the level of individual participants. Participants who shifted their gaze away from the target relatively soon after contact exhibited few if any delayed exits on catch hits. Participants who generated later gaze shifts exhibited more delayed exits on catch trials.) In contrast to gaze exits, in both the handle-visible and invisible conditions, the distributions of gaze arrival times for correct hits and catch hits were quite similar. This suggests that the delayed gaze exits, seen in approximately 30 and 40 % of catch hits in the handle-invisible and visible conditions, respectively, were not associated with delayed gaze arrivals.
Figure 5. Catch hits. Cumulative distributions of gaze arrivals (gray traces) and exits (black traces), relative to contact, for correct hits and correct catch hits in both the handle-visible and invisible conditions. The vertical solid lines marks 130 ms after contact. Exit times greater than 1,000 ms were set to 1,000 ms.
In catch hits in the handle-invisible condition, participants received no sensory feedback indicating that the target was contacted and, in 60 % of these events, they made one or more corrective hand movements in an attempt to contact the target before continuing. In contrast, in catch hits in the hand visible condition, participants received visual information indicating that the target was contacted even though tactile feedback related to contact force was absent. That is, they saw the circle representing the handle move through the target. In this condition, participants made corrective hand movements in an attempt to hit (or re-hit) the target in only 15 % of the catch contacts.

3.5 Discussion
We have shown that in our sequential target contact task, participants fixated each target and, on average, maintained fixation at the target until shortly after it was contacted by the grasped handle. Similar gaze behaviour was observed regardless of whether visual feedback representing the position of the handle was present or absent. This indicates that the mechanisms responsible for generating gaze shifts away from the target can be driven by non-visual feedback loops; i.e., they do not require visual feedback about the relative positions of the handle and target.

In order to examine whether gaze shifts away from the target were triggered reactively in response to sensory feedback related to contact force, we included occasional catch hits in which contact force was removed. In both the handle-visible and invisible conditions, we found that the timing of the majority of gaze exits in catch hits was similar to the timing of gaze exits in correct hits involving force feedback. However, in 40 % of catch hits in the handle-visible condition and 30 % of catch hits in the handle-
invisible condition, gaze shifts were delayed. These percentages corresponded to the percentages of correct hits, in the two conditions, in which gaze shifted later than 130 ms after contact. Our interpretation of these results is that saccadic gaze shifts between targets are generally proactive but can be delayed if, prior to saccade initiation, there is a mismatch between predicted and actual tactile (and possibly proprioceptive) feedback related to contact. In object manipulation tasks, mismatches between predicted and actual tactile feedback result in corrections to fingertip forces within about 100 ms (Jenmalm and Johansson 1997; Jenmalm et al. 2000; Johansson and Birznieks 2004; Johansson and Westling 1988, 1984). Our results suggest that such mismatches can also influence task-specific eye movements within about 130 ms. Using an eye movement countermanding task, Akerfelt and colleagues (2006) demonstrated that a tactile stimulus can be an effective stop signal. These authors report that participants can inhibit saccades to a visual target 90-140 ms after receiving a vibratory stimulus to the hand. Our results indicate that the absence of an expected tactile signal can inhibit or delay the execution of saccades within a similar time frame. Note that these saccade inhibition times are considerably shorter than the 200 ms required to generate a saccade toward the location of a tactile (vibratory) stimulus applied to the hand (Groh and Sparks 1996). Gaze exits that were delayed in catch hits were far more delayed, on average, in the hand invisible condition than in the handle-visible condition. These results indicate that although the absence of expected tactile feedback can suppress the saccade to the next target (if it has not yet been launched), in many cases visual feedback can be used to confirm contact and allow eye movements in the sequential task to continue within 100-200 ms.
An alternative explanation for our results is that 40 and 30 % of all gaze shifts in the handle-visible and invisible conditions, respectively, were reactively triggered based on sensory feedback related to contact forces. As a consequence, the same percentage of gaze shifts would be expected to be delayed in catch hits. Although we cannot rule out this explanation, we note that all of our participants exhibited approximately normal distributions of gaze exit times that included a substantial proportion of exit times that occurred less than 130 ms after contact (Fig. 4B). Therefore, we suggest that, in general, participants employed a proactive gaze strategy rather than a reactive strategy in which gaze shifts are triggered in response to tactile or visual signals signaling that contact has occurred. That is, we suggest that the sensorimotor system launches each saccade in anticipation that the target will be contacted; i.e., that the goal of that current action phase will be attained. This conclusion agrees with a number of previous studies of gaze behaviour in object manipulation tasks showing that, in many instances, gaze shifts away from a given contact location around the time, even before, contact occurs (Ballard et al. 1992; Epelboim et al. 1995; Johnasson et al. 2001; Land et al. 1999; Flanagan and Johansson 2003).

To assess how haptic contact information influenced the timing of gaze shifts from one target to the next, we included occasional trials in which we removed force feedback when one of the middle three targets was contacted. If gaze shifts from one target to the next were reactively triggered, based on haptic contact cues, we would expect to see a delay in the gaze exit time referenced to the instance of contact. In our analysis of contact events not involving force feedback, we only included correct hits and will therefore refer to these events as catch hits. (As only a handful of catch mishits and
catch misses were observed, these attempts were not analyzed.) Figure 5 shows, for both the handle-visible and handle-invisible conditions, cumulative frequency distributions of gaze arrival and exit times, relative to contact for correct hits and catch hits. The data for correct hits were taken from the middle three targets only so that they can be directly compared to the catch hits. Each distribution shows data from all participants. Nevertheless, it should be emphasized that, in general, the timing of gaze shifts is task specific. Although the gaze shifts observed in our task appear to be predictive, reactive gaze shifts would be expected under some task conditions. For example, in a version of our task in which the five targets disappear prior to hand movement onset, manual performance is impaired and reactive gaze shifts are seen (unpublished observations).

Neggers and Bekkering (2001; 2000) examined the coordination of gaze and hand movements in visually guided pointing using a task in which participants were required to point to a reach target. During the reach and while gaze was directed to the reach target, a second gaze target could be presented and participants were instructed to shift their gaze to this target as quickly as possible. These authors found that participants could not execute a saccade away from the reach target until around the time the fingertip arrived at the reach target. Such gaze anchoring was seen both when vision of the hand was available and when it was not (Neggers and Bekkering 2001). On average, gaze shifted to the second gaze target about 50 ms after the finger contacted the reach target. Saccadic reaction time was found to be about 220 ms, indicating that the preparation of these saccades was initiated about 170 ms before the fingertip contacted the reach target (Neggers and Bekkering 2001). These results indicate that,
as in the task that we have examined, gaze shifts were planned predictively rather than reactively in response to sensory information confirming that the movement goal was achieved. These findings also suggest that an internal signal directly related to the arm movement command, rather than a visual signal related to the image of the moving arm, can be used to program the oculomotor system and that this signal can only be effectively exploited up until 170 ms before predicted target contact. This interpretation agrees with our results showing that removing vision of the handle has little effect on the timing of gaze shifts between targets and that these shifts are generated predictively.

Previous studies of reaching to visible targets have shown that removing vision of the hand only slightly degrades pointing accuracy, provided the visual information about the initial hand position is available (Jeannerod 1988; Prablanc et al. 1979; Prablanc et al. 1986). Consistent with this observation, our participants were generally successful at performing the sequential target contact task in the handle-invisible condition in which they received visual feedback about the initial position of the handle but were unable to see the handle position during the task. However, because they received haptic feedback when contacting the visible targets, they effectively received visual feedback related to handle position at contact. That is, at contact, the viewed location of the target could provide an estimate, based on haptic information, of the position of the handle (with an offset in the z position and some uncertainty in the x position).

We have suggested that one reason why gaze may be directed at target contact locations, during contact events, is so that central visual information related to these events can be obtained and compared to predicted information (Flanagan et al. 2006; Johansson et al. 2001). Just as predicted and actual tactile information related to contact
is compared in object manipulation tasks (Jenmalm and Johansson 1997; Jenmalm et al. 2000; Johansson and Westling 1988, 1984), so too might predicted and actual foveal information. If mismatches between predicted and actual sensory information are detected, the sensorimotor system can take corrective actions and update representations of objects in the environment so as to improve future control and prediction (Flanagan et al. 2006; Johansson and Flanagan 2007; Land et al. 1999; Wolpert and Flanagan 2001; Wolpert and Ghahramani 2000; Wolpert et al. 2001). By directing gaze to contact locations, during contact events, the sensorimotor system may also be able to maintain spatial and temporal alignment among different sensory signals. Because contact events give rise to salient sensory signals from multiple modalities (including tactile, proprioceptive, auditory, and visual signals) that are linked in time and space, these events provide an opportunity for inter-modal alignment of sensory signals (Flanagan et al. 2006; Johansson and Flanagan 2007).
Chapter 4

Object-based sensory information in sequential tasks

Planning manual action typically involves gaze actively gathering information by leading, in time and space, the intended action of the hand (Aivar et al., 2005; Ballard et al., 1992; Buneo et al., 1998; Buneo et al., 2002; Buneo & Andersen, 2006; Epelboim et al., 1995; Flanagan & Johansson, 2003; Hayhoe et al., 2003; Johansson et al., 2001; Land et al., 1999; Neggers & Bekkering, 2000; Mennie et al., 2007; van Donkelaar, 1997).

Although a number of previous studies of gaze behaviour in object manipulation tasks have shown that gaze often shifts away from a site of contact around the time of, or just prior to, contact (Ballard et al. 1992; Epelboim et al. 1995; Johnasson et al. 2001; Land et al. 1999; Flanagan & Johansson, 2003) other researchers have suggested that the timing of gaze movements serve an additional function beyond directing the hand to the location of a target. For example, through repeated fixations the accuracy of the representation of the current workspace may be improved by noting obstacles that might influence forthcoming action while also monitoring components of the workspace that, if changed, would impede performance (Aivar et al., 2005, Ballard et al., 1995; Hayhoe et al., 2003; Land et al., 1999; Mennie et al., 2007; Treisch et al., 2003). Thus, placing gaze ahead of hand action may provide additional benefits beyond aiding in guiding the hand to a location, especially when the movement is part of an inter-related sequence.

Unfortunately, the degree to which gaze and hand movements are linked in the period immediately following a planned action and the effect it has on future actions that are directly linked to the preceding action has been poorly studied.
We (Bowman et al., 2009) have shown that in a task in which participants reach out and sequentially tap a series of static objects that gaze was positioned at each contact site before the hand arrived and typically stayed until just after contact. Gaze appeared to be controlled such that the completion of a goal with the hand was registered in central vision before diverting gaze to the position of the next goal. Our findings are not unlike the findings of Neggers and Bekkering (2001) who also demonstrated that the linkage between gaze and hand movements can be yoked to non-visual (e.g., hand-based) feedback. Nevertheless these gaze movements are likely generated by predicting when key events in the task will occur (Bowman et al., 2009). Directing gaze ahead of action can enable efficient registration of task-critical feedback required to generate predictions related to upcoming movements and allow gaze movements to precede the next phase of hand action rather than reacting to it (Flanagan et al., 2006). As a result of gaze leading the hand, smooth transitions through multiple components of action are possible. Using such a strategy, gaze may also contribute to maintaining and adapting the ongoing motor plan in a variety of task-dependent capacities beyond accurately directing the hand to a viewed location (Flanagan et al., 2006). However, the exact components of action registered by gaze that contribute to successful action planning remain unclear. What is gaze looking for?

In manipulation tasks the consequence of contacting an object can vary depending on whether the object moves in response to contact. Maintaining the representations of both the hand and the workspace are necessary for planning such action since the consequences of just-completed action might directly impact subsequent actions. For example, different demands are elicited by reaching to grasp
movable and immoveable objects. Contacting an object that moves can result in different computational challenges for the CNS than a stationary object when planning how to move to the next location of action. While the position of the hand must be determined to guide action, changes brought about by action must also be accounted for so as to avoid such problems as mistakenly contacting an object set in motion or a new obstacle in the planned path of the hand. Because stationary objects do not move, there would be fewer pressures to update the representation of the workspace following action. In order to maintain accurate representations, gaze might be used to capture task-related information at key sites (Johansson et al., 2001; Flanagan et al., 2006), particularly when the workspace can change as a result of action. A viable strategy might therefore be to control gaze so as to guide the hand while maintaining this position long enough to also capture just-completed components of action. Importantly, this strategy would require that gaze movements be made based on predicted events so as to allow gaze position to precede hand action to the next object but that reactions to errors related to key events would also feasibly influence action execution where necessary.

Therefore our first hypothesis is that gaze control is influenced by dynamic consequences of interactions within the workspace that occur following contact (e.g. resulting object motion) rather than simply directing the hand to future locations. It is possible that goal-related feedback indicating a moving object’s location might differently influence behaviour than feedback indicating an immovable object’s location. Because feedback of the hand may be important for determining action relative to object locations, hand visibility might also influence gaze positioning with both static and movable objects. In the two experiments presented here, we used our sequential contact task—in which
participants reach to contact five virtual objects in quick succession—and incorporated objects that move in response to contact to test this hypothesis.

Previous researchers have demonstrated that when the cursor representing the position of the hand is removed, the known position of the hand is compromised and accuracy degrades (Pellison et al., 1986; Prablanc et al., 1986, Bowman et al., 2009). As such, we expected the accuracy in reaching to and contacting objects might be reduced when the cursor is invisible. We previously established that when the hand is invisible tactile feedback could influence gaze shifts such that that gaze position is maintained until after the hand contacts a static object (Bowman et al., 2009). It is possible that somatosensory feedback obtained at contact may have aided in maintaining a stable representation of the workspace by confirming expected tactile contact and providing information about the location of this event through proprioception (Buneo & Andersen, 2006). By introducing object motion resulting from contact with the hand, the sensory consequences of contacting an object could now continue past the initial time and position of contact. If gaze is positioned to capture sensory consequences rather than the hand’s reaching the object position, we additionally hypothesize that gaze will remain longer at sites of sensory consequence with moving objects than with static objects that do not move when contacted. Alternatively, if gaze is strictly controlled to direct the hand to an object location, object motion resulting from contact should have no effect on accuracy of contacts nor on the relational timing between gaze and hand movements.

Our second hypothesis is that gaze is positioned to capture sensory consequences, and therefore gaze will remain at contact sites longer when objects move irrespective of whether they remain visible. Importantly this gaze strategy makes use of
predicted gaze movement timing and is not driven by reactions to sensory consequences. Because previous studies have reported that the visibility of the target is crucial in guiding action when the hand cannot be seen (Pellision et al., 1986; Prablanc et al., 1986), it is feasible that when the objects disappear accuracy will degrade further as key reference points for guiding behaviour have been removed. We again expect that accuracy will decline when the cursor is invisible. Thus, as sensory information becomes unavailable, gathering alternate means of confirming task-progress might become especially important for retaining control. One means of measuring whether gaze is positioned at a site to gather sensory information will be to quantify the duration of gaze placement at each site. Therefore, we expect that gaze will remain longer at locations where critical information for continuing a task might be gathered (i.e. the first object in a sequence for guiding the hand, or the last object in a sequence for assessing performance across the task). Finally, it is possible that removing a substantial portion of the information on which predicted sensory consequences are based may cause participants to transition to reactive control to complete the task. Here, we would expect greater inaccuracy paired with delays in gaze and hand movements across the task.

We found in Experiment 1 that gaze movements were delayed when the cursor was invisible but only when the objects moved after contact, an effect not apparent with stationary objects. This observation is consistent with our hypothesis that gaze is controlled to assess just completed action as well as direct the hand. When the cursor is invisible, gaze may be positioned such that central vision could reliably capture the consequences of action (e.g., resultant object motion, the position of tactile feedback). The timing of gaze movements may also be delayed so as to gather more information.
about changes made within the workspace that will need to be accounted for to plan motion to the next target and may even have resulted from a mode of control in which gaze movements were triggered by sensory confirmation.

To investigate whether gaze movements were delayed to capture visual and or non-visual consequences or were alternatively reactively triggered by them, we further manipulated the object-based sensory information when the cursor was invisible. It was not clear whether gaze would be used to monitor visual and non-visual consequences of action. We attempted to dissociate whether gaze was positioned to a) guide the hand and capture the hand reaching this location or b) to monitor visual and non-visual sensory consequences related to contact. To do this we introduced a strong-spring condition in which the object moved but quickly returned to its initial position. A delay in gaze movements here would suggest that gaze exits are delayed to capture the sensory consequences resulting from contact and not simply changes in object position (since these objects quickly return to their original position). We additionally tested whether gaze movement timing is linked to a visual reference of the contact site—indeed independent of resultant motion—by having the objects disappear when contacted but still provide tactile feedback. We used both static objects and loose-spring objects (used in Experiment 1) to determine whether tactile feedback linked to a static position or a moving reference might influence gaze movements. If gaze movements are only delayed with static objects, this may suggest that gaze is positioned to capture the hand reaching the initial location to which action is directed. If gaze movements are also delayed with the loose-spring objects, this may suggest that gaze is positioned to capture the resulting consequences of action (here linked to the tactile feedback administered to the hand as
it moves the object). In both cases, if gaze is delayed beyond contact this may suggest that a simple visual motion is not determining the timing of gaze movements; delays here would support the idea that gaze timing is linked to the predicted timing of multisensory feedback arising from manual action.

4.1 General Methods

4.1.1 Participants

We tested sixteen participants (18-30 y). Eight participants took part in Experiment 1 and eight took part in Experiment 2. All participants had normal or corrected-to-normal vision and each provided informed consent prior to testing. The experimental protocol complied with Queen’s University General Research Ethics Board and the Declaration of Helsinki, and the participants were compensated for their time.

4.2 Experiment 1 Methods

4.2.1 Apparatus and stimuli

Participants moved a handle attached to a lightweight force-reflecting robotic device (Phantom Haptic Interface 3.0L, Sensable Technologies, Woburn MA) with their right hand to contact a series of five visible virtual objects located in a horizontal plane approximately 40 cm below the eyes (Figure 6). The handle was a vertically oriented cylinder (2 cm in diameter and 10 cm in height) mounted on an air sled that allowed low-friction movement across a horizontal glass surface. The position of the handle was recorded at 1000 Hz with a spatial resolution of 0.1 mm. While seated, participants could not see their actual hand or the handle positioned below the virtual display. The virtual
display included the objects (2 by 2 cm squares), a start position for the cursor (2 cm diameter circle), and a cursor representing the position of the handle (2 cm diameter circle), all aligned with the top of the handle and matching the location where forces were imparted to the handle by the robot. Because handle position was represented by the cursor it will hereafter be referred to as cursor position. Each object was located randomly within a 4 by 4 cm region subject to the constraint that the lateral distance between any two objects was not less than 1 cm. The start position was located in the participant’s midsagittal plane approximately 35 cm below and 22 cm in front of the participant's eyes.

Images were displayed using an LCD projector (LC-XNB3S, Eiki Canada, Midland, ON) with a refresh rate of 60 Hz and a fixed (minimum) delay of 13 ms, yielding an average delay of ~21 ms. The objects were modeled with slightly compliant sides linked to the center of the object by way of a damped spring with stiffness and viscosity of 1000 N/m and $0.9^{-4}$ Ns/m, respectively. Because of the high stiffness of the objects, the sides did not move appreciably during contact and we did not render deformation visually. Two distinct objects were created: static objects and loose-spring objects. Static objects did not displace when contacted. Loose-spring objects would displace when contacted and gradually return to their start position by way of a modeled spring (mass 0.45 Kg, viscosity 0.8 Ns/m, and stiffness 1 N/m). This object was therefore very light and responsive to contact.
Figure 6. Apparatus and task. While seated, participants held a handle attached to a lightweight robot arm. The handle was mounted on air sleds and could be easily moved over a horizontal glass surface. An image from a projector was cast onto a screen via a 45° mirror and viewed by the participant in a semi-silvered mirror. Because the distance between the screen and mirror matched the distance between the mirror and the top of the handle, the image appeared at the level of the handle top. The projector displayed the objects, the start position for the hand and gaze, and, in some conditions, a circular cursor representing the position of the handle. A video-based eye tracker was used to record the position of the right eye and a forehead strap and small bite bar were used to stabilize the head.
Eye movements were recorded on each trial. An infrared video-based eye-tracking system (ETL 500 pupil/corneal tracking system, ISCAN Inc. Burlington, MA), recorded the gaze position of the left eye at 240 Hz. A bite-bar was used to stabilize the head and participants rested their foreheads against a fixed headband. Gaze was calibrated using a two-step procedure: an initial 5-point calibration using ISCAN’s Line-of-Sight Plane Intersection Software followed by a 25-point calibration routine. During calibration, points (4 mm diameter circles) were projected onto the horizontal plane distributed over a region that incorporated the start location and all possible locations of the objects. Raw gaze signals were converted into the coordinates of the Phantom robot in the horizontal plane. Gaze was calibrated at the start of the experiment, checked following each block of trials (see below), and re-calibrated as necessary. The spatial resolution of gaze, defined as the average standard deviation of all calibration fixations, was 0.36° visual angle. This corresponded to ~3 mm when gaze was directed to the center of the object zone for the middle object.

Hand and gaze position and hand forces were sampled at 1000 Hz, and so the gaze data provided by the ISCAN system at 240 Hz was over-sampled to correspond with this sample rate. The ISCAN software applied a ten-point moving average to the gaze data resulting in a delay of 20 ms that we manually corrected in the data. In order to detect saccades we: (1) smoothed the x and z gaze-position signals using a fourth order low pass Butterworth filter with a cutoff frequency of 6 Hz, (2) differentiated these signals to obtain x and z velocities, (3) computed the magnitude of the resultant velocity or gaze speed, and (4) differentiated this signal to obtain gaze speed slope. A saccade was deemed to occur when gaze speed was greater than 5 m/s² two times within 150
ms. Once a saccade was detected, saccadic onset and offset times were defined as the times at which saccadic velocity first exceeded and dropped below 0.2 m/s, respectively. Here we computed velocity based on the x and z gaze positions from the ISCAN (i.e., without additional smoothing). The x and z hand position signals were smoothed using a low pass fourth order Butterworth filter with a cutoff frequency of 14 Hz and differentiated to obtain x and z hand velocities.

4.2.2 General Procedure
To initiate a trial, participants maintained the handle and gaze within 5 and 60 mm, respectively, from the center of start position. The cursor was always shown during this phase of the trial. After 200 ms, five objects appeared and participants reached out and lightly contacted the near surface of each object moving from the leftmost to the rightmost object before returning to the start position. Feedback on movement speed and correct contact order was displayed for 1 s. “Too Fast” or “Too Slow” was displayed if the average time between contacts (not including the interval to reach the first target or leave from the last target) was less than 350 ms or greater than 750 ms, “Wrong Order” was displayed when the objects were not contacted in sequence from left to right. Otherwise, “Good” was displayed.

During the 30 trial training sessions the objects were the loose-spring type and participants could see the cursor. Training was followed by the test conditions (see below), presented in the same order for each participant. Participants were not instructed where to look during the task.
4.2.3 Design

Each participant performed a total of 120 trials, administered in two blocks of 60 trials. Every five trials the stimulus condition would change pseudo-randomly among six possible variations. Each stimulus condition appeared four times for a total of 24 trials. The 6 stimulus conditions included the following combinations of object type, cursor visibility, and tactile feedback (with contact force provided or removed):

- Static object, cursor visible, tactile feedback
- Static object, cursor invisible, tactile feedback
- Loose-spring object, cursor visible, tactile feedback
- Loose-spring object, cursor invisible, tactile feedback
- Loose-spring object, cursor visible, no tactile feedback
- Loose-spring object, cursor invisible, no tactile feedback

The current analysis focuses on the four stimulus conditions in which tactile feedback was provided. Thus, the analysis will center on the effects of two factors: object type (static or loose-spring objects) and cursor visibility (visible or invisible).

4.2.4 Analyses

We focused our analysis around contact attempts that we coded into three categories: correct contacts, misses, and erroneous contacts. A correct contact occurred when the cursor contacted the near surface of the object; an erroneous contact occurred when the cursor contacted any other surface of the object; and a miss occurred when the cursor
moved toward the object and back but failed to make contact. Trials in which the objects were not contacted in the correct order were excluded.

In order to investigate how eye-hand coordination is affected by our experimental manipulations, it is important to first examine how hand behaviour, \textit{per se}, is affected. We therefore computed a number of dependent variables to assess the path traveled by the hand, how the hand approached each target, and the speed of hand movement throughout the trial. For each trial we measured the hand path distance, defined as the displacement of the hand between contacting the first and fifth objects. For each object, we calculated hit interval, hand approach angle, contact location, hand velocity at contact, and hand withdrawal time. Hit time was defined as the time between contacting the previous object to the time of the current object contact. Hand approach angle was computed based on a vector between the location of the cursor at contact and 3 cm before this contact location. Hand velocity at contact is the resultant of the $x$ and $z$ velocity of the hand as it contacted each object. Hand withdrawal time is the interval of time between contact and the hand attaining maximum velocity during withdrawal from an object. Contact position was calculated separately for each contact type: For correct contacts, the contact position was defined as the $x$ position of the cursor at contact relative to the $x$ position of the centre of the object. For erroneous contacts and misses, we used the $x$ position of the center of the cursor when the perimeter of the cursor crossed the $z$ position of the near surface of the object (i.e., the location of contact had the object been wider). If the cursor did not reach this $z$ position, we took the $x$ position of the center of the cursor at the maximum $z$ position of the handle (furthest from the start position).
We assessed gaze exit times to investigate the temporal coupling between gaze and hand movements. Gaze exit latency is the difference in time between the onset of gaze movement away from an object and the time that the cursor contacted the object.

Our dependent measures were compared across the experimental factors of cursor availability (visible vs. invisible) and object type (static vs. loose-spring) in a 2 x 2 repeated measures ANOVA. For all analyses, alpha was set at 0.05. We also included planned comparisons between the four experimental conditions. To protect against Type 1 error across these multiple comparisons, we set alpha to 0.005.

4.3 Results Experiment 1
Participants in Experiment 1 exhibited a similar stereotypy to the general behaviour we reported in our previous work (Bowman et al., 2009). Figure 7 shows representative trials detailing how two participants moved throughout the trial. Generally gaze led hand position as the objects were contacted in order from left to right and the hand moved between objects with a u-shaped profile. Across conditions, we observed changes in our dependent measures depending on the visibility of the cursor as well as the object type. We report how accuracy and the temporal coupling between hand and gaze were differentially affected by these manipulations.

4.3.1 Accuracy
In examining the accuracy with which the hand contacts the objects, we focused on contacts made to the middle three objects. The first object was excluded from this analysis because participants were free to begin their movements at any time after the display appeared. With no time constraint placed on initial movement, participants were
Figure 7. Sample trials from two participants across experimental factors. Displayed is a top view of participants' performance where the large light gray squares represent the possible center locations of the 5 objects (dark gray squares) and the gray and black traces show the paths of the hand and gaze, respectively. A. Visible cursor and static objects. B. Visible cursor and loose-spring objects. The single gray lines starting from each object location denote the path of the object over the course of the trial once it was contacted. C. Invisible cursor and static objects. D. Invisible cursor and loose-spring objects. The single gray lines denote the same object movement as in B. Note. The objects moved further in response to contact in D compared to B. The hand path is exaggerated when comparing the left column (A, C) to the right column (B, D).
able to take as long as they wished to plan this initial movement. Since we were interested in performance during a sequenced task, when pressures to continue moving were high, we excluded the first object from analysis. In addition, because there were no pressures to continue moving gaze or the hand following contact with the fifth object, the coordination of gaze and hand movements to and from this object may also have varied. Consequently, this object was also excluded from analysis.

The percentage of contact attempts depended on the visibility of the cursor, as shown in Figure 8, which shows the percentages (and frequencies) for all contact attempts collapsed across participants. When the cursor was visible, participants were very accurate independent of object type. For static objects, only five attempts were misses (0.45%) and 49 attempts were erroneous contacts (7.4%); for loose-spring objects, only three attempts were misses (0.76%) and 46 attempts were erroneous contacts (7.40%). When the cursor was not visible, accuracy was markedly poorer. With static objects, participants missed 98 times (10.1%) and 158 attempts were erroneous contacts (24.8%); for loose-spring objects, 27 attempts were misses (4.2%) and 98 attempts were erroneous contacts (15.1%).

We coded contact attempts into three categories: correct contacts, erroneous contacts and misses. Only the initial attempt at contact was coded (corrections were excluded) resulting in 2609 attempts. A correct contact occurred when an object was hit in the proper order and the cursor contacted the near surface; there were 2159 (82.75%) correct contacts. Erroneous contacts occurred 395 times when the cursor contacted any other side of the object (13.45%). Misses occurred 99 times, when the cursor moved toward the object and back but failed to make contact (3.79%).
Figure 8. Hit type totals for Experiment 1. Percentage of correct contacts (black) and incorrect contacts (gray) across conditions in Experiment 1. Each pair of bars represents the total summed across all participants, for a stimulus condition. Note. The n of each bar is displayed in white text within the bar.
We performed a two-way repeated measures ANOVA on the percentage of correct contacts across the two experimental factors (cursor visible vs. invisible and static vs. loose-spring objects) and observed a main effect of cursor visibility $F(1, 7) = 15.4, p < .006$. A greater number of correct contacts occurred when the cursor was visible ($M = 76.2\%, SD = 1.26\%)$ than when it was invisible ($M = 58.7\%, SD = 3.75\%)$. There was also a main effect of object type, $F(1, 7) = 10.6, p < .014$, with a greater number of correct contacts with loose-spring objects ($M = 71.06\%, SD = 0.71\%)$ compared to static objects ($M = 63.88\%, SD = 2.77\%)$. The interaction between cursor visibility and object type approached significance, $F(1, 7) = 4.8, p = .065$. Cursor visibility appeared to have a larger effect on the number of correct contacts with static compared to loose-spring objects.

### 4.3.2 Hand trajectories

Figure 7 shows representative hand paths of two participants when performing the five-object contact task. In all conditions, participants produced stereotypical U-shaped hand paths between successive objects (c.f. Bowman et al., 2009). However, when the cursor was invisible the hand path curvature became exaggerated. We quantified this change by comparing the median hand path distance, for each participant, across the two experimental factors (cursor visible vs. invisible x static vs. loose-spring objects). Our analysis revealed a significant main effect of cursor visibility, $F(1, 7) = 10, p = .016$. When the cursor was visible, participants’ hand path distance was shorter ($M = 95.52$ mm, $SD = 3.37$ mm) than when the cursor was invisible ($M = 122.53$ mm, $SD = 10.44$ mm). There was no main effect of object type $F(1, 7) = 2.921, p = .131$, nor an interaction between the factors, $F(1, 7) = .754, p = .414$. 
Given the increase in hand path distance when the cursor was invisible, it is reasonable to expect a corresponding increase in the hit interval. We compared median hit intervals, computed for each participant, across the experimental factors (cursor visible vs. invisible and static vs. loose-spring objects) and observed a main effect of cursor visibility, $F(1, 7) = 13.2, p = .008$. Hit intervals were shorter when the cursor was visible ($M = 398$ ms, $SE = 7$ ms) than when it was invisible ($M = 443$ ms, $SE = 18$ ms). There was no main effect of object type, $F(1, 7) = .6, p = .48$, nor an interaction between the factors, $F(1, 7) = .2, p = .693$. Participants had similar hit intervals with static objects ($M = 420$ ms, $SE = 13$ ms) and loose-spring objects ($M = 422$ ms, $SE = 12$ ms).

One reason for the increase in hand path distance may be that participants were trying to align the approach of the hand more perpendicularly to the near surface of the target to increase the chances of successful contact (Bowman et al., 2009; Cuijpers et al., 2004; Kleinholdermann et al., 2007; Smeet & Brenner, 1999). An inspection of Figure 7 suggests that approach angle varied as a function of our manipulations in Experiment 1 as well. For each participant across the two experimental factors (cursor visible vs. invisible and static vs. loose-spring objects) we calculated the median approach angle and plotted these in Figure 9A. The grey lines illustrate each individual’s median approach angle where $0^\circ$ represents approach perpendicular to the right side of the object, $90^\circ$ a normal approach. The thick black lines illustrate the mean approach angles averaged across participant medians. Note that when the cursor was invisible, participants’ approach angle was more perpendicular to the bottom surface of the object. Our analysis revealed a main effect of cursor visibility, $F(1, 7) = 21.4, p = .002$, but not object type, $F(1, 7) = .5, p = .498$ and no interaction between the factors, $F(1, 7) = .8, p =
Figure 9. Hand Trajectories. A. Top views of cursor approach angles across the experimental factors. In each panel, the two gray circles show, the average locations (based on participant medians) of the handle when it approached within 3 cm of the contact position, and contact position. The left column shows visible cursor trials, and the right column shows invisible cursor trials. The top row shows static object trials, the bottom row, loose-spring object trials. B. Average approach angles, based on participant medians, averaged for all participants across the experimental factors. Perpendicular approach (90 degrees) to the object is denoted by the dotted line. Error bars represent ± 1 SE. C. Average hand withdrawal time, based on participant medians for the four stimulus conditions. Error bars represent ± 1 SE.
Approach angles were less perpendicular with the visible cursor ($M = 111^\circ$, $SE = 2^\circ$) than with the invisible cursor ($M = 101^\circ$, $SE = 3^\circ$) suggesting that cursor visibility facilitates the planned approach to the object.

When approaching an object, greater precision requirements can influence the velocity profile of the hand such that hand velocity is slowed (Fitts, 1954, Fitts & Petersen, 1964, Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Milner, 1992). Without a visible cursor, the accuracy with which the position of the hand relative to object—and hence the prediction of when and where contact will take place—may be degraded. As a consequence, we might expect differences between the cursor visible and invisible conditions in the velocity of the hand (and hence contact force) at contact. For each participant, we compared median hand velocity at contact across the two experimental factors. This analysis revealed a main effect of cursor visibility, $F(1, 7) = 14.8, p = .006$, such that participants contacted the object with greater velocity ($M = 548.7 \text{ mm/s, } SE = 28.6 \text{ mm/s}$) when the cursor was invisible than when the cursor was visible ($M = 524.3 \text{ mm/s, } SE = 27.9 \text{ mm/s}$). There was no main effect of object type, $F(1, 7) = 1.84, p = .217$, nor was there a significant interaction between the two factors, $F(1, 7) = 1.9, p = .21$. Our findings suggest that when approaching an object, vision of the cursor can be used to predict when contact will take place and scale the velocity of the hand appropriately (Desmurget and Grafton, 2000). Without vision of the cursor, scaling of hand velocity during the approach is done less well.

To examine the timing of hand movements to the next object following contact, for each participant we calculated the hand withdrawal time – the time to reach peak
velocity when withdrawing from the object, relative to the time that the cursor contacted that object (Figure 9C). Analysis of the median hand withdrawal time for each participant across the two experimental factors revealed a main effect of cursor visibility, $F(1, 7) = 15.1, p = .006$, but no main effect of object type, $F(1, 7) = .2, p = .642$, nor an interaction between the factors, $F(1, 7) = .2, p = .672$. Hand withdrawal time was longer when the cursor was invisible ($M = 223$ ms, $SE = 10$ ms) than when it was visible ($M = 195$, $SE = 5$ ms) but unaffected by object type (static: $M = 208$ ms, $SE = 7$ ms; loose spring: $M = 210$ ms, $SE = 7$ ms). Participants' withdrawal from objects was slower when the cursor was invisible. Following a less certain contact, slower hand withdrawal may have enabled required changes in hand path to be incorporated more quickly.

In comparison to the above hand measures, cursor visibility did not affect contact $x$ position variability. For each participant, we calculated the standard deviation of the $x$ contact position. We found no significant differences as a function of cursor visibility, $F(1, 7) = 1.1, p = .3$, or object type, $F(1, 7) = 3.2, p = .1$, nor was there an interaction between the factors, $F(1, 7) = .1$ $p = .7$. Across participants, the average standard deviation of the contact position was $M = 8.6$ mm ($SE = .5$ mm). We also calculated the median $x$ contact position for each participant across our experimental factors, finding main effects of cursor visibility, $F(1, 7) = 52.2, p < .001$, and object type, $F(1, 7) = 10.9, p = .01$, but no significant interaction between the factors, $F(1, 7) = 189, p = .68$. Participants contacted further to the right of the object center when the cursor was invisible ($M = 6.1$ mm, $SE = .78$ mm) than when the cursor was visible ($M = 3.2$ mm, $SE = .75$ mm) and contacted further to the right with static objects ($M = 5.77$ mm, $SE = .72$ mm) compared to moving objects ($M = 3.55$ mm, $SE = .89$ mm). These results require careful interpretation; it is
difficult to determine the exact influences on contact position since variability is limited by available contact surface. Nevertheless, with static objects and an invisible cursor, participants contacted the objects further off-center.

In sum, when the cursor was invisible participants markedly changed their hand paths. They scaled down hand velocity less at contact, and moved away from contacted objects more slowly. When contacting objects, the approach angle was more direct, and to facilitate this approach the hand path distance increased. These changes in how participants engage the hand in and around the site of contact may be adaptations to compensate for the uncertainty of the position of the hand relative to the position of the object. Despite this putative adaptation, participants were less accurate when the cursor was invisible and produced fewer correct hits.

4.3.3 Temporal coordination of gaze and hand movements
We were principally interested in how gaze movements serve manual action in planning sequential movements and assessed this by examining the correlation between gaze and hand movements. To determine the temporal coupling between gaze and hand movements in our sequential task we measured gaze exit latency, the interval between object contact and when gaze exited the viewed object. We sought to measure potential changes in gaze exit latency that occurred as a function of the experimental factors.

Figure 10A shows cumulative frequency distributions of median gaze exit latency for the correct contacts from all participants as a function of the two experimental factors. Figure 10B shows individuals’ cumulative frequencies across the four experimental conditions and demonstrates that no one individual was responsible for our observed effects. Our
analysis of the median gaze exit latency for each participant demonstrated a main effect of cursor visibility, \( F(1, 7) = 27.4, \ p = .001 \), and object type, \( F(1, 7) = 18.0, \ p = .004 \). Importantly, we also observed a significant interaction between the factors, \( F(1, 7) = 8.8, \ p = .021 \). Gaze exit latency increased when the cursor was invisible but increased more with loose-spring objects (\( M = 151 \ ms, \ SE = 18 \ ms \)) than with static objects (\( M = 105 \ ms, \ SE = 16 \ ms \)). Median gaze exit latency was least delayed when the cursor was visible and was similar for both object types (static: \( M = 88 \ ms, \ SE = 15 \ ms \); loose-spring: \( M = 85 \ ms, \ SE = 12 \ ms \)). When the cursor was invisible, gaze remained at an object longer; this effect was strongest when that object moved in response to contact. Pairwise comparisons between the four conditions revealed significantly later gaze exit latencies occurred with the invisible cursor and loose-spring objects than all other conditions (all values \( p \leq .004 \)). There were no differences between the other conditions.
Figure 10. Gaze Exit Latencies. A. Cumulative distributions of gaze exit times relative to contact across the experimental factors. Each distribution combines data from all 8 participants. B. Cumulative distributions of gaze exit latencies for each participant in each of the four experimental factors. The left column shows visible cursor trials the right column shows invisible trials. The top row shows static object trials, the bottom row shows loose-spring trials. Note. The gray areas in each distribution denote the epoch containing gaze exits that occurred before 130 ms during which time it was unlikely that gaze exits were triggered (c.f. Bowman et al., 2009).
4.4 Experiment 1 Discussion

Considerable research has indicated that directing gaze to a reach target improves manual accuracy through the use of signals related to gaze position and, when available, visual feedback of the hand (Crawford et al., 2004; Desmurget, Gaveau, Vindras, Broussolle & Thobois, 2004; Johansson et al., 2001; Land et al., 1999; Medendorp et al., 2003; Paillard, 1996; Sarlegna et al., 2004; Saunders & Knill, 2004). Used solely for this function, there would be little reason for gaze to remain at a site of planned action beyond when contact occurs. Indeed, we might expect gaze to shift before contact when gaze signals can no longer be used to update hand movement due to time delays in sensory loops. However, we have demonstrated that gaze does not leave before contact when contacting a series of static objects (Bowman et al., 2009). Here, we manipulated the feedback that contributes to determining the timing and location of planned sensory consequences (i.e., cursor visibility and object response to contact). Our results support the hypothesis that gaze placement matters for more than directing the hand to a target; accuracy and the coupling of gaze and hand movement timing were differentially affected by our experimental manipulations. Changes in contact accuracy occurred independently of gaze exit latency; accuracy was lowest when the cursor was invisible and static objects were contacted while gaze exit latency was longer with an invisible cursor and loose-spring objects were contacted (i.e., when the cursor was visible there was no difference in accuracy or gaze latency). These results might indicate that the parameters responsible for accuracy may be separable from those controlling coordinated timing between gaze and hand movements.
Owing to the removal of sensory information that is otherwise normally available (i.e., cursor visibility), it may be possible that participants were less able to determine the exact location and timing of forthcoming contact with the objects. The delayed gaze exit latencies seen with the invisible cursor and the loose-spring objects might indicate further degradation in the estimates needed for predicting the timing and location of key events. Though generally delayed, gaze exit times here are nevertheless similar to those observed in our earlier work where participants sequentially contacted static objects (c.f. Bowman et al., 2009). In the cursor visible conditions gaze exits continued to occur within an epoch denoting movements based on predicted events. When the cursor was invisible and static objects were contacted, gaze did not remain long after contact, perhaps because additional visual information was not available (c.f., Bowman et al., 2009). The delays in gaze timing might owe to the frequency of the changing stimuli (i.e., changing every 5 trials) making it difficult to predict what feedback would be available and when contact would occur. Recall that with an invisible cursor there were a greater number of erroneous contacts for both loose-spring and static objects (Figure 8) indicating a plausible detriment in determining the location of the hand relative to the object. Moreover, participants adapted many components of the hand approach to the objects when the cursor was invisible. These reported compensatory changes in hand behaviour could support the supposition that the timing and location of contact were less well determined without cursor feedback.

Given the detriment in determining the location and timing of planned events, participants may have adopted one of two compensatory strategies that are currently indistinguishable in the present results. Participants may have 1) delayed gaze to
capture object motion and tactile feedback signaling contact in central and/or parafoveal vision, or 2) as a result of limited feedback may have begun to shift to a reactive mode of planning movements (c.f., Zorn et al. 2007). Maintaining gaze position until the hand arrives might result—as some have suggested—via a shared motor plan between the hand and eyes that necessarily anchors gaze to a reach position until the hand has arrived (Neggers & Bekkering 2001; Neggers & Bekkering, 2002). In addition, maintaining gaze until contact might allow the consequences of action to be captured in central vision and compared to predictions about these consequences (Bowman et al., 2009; Flanagan et al., 2006; Johansson et al., 2001; but see also Miall & Cole, 2007). With sufficiently delayed gaze exits, sensory information arising from just-completed action could be registered and integrated to update errors in the motor plan, while still not necessarily triggering the next movement (Bowman et al., 2009). If gaze leaves an object before this contact information is registered in central vision it is less likely to contribute to this process. Alternatively, gaze movements may be reactively executed when predictions are sufficiently poor. With an invisible cursor and the loose-spring objects gaze delays were long enough that either strategy of capturing sensory consequences to generate an appropriate response in moving to the next object could have been used.

It remains difficult to differentiate whether delays in gaze movements reported here were planned or reactive. We designed Experiment 2 to test the hypothesis that gaze movements are delayed to better align and integrate key information related to contact (or a goal of movement); removing goal-related sensory information should interrupt gaze movements, and potentially have detrimental effects on performance
accuracy. Moreover, if information arising from one contact is used to guide movements to the next object, performance might also be negatively impacted when the visual references of object position are changed following contact. Alternatively, reactive motor programming might be based on goal-related feedback and could only be used following contact. If this is the case, removing features of a goal to which action has been directed following the completion of that goal should produce few changes in the temporal profile of movement. Thus, Experiment 2 was designed to determine whether the delayed gaze movements seen with an invisible cursor and moving objects resulted from removing a goal-related reference used in confirming completed action (and integrating sensory feedback important to the task) or for reactively planning subsequent movements.

4.5 Experiment 2

The gaze movements observed when contacting loose-spring objects with an invisible cursor (Experiment 1) might have been delayed because they were reactively triggered by confirmation of contact (e.g., resultant object motion) or because gaze was being used to register, in central vision, sensory signals needed for generating accurate predictions of the consequences of action. To further investigate this difference, in Experiment 2 we returned to the blocked design used by Bowman and colleagues (2009) and introduced stimulus conditions that removed object visibility following contact or involved a new object type that moved when contacted but rapidly returned to its initial position as the hand moved away (strong-spring object). We examined changes in hand measures and the temporal coupling between hand and gaze movements following these manipulations. We were specifically interested in how the timing of gaze
movements might change as function of the availability of object-based sensory information when the cursor was invisible.

The gaze delays with an invisible cursor and moving objects in Experiment 1 may have resulted because a reference used to guide the hand (e.g., object position) changed. As such, gaze may have been delayed to capture object motion and update the representation of the workspace in which action occurs. Indeed such a strategy might be evident irrespective of the type of object motion. Should gaze be delayed to capture any object motion we hypothesize gaze will be delayed with loose-spring and strong-spring objects. We have previously suggested that in sequential contact tasks gaze is used to capture visual and possibly non-visual information following contact (Bowman et al., 2009). To test this we included two conditions in which the object disappeared following contact; one condition in which the object moved (a loose-spring object) and one in which the object was static. Gaze positioning to capture resultant motion from contact would not prompt longer gaze maintenance when the objects remained static. Alternatively, this gaze behaviour may have occurred so as to capture sensory information needed to align and integrate sensory information (and thus contribute to accurate movements in the future). Therefore, we hypothesize that gaze should remain longer upon an object (where visual and non-visual signals related to contact may be registered) even when that position is no longer visible and irrespective of whether the object moves. Finally, we also tested the contribution of tactile feedback in coordinating gaze and hand movements by including tactile catch trials in the invisible cursor conditions. It remains a possibility that with long enough delays gaze movements could be triggered by tactile confirmation of contact and removing this tactile information.
might therefore inhibit these gaze movements. However if gaze movements were
delayed to capture key tactile information arising from planned actions, removing this
expected information would be unlikely to interrupt planned gaze movements.

4.5.1 Apparatus and Stimuli
The apparatus were the same as in Experiment 1 with the following exceptions: first, the
projection unit was upgraded to a faster CRT projector (Marquis 8500, VDC Display
Systems) with a refresh rate of 120 Hz with a fixed computer to screen delay of 1 ms
resulting in an average delay of 8 ms; second, the ISCAN software was upgraded
allowing us to remove the moving average feature that was previously applied to the raw
data. We were therefore able to collect raw gaze signal data sampled at 240 Hz. In
Experiment 2 we introduced an additional object type, the strong-spring object. This
object resisted moving when contacted, generally staying in contact with or within close
proximity to the hand and returned to its original position when the hand withdrew from
contact. The strong-spring object was simulated as having a mass of 0.45 Kg attached
to a spring with viscosity 5 Ns/m and stiffness 50 N/m.

4.5.2 Procedure
Training trials were the same as in Experiment 1. Thus, the training trials provided a
baseline measure of performance for comparison with Experiment 1. After training,
participants performed four test blocks of 30 trials. The cursor was invisible in all four
test blocks. This resulted in 5 stimulus conditions: baseline and four test blocks. The four
test blocks were administered in the same order for all participants. The first condition
contained loose-spring objects that disappeared when contacted. The second condition
contained strong-spring objects that remained visible after contact. The third condition contained loose-spring objects that remained visible after contact (matching the loose-spring condition in Experiment 1). Finally the fourth condition contained static objects that disappeared when contacted.

To assess whether gaze shifts might be triggered by tactile information related to contact we included catch trials in which the tactile information normally provided at contact was removed. Each test block contained six randomly selected catch trials in which tactile feedback was removed for one of the middle three objects in the sequence (each object was used twice and the same sequence of catch trials was used for all participants). We opted to keep the catch rate very low to guard against the possibility that catches would alter gaze or hand movement behaviour; out of the 150 contact events in a test block (30 trials x 5 objects), approximately 4% were catches. The baseline block contained no catch trials.

4.5.3 Analyses

We analyzed the same dependent variables used in Experiment 1 and added two new variables, gaze arrival latency and fixation time. Together these measures can more fully describe gaze behaviour at each object. Gaze arrival latency is the interval between the end of a saccade bringing gaze to an object and when the hand contacted the object. Fixation time is the epoch from the end of a saccade that brings gaze to an object to the beginning of a saccade exiting from that object.

In Experiment 2 we compared the effects of our five conditions (baseline, loose-spring disappearing objects, strong-spring objects, loose-spring objects, and static
disappearing objects) in a five-way repeated measures ANOVA. We followed up with planned comparisons to answer four main questions. First, to assess the overall effects of removing vision of the cursor we compared the baseline condition (where the cursor was visible) to all the other conditions combined (where the cursor was invisible). Second, to assess whether the type of object motion influences behaviour, we compared the strong-spring and loose-spring conditions. Third, to assess how removing visual feedback of the just-contacted object influenced hand and gaze behaviour we compared the disappearing loose-spring condition to the loose spring condition. Finally, to determine whether gaze timing changed when the visual position of the object was removed and its felt position changed or remained at the last seen location of the object we compared the disappearing loose-spring condition to the disappearing static condition. There is a small degree of overlap amongst the four comparisons between these conditions of which we are aware. Although most object pairs are orthogonal (e.g. disappearing loose-spring vs. loose-spring; loose-spring vs. strong-spring objects; disappearing loose-spring vs. disappearing static) the first comparison involves a combination of all these cursor invisible conditions to the baseline condition. However, because the tests are mostly independent we opted to use an alpha level of 0.05.

We further examined gaze performance throughout the task by comparing our gaze measures at each of the five objects across the five conditions in a 5 x 5 ANOVA. For these tests, in addition to the comparisons among the conditions described above we used planned comparisons across successive object numbers comparing each object to the average of the remaining objects to assess performance as the task unfolded.
4.6 Results Experiment 2

The behavioural profiles in Experiment 2 were mostly consistent with Experiment 1 but demonstrated some new effects. When the objects disappeared participants were challenged to a greater degree. In the first instance of this manipulation (i.e., cursor invisible, loose-spring disappearing object) 3 participants became so disoriented that they were unable to locate the objects and testing was stopped. These participants were excluded from further analysis and three additional participants were recruited in their stead. To further examine the contribution of feedback related to the contact goal, we report accuracy and describe the temporal and spatial coupling between gaze and hand movements.

4.6.1 Accuracy

The same definitions for contact accuracy used in Experiment 1 apply here. Of the 6181 contact events analyzed, 3683 (59.6%) were correct contacts, 1872 (30.3%) were erroneous contacts, and 292 (4.7%) were misses. As can be seen in Figure 11 the proportion of correct contacts, erroneous contacts, and misses varied as a function of condition. During baseline participants mostly correctly contacted the objects, while accuracy declined when the object moved and/or disappeared.

We analyzed the number of incorrect hits (pooling the erroneous hits and misses) across the conditions. During the disappearing loose-spring trials one individual struggled greatly with the task and produced so many misses that the group miss average was skewed to a value larger than the total number of misses for all other participants (group average =14.5; S3 = 65; all other participants’ miss total ≤ 14). Since
this individual was an outlier in only this condition we substituted the number of misses they produced with the value of 15 (the mean rounded up), a value still greater than the number of misses produced by any other subject. We then summed the erroneous contacts and misses for each participant to produce the number of incorrect hits made in each condition. This action was taken to protect against the skewed data potentially bringing about a significant difference across conditions where there was none.

We next calculated for each participant and block the percentage of incorrect hits. A repeated measures ANOVA on the percentage of incorrect contacts demonstrated the main effect of condition, $F(4, 28) = 12.7, p < .001$ (see Figure 11). A planned comparison revealed fewer incorrect hits were made in the baseline condition than the remaining conditions combined, $F(1, 7) = 41.7, p < .001$. With strong-spring objects there were fewer incorrect hits than with loose-spring objects, $F(1, 7) = 10.1, p = .015$. Loose-spring objects produced fewer incorrect hits than disappearing loose-spring objects $F(1, 7) = 6.8, p = .035$. Finally, the number of incorrect contacts produced for disappearing loose-spring objects did not differ from those for disappearing static objects $F(1, 7) = .1, p = .80$. Generally, when the cursor was invisible accuracy diminished and accuracy degraded further when the objects disappeared following contact. Together these results suggest that feedback related to the just contacted object may be helpful in guiding the hand to the next target.
Figure 11. Hit type totals for Experiment 2. Percentage of correct contacts (black) and incorrect contacts (gray) in Experiment 2. Each pair of bars represents total summed across all participants, for each of the five block types. Note. The n of each bar is displayed in white text within the bar.
4.6.2 Hand trajectories

Figure 12 shows representative hand paths of four participants across the four testing conditions of loose-spring disappearing (Fig. 12A), strong-spring (Fig. 12B), loose-spring (Fig. 12C) and static disappearing (Fig. 12D). Each panel depicts one individual and demonstrates normal performance in the condition. During baseline we observed that participants exhibited the typical u-shaped hand paths between objects (Bowman et al., 2009); these data are not depicted in Figure 12. As in Experiment 1, hand path curvature (and therefore distance) was markedly exaggerated with the invisible cursor. Note that this comparison is difficult with the static objects because there is no visible cursor static object condition in Experiment 2 (c.f. Figure 7).

We examined hand path distance based on participant medians, comparing correct contacts across the five conditions and observed a main effect of condition $F(4, 28) = 7.1, p < .001$. As shown in Table 1, hand path distances were short during baseline (when the cursor was visible) and shortest with an invisible cursor and disappearing/static objects when the hand would have been stopped by object contact. Thus, a shorter hand path distance occurred in the static object condition than the remaining invisible cursor conditions possibly because the hand was stopped at each contact.
Figure 12. Representative trial examples. Displayed is a top view of four individuals' performance in the 4 invisible cursor conditions; a different individual represents each condition. The large light gray squares represent the possible center locations of the 5 objects (dark gray squares), and the thin dark gray lines denote object motion resulting from contact. The thick gray and black traces show the paths of the hand and gaze, respectively. Trial types are labeled across the horizontal and vertical axes.
In *Experiment 1* hand path distance and trial duration both increased when the
cursor was invisible. Here too, our analysis of trial duration, based on participant
medians, revealed a significant difference amongst the conditions $F(4, 28) = 2.7, p = .047$ (Table 1). Planned comparisons confirmed that participants tended to take the least
time to complete baseline trials compared to the other conditions combined, $F(1, 7) = 5.2$
$p = .056$); none of the other conditions differed ($p > .05$).

Table 1:

<table>
<thead>
<tr>
<th>Condition</th>
<th>Correct hits</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Hand path distance (mm)</td>
</tr>
<tr>
<td></td>
<td>Hand velocity at contact (mm/s)</td>
</tr>
<tr>
<td></td>
<td>Approach angle (degrees)</td>
</tr>
<tr>
<td></td>
<td>Trial Duration (seconds)</td>
</tr>
<tr>
<td>----------------------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>Baseline</td>
<td>177.22 32.78 877.44 87.73 109.95 12.66 2.015 .064</td>
</tr>
<tr>
<td>Disappearing/loose-spring</td>
<td>217.02 43.72 1008.48 74.77 100.70 11.39 2.196 .087</td>
</tr>
<tr>
<td>Strong-spring</td>
<td>207.94 34.90 1025.32 64.55 100.86 7.83 2.295 .044</td>
</tr>
<tr>
<td>Loose-spring</td>
<td>194.90 37.21 978.46 63.14 103.76 10.80 2.159 .100</td>
</tr>
<tr>
<td>Disappearing/static</td>
<td>173.81 26.26 681.80 38.94 103.12 11.00 2.143 .072</td>
</tr>
</tbody>
</table>

*Note.* a main effect at $p < .01$. b main effect at $p < .001$. c main effect at $p < .05$

As was observed in *Experiment 1*, hand trajectories in *Experiment 2* changed
when the cursor was invisible with a more perpendicular approach to the bottom of the
object (see Table 1). We quantified the median approach angle for correct contacts for
each participant and condition. We compared these values across the conditions finding
only a trend toward a main effect of both condition, $F(4, 28) = 2.5, p = .062$. The
approach angle tended to be more perpendicular (see Table 1) when participants were
unable to see their hand, replicating our observation that participants align hand
approach to be perpendicular to the bottom of the object (Bowman et al., 2009;
*Experiment 1*). This result may have failed to reach significance because of the static
object condition in which the hand was differently controlled to reach and contact objects.

In comparison to hand approach angles, where participants appeared to take a more perpendicular approach to moving objects, we might expect that prior to contacting static objects hand velocity at contact be damped more so as to avoid colliding with an object with too much force. Moving toward moving objects might be less well predicted, but without the same penalty of collision; and thus contact with moving objects might differ. We examined hand velocity at contact, based on participant medians, for correct hits across the five conditions and observed a main effect $F(4, 28) = 13.5, p < .001$. As seen in Table 1, hand velocity at contact was damped most for the static objects compared to the cursor invisible conditions but also damped more before contacting objects in baseline. Since different behavioural contrasts were expected among the conditions we conducted Bonferroni corrected comparisons across the groups. This analysis revealed that hand velocity at contact was significantly less damped with the static objects than with disappearing loose-spring objects ($p = .002$), strong spring objects ($p = .004$) or loose-spring objects ($p = .005$); however, hand velocity at contact was not different than baseline ($p = .201$). These differences support the argument that the precision of the planned contact may have influenced how the hand was controlled in approaching the objects.

4.6.3 Gaze hand coordination

Our previous results showed that sensory information resulting from object contact could influence the timing of gaze movements (Bowman et al., 2009; Experiment 1). Here, we
measured the temporal coupling between gaze and hand movements in response to our experimental manipulations, examining gaze arrival latency (i.e., the time from gaze arrival to when contact of the object occurred), gaze exit latency, and fixation time (i.e., the interval between gaze arrival to and gaze exit from an object). Figure 13A shows cumulative frequency distributions of gaze arrival and exit latencies for correct contacts as a function of object number. Using the values from correct contacts, exit and arrival latencies for each participant were calculated for each object across the five conditions and evaluated in separate 5 x 5 repeated measures ANOVAs.

Gaze arrival latency for correct contacts depended on object number (Figure 13B), \( F(4,28) = 50.5, p < .001 \), but not condition, \( F(4, 28) = .9, p = .494 \), nor was there a significant interaction, \( F(16, 112) = 2, p = .146 \). Planned comparisons were carried out to compare the gaze arrival latency of each object number with the average of the remaining objects in the sequence. Gaze arrival latency for the first object (\( M = 452 \) ms, \( SE = 29 \) ms), was greater than all the other objects combined (\( F(1, 7) = 61.1, p < .001 \); Figure 13A). Gaze arrival latency to the second object (\( M = 244 \) ms, \( SE = 16 \) ms) was not different from the remaining objects, \( F(1, 7) = 1.9, p = .213 \). However, the arrival latency of the third object (\( M = 246 \) ms, \( SE = 19 \) ms) was greater than to the two remaining objects, \( F(1, 7) = 6.2, p = .042 \). Finally, gaze arrival latencies between the fourth object (\( M = 241 \) ms, \( SE = 17 \) ms) and fifth object (\( M = 209 \) ms, \( SE = 13 \) ms) were significantly different, \( F(1, 7) = 11.2, p = .012 \). As the trial unfolded gaze arrival latency tended to diminish, bringing gaze arrival closer to contact time.
Figure 13. Average gaze arrival and exit latencies. A. Cumulative percentage distributions of gaze arrival latencies (left) and gaze exits latencies (right) for each object number across each of the block types. Each distribution contains data from all participants. The gray region denotes the < 130 ms epoch in which it is unlikely that triggered saccades will occur (Bowman et al., 2009). B. Average gaze arrival latency relative to contact of each object pooled across all block types. Error bars represent ± 1 SE. C. Average gaze exit latency relative to contact for each object pooled across all block types. Error bars represent ± 1 SE. D. Average gaze exit latency relative to contact for each block type pooled across object position. Error bars represent ± 1 SE. Note. * denotes $p < .05$; **denotes $p < .01$; *** denotes $p < .001$. 


Gaze exit latency for correct contacts depended on object number (Figure 13C), $F(4, 28) = 19.6, p < .001$, condition (Figure 13D), $F(4, 28) = 26.3, p < .001$, and the interaction between the factors, $F(16, 112) = 2, p = .019$. Planned comparisons were carried out to compare each object to the average of the remaining objects in the sequence. Gaze exit latency increased from each object to the next, from the first through to the fifth object (all values $p < .01$). Planned comparisons across conditions revealed that shorter gaze exit latencies occurred during baseline ($M = 116$ ms, $SE = 11$ ms) compared to all the other conditions combined ($p < .001$). Gaze exit latencies for strong-spring objects ($218$ ms, $SE = 7$ ms) and loose-spring objects ($M = 185$ ms, $SE = 11$ ms) were significantly different, $F(1, 7) = 31.7, p = .001$; however, gaze exit latencies between loose-spring objects and disappearing loose-spring objects ($M = 184$ ms, $SE = 7$ ms) did not differ, $F(1, 7) = .01, p = .9$; nor were gaze exit latencies between disappearing loose-spring objects and disappearing static objects ($171$ ms, $SE = 10$ ms) different, $F(1, 7) = 1.3, p = .285$. Thus, gaze position was maintained longest with strong-spring objects possibly because it resisted the hand and may have provided meaningful feedback after contact. Disappearing objects had no additional effect on gaze timing irrespective of whether the object moved. Together these results point to gaze being used to capture sensory information following contact. Finally the interaction resulted from relatively longer gaze exit latencies from the fifth object in cursor invisible conditions (especially strong-spring and loose-spring conditions) compared to baseline as well as relatively shorter gaze exit latencies from the first two objects in the baseline and disappearing static object conditions compared to the other conditions.
We examined the fixation time for correct hits across the five objects and conditions. For each participant we calculated the median fixation time for each object number across the conditions. Our analysis of fixation times showed main effects of object number, $F(4, 28) = 4.4, p = .007$, and condition, $F(4, 28) = 25.9, p < .001$, but no interaction of the factors, $F(16, 112) = 1.0, p = .419$. Planned comparisons across object number revealed longer fixation times on the first object than any other object and shorter fixation times on the second and third objects compared to the remaining objects (all values, $p \leq .03$). On average, participants fixated the first object for 596 ms and the remaining objects for 392, 395, 414, and 445 ms for the 2nd, 3rd, 4th, and 5th objects, respectively. Planned comparisons across conditions revealed that median fixation time during baseline ($M = 392$ ms, $SE = 22$ ms) was shorter than for all other block types combined $F(1, 7) = 11.1, p = .013$. Fixation times between the loose-spring objects ($M = 448$ ms, $SE = 15$ ms) and disappearing loose-spring objects ($M = 485$ ms, $SE = 30$ ms) were not different $F(1, 7) = 2.7, p = .142$ but fixation times were significantly longer for strong-spring objects ($M = 482$ ms, $SE = 10$ ms) than for loose-spring objects $F(1, 7) = 6.4, p = .039$. Fixation times for disappearing loose-spring and disappearing static objects ($M = 434$ ms, $SE = 27$ ms; $p = .014$) were not different $F(1, 7) = 1.8, p = .218$.

These results are consistent with an interpretation in which sensory information is sought out, with gaze, under impoverished circumstances. Because the strong-spring objects moved but returned quickly to their positions it is not surprising that fixation times may have been longest in this condition. If positions of just-contacted objects are used in guiding the hand to the next object, gaze may have been maintained longer in this condition so as to capture the object returning to its initial position.
4.6.4 Catch hit analysis

Saccadic movements in our previous work in this paradigm did not follow a time course that was would indicate that sensory confirmation was triggering movements but we were unable completely to rule out this possibility (Bowman et al., 2009, but see also Experiment 1). Here, gaze exit latencies were considerably longer across all of the invisible cursor block types, with the majority of gaze exits taking place 130 ms (or more) after contact. Because of this delay, it remains difficult to determine whether gaze exits were triggered by sensory confirmation or based on a predicted event. Following a considerable delay some gaze exits may have been generated reactively based on feedback arising from contact. However when sensory information is unexpectedly removed—as with the tactile catch trials—triggered gaze exits may be interrupted. In contrast, if gaze exits occurred based on a prediction, albeit a delayed one, gaze exits might continue to occur along a similar time course when tactile information is unexpectedly removed. There is a caveat though; with sufficiently delayed gaze movements, the absence of expected tactile information could also result in planned saccades being inhibited, resulting in greatly delayed (and presumably reactively triggered) saccades. Figure 14A shows cumulative frequency distributions of gaze exit latencies relative to contact of the middle three objects in the sequence summed across all participants for correct contacts (top), incorrect contacts (middle), and catch hits (bottom). Here, regular trials can be appropriately compared to catch trials since catch hits did not occur for the first and fifth objects. Figure 14B shows gaze exit latencies for each individual’s catch trials and separate plots are shown for each condition. The variability across participants and conditions in the four panels of Figure 14B suggests
Figure 14. Gaze exits by hit type. A. Cumulative distributions of gaze exit latency across the 5 block types. Each distribution combines data from all 8 participants. Top distribution depicts gaze exits for correct contacts; middle depicts incorrect hits (summed total of erroneous contacts and misses); bottom depicts all catch hits. The gray area denotes the < 130 ms epoch in which it is unlikely that saccadic triggered saccades will occur (Bowman et al., 2009). B. Individual cumulative distributions of gaze exit latency for catch hits. Each distribution shows catch hits for each individual in one of the block types. Note. There were no catch hits in the baseline condition; it is not represented in Figure 14A.
that many of the gaze exits observed here could still have been generated based on a prediction.

We compared median gaze exit latencies across the four conditions containing catch trials (disappearing loose-spring, strong-spring, loose-spring, and disappearing static target object conditions) and between hit types (correct contacts vs. catch hits) in a 4 x 2 repeated measures ANOVA observing a main effect of condition, $F(3, 21) = 14.4$, $p < .001$, and hit type $F(1, 7) = 53$, $p < .001$. Gaze exit latency was shorter for correct contacts ($M = 185$ ms, $SE = 6$ ms) than for catch hits ($M = 235$ ms, $SE = 9$ ms) indicating a delay in the execution of saccades following catch hits (n.b. gaze exit latencies for correct contacts are reported in section 4.6.3.). Critically, we also observed an interaction, $F(3, 21) = 4.977$, $p < .009$. Shown in the top and bottom panel of Figure 14A, the difference between the mean gaze latencies for correct contacts and catch hits with disappearing static objects was smaller (producing an additional ~17 ms delay) than for disappearing loose-spring objects (~53 ms), or loose-spring objects (~53 ms), and was longest for strong-spring objects (~77 ms). Thus, for static object trials catch hits produced a shorter delay in gaze exit latency; gaze exit latencies lengthened most in conditions in which gaze exits were already delayed.

4.7 Discussion Experiment 2

Experiment 2 was designed to further test whether gaze is positioned longer at a site of action to gather object-based sensory consequences resulting from contact or reactively trigger movements based on confirmation of contact. We directly tested whether feedback, resulting from contact and captured with gaze, influenced behaviour. Our
results are consistent with our hypothesis that gaze is controlled to capture sensory consequences resulting from action. Participants’ reach accuracy declined in all cursor invisible conditions and was worst when the objects disappeared after contact. When the cursor was invisible participants tended to change their hand path trajectory, perhaps to compensate for the lack of information signaling hand position relative to objects. Gaze was positioned upon the source of sensory consequence between the hand and object (i.e., contact) and not the resultant position of the object – even when objects disappeared following contact. Gaze position was maintained well after contact suggesting part of delaying gaze movements may have been to capture visual and non-visual feedback occurring after contact. The timing of gaze movements varied across objects as well as across conditions indicating that the strategy of capturing resultant feedback from contact was influenced by task requirements. Interestingly, interactions with an object may have provided feedback after contact (as with the strong-spring objects) gaze position was maintained for a longer time. Taken together, these results further indicate that gaze positioning is used for registering feedback (both visual and non-visual) related to just-completed actions and that a large proportion of these movements are based on predictions of key sensory events.

4.7.1 Accuracy

Our reported contact accuracy rates generally replicate the findings in Experiment 1. When the cursor was invisible, accuracy decreased; performance was more accurate with a visible cursor. Accuracy was lowest with the disappearing static object, but was also very low with the disappearing loose-spring objects. In these two conditions vision of the just-contacted object was removed and this significantly impacted how the hand
was directed to the next object. Recall that this effect was so disorienting that three participants were unable to complete the disappearing loose-spring objects condition and testing was stopped. Together these results strongly suggest that visual feedback of object position contributes to directing the hand to the next site of action possibly by helping to locate the unseen hand relative to the just-contacted object. This is not unlike previous studies that have demonstrated that a starting visual marker is required to orient participants as they perform a reach (Prablanc et al., 1986). The known position of the hand may, in fact, be of great benefit in programming a vector by which to move the hand to the next target (Sober & Sabes, 2003; Sober & Sabes, 2005). These findings provide support for this interpretation while also developing upon our suggested role that gaze is used to monitor the outcome of planned events.

4.7.2 Hand trajectories

Participants in *Experiment 2* altered their hand trajectory when the cursor was invisible just as we reported in *Experiment 1* and our previous work (Bowman et al., 2009). As the hand approached the object it tended to be aligned more perpendicularly to the bottom surface of the object. Perpendicular alignment to the to-be-contacted surface is a known approach strategy in manipulation by which the most precise control can be exacted upon an object (Cuijpers et al., 2004; Kleinholdermann et al., 2007; Smeets & Brenner, 1999). Here, perpendicular-like approach tended to occur when the objects moved. By aligning to the bottom surface, the potential surface area of contact is increased and hand approach can be simplified to a movement that would best intersect the targeted contact surface. In contacting an object that moves, control could be such that the hand moves along a vector through the contact surface. Such a strategy might decrease the
calculations required for determining the precise timing and location of contact since this event could be predicted with less precision in depth so long as the hand passed through the contact zone. Movements based on such predictions might also explain why hand velocity at contact was less with the static objects – the hand needed to be controlled to stop near the surface of contact so as not to inappropriately collide with the object whereas hand turnaround with moving objects needed to be less precisely controlled. It should be noted that participants were told to avoid contacting the objects with too much force because it could overload the Phantom’s force capabilities. Not surprisingly, hand velocity at contact was less in *Experiment 1* than in *Experiment 2* because the objects could unpredictably change to static objects. When the location of the hand relative to the objects was less easily determinable (because the cursor was invisible and object related information was sometimes removed), hand movements were often less well controlled.

### 4.7.3 Gaze hand coordination

Relative to contact, gaze exits were delayed more in *Experiment 2* than our previous work. Because gaze arrival latency did not change, however, this did not reflect a general delay in gaze movements. Rather, the epoch of fixation increased in conditions in which sensory information related to contact was limited. These fixation times tended to be longest to the first object, shorter to the middle three objects and sometimes increased again to the last object. Fixation times were longest while the hand approached the first object, while task pressures to locate the next object likely resulted in shorter fixations during the middle of the task and as task pressures abated at the end of the sequence, fixation times again increased. Thus the strategy of using gaze to
register the sensory consequences of action must be balanced with task pressures – fixation timing varied across the task and conditions but when sensory information was limited most fixation times and movement times increased. An interest in the beginning and end of a series of coordinated eye and hand movements corroborate recent findings by Mushiake and colleagues (2006) showing greater neuronal activity in monkey PFC corresponding to the first and last stages of such movements. These authors suggest that information at the beginning and end of a sequence of movement may be particularly important in assessing performance relative to a desired a goal state thought to be represented in the PFC (Mushiake et al., 2006). It is noteworthy that our reported gaze patterns show evidence of being used to monitor the outcomes of planned goals rather than simply guiding the hand.

4.7.4 Catch hits
When visual information signaling contact was available, gaze was positioned such that this information could be registered; however, our results do not support the idea that gaze exits were necessarily triggered by a visual signal. In the disappearing object conditions the triggering visual signal was equivalent and yet gaze exits for catch hits were longer than correct hits. In fact, we report gaze exit latency with disappearing moving objects (181 ms) was generally later than with disappearing static objects (164 ms; a 17 ms difference). Moreover, because gaze exits were delayed longer still with the moving objects when the cursor was visible, the strong-spring and loose-spring conditions were even further separated in time for catch hits (a ~53 ms difference). It is unlikely that gaze exits were triggered by a tactile signal since contact was equivalently represented between these conditions. Besides, triggered gaze movements typically
show considerable consistency in their timing compared to predictive saccades (Shelhamer, 2005; Shelhamer & Joiner, 2003); we do see this level of consistency. Based on the differing gaze exit latencies across catch trials (Figure 14) triggering seems an unlikely explanation in comparison to movements based on predicted timing and location of contact events. Nevertheless, our data also demonstrate that when the prediction of the timing and location of these events produced sufficiently delayed gaze exit latencies the probability of a gaze exit being inhibited following a catch trial greatly increased because there was now sufficient time to register the lack of expected sensory information. In Experiment 2 a much larger proportion of gaze exits during catch trials were delayed than in our previous work (c.f., Bowman et al., 2009).

4.7.5 Dissociation

Taken together these results indicate that during sequential action gaze placement is used to guide the hand to forthcoming sites of action and also to register the sensory consequences resulting from a just completed action. It is not surprising gaze arrivals and exits appear to be independently controlled. However, the factors that directly influence arrival and exit times remain unclear. Moreover distinguishing the factors that influence accuracy or movement timing continue to warrant further exploration. The visibility of the hand appears to most affect the accuracy of approach while the sensory consequences related to the just-completed action appear to affect the timing of gaze and hand coupling. It may be that using gaze to direct the hand is a dissociable quality from gaze as a mechanism for monitoring the sensory feedback resulting from planned movements.
4.8 General Discussion

In these experiments we set out to differentiate whether gaze is controlled so as to register and react to the hand completing a movement to a planned goal location or purposefully delayed to monitor visual and non-visual sensory consequences of action while still moving to the next site of action based on the predicted events. Our results support the latter conclusion; the gaze movements we report may be the result of a need to monitor just-completed action, comparing it to predicted outcomes rather than triggering gaze exits by sensory confirmation. Accuracy and hand approach measures were differently affected by our manipulations than coupled gaze and hand movements away from the objects. Perhaps these measures reflect separable components of planned behaviour that may be differently influenced by the availability of sensory information at a goal site.

4.8.1 Predicted and reactive action

Predicting action might be achieved by registering task related information at key events that allow compensatory adjustments to be made to ongoing plans (Flanagan et al., 2006). Registering this sensory information at key events is more likely when it gives rise to diverse feedback associated in time and space (Amlot et al., 2003; Kennett & Spence, 2002; Maravita et al., 2003; Wallace et al., 1993; Wallace et al., 1998). Moreover, aligning and integrating this available feedback can facilitate the construction of the representation of the body and its position in the workspace (Maravita et al., 2003; Spence et al., 2001) needed for planning action. By positioning gaze at key events the probability that task-critical events will be registered in more than one modality increases as interactions between the hand and objects frequently give rise to multimodal feedback
(Flanagan et al., 2006; Johansson et al., 2001). Sensory information obtained at these key sites can then be compared against predicted consequences to compute potential errors (Flanagan & Wolpert, 2001; Wolpert & Ghahramani, 2000; Wolpert et al., 2001). Therefore detected errors can influence predictions by adapting currently held representations that are inter-modal, as when aligning sensory information in a single modality (Flanagan et al., 2006; Johansson & Flanagan 2007), or possibly intra-modal, as when aligning sensory information spanning more than one modality (Bowman et al., 2009). It follows that the reverse may also be true – limiting sensory information signaling task progress would decrease the probability of registering task-specific sensory information and as a consequence, the precision of predicted sensory consequences may also be reduced.

### 4.8.2 Accuracy
An invisible cursor most likely impacted upon accuracy by degrading the precision of the predicted timing and location of contact between the cursor and the objects. Without the cursor participants were less able to gauge hand position and may have been limited to determining its position through brief tactile feedback received upon contact. When the cursor was invisible approaches toward the objects tended to be more perpendicular and the hand contact velocity was damped more. Yet despite attempts to more carefully approach the objects, participants in both experiments produced more incorrect contacts when the cursor was invisible. Thus without a visual marker of cursor position throughout the task, estimated contacts became inaccurate. In *Experiment 2*, when the objects disappeared following contact, performance degraded further. Here, when the objects disappeared three participants were unable to finish the task, while the remaining
participants were increasingly inaccurate in contacting the objects. These results help illustrate that in addition to the hand-in-motion, task performance is assessed relative to object locations. Indeed, Mennie and colleagues (2007) have recently suggested that during a complex task, object positions in the workspace are estimated with greater accuracy when they remain stable. It is possible that accuracy decreased when the objects disappeared because participants were forced to plan action and confirm just-completed action based on remembered positions. Thus the behaviour reported here is consistent with the idea that visual markers of forthcoming and just-completed action contribute to manual performance. When this information is removed, positioning gaze upon key events may become increasingly important so as to register any available information related to these key sites.

4.8.3 Gaze monitoring

Our results further the understanding of the gaze positioning strategy used to capture, with the fovea, sources of sensory input linked to task progress (Johansson et al., 2001; Flanagan and Johansson, 2003; Sailer et al., 2005). Gaze tended to persist longer when sensory information related to the hand was removed (e.g., invisible cursor) and persisted longer still when feedback related to the object positions was changed or limited (e.g., moving or disappearing objects). The present results are consistent with the supposition that without vision of the hand a non-visual signal (e.g. retinal efference copy) may hold gaze at a site of forthcoming action (c.f., Neggers & Bekkering, 2001; Neggers & Bekkering, 2002). Gaze could potentially remain as a result of a shared motor plan directing the two effectors to the target using shared coordinates and a common motor plan (Neggers & Bekkering, 2002). However, gaze exits here occurred well after
hand arrival and the time course of the latencies more probably indicates reactively programmed movements or a strategy of planning gaze exits within an increasingly later and broader epoch when the hand position relative to the object and/or object response is less determinable. Thus, our results more credibly support the notion that when task-relevant sensory information is limited gaze is positioned and maintained upon key sites of feedback in order to gather any available task-related information on which further predictions might be made.

When information that is otherwise available is limited or removed, positioning gaze at the site of expected feedback may be a compensatory strategy to continue registering visual and or non-visual consequences related to planned interactions. When the cursor was visible, visual feedback of its position could be used to assess performance and guide the hand. With an invisible cursor, however, the timing and location of contact might be less easily predicted. Determining hand position here would be limited to visual input at the start of the trial and, until the first object was contacted, proprioceptive inputs. Participants may therefore have kept gaze upon sites of contact to register alternative consequences of contact be they visual (e.g. object motion) or non-visual (e.g., tactile confirmation). Following contact, a rich source of information would become available via tactile receptors in the hand and this new information could assist in calibrating the mapping between vision and proprioception. When predictions were sufficiently poor, as with the invisible cursor conditions and moving objects, participants may have used any available feedback from these key sites to generate predictions or even to transfer into a reactive mode of control.
4.8.4 Summary and conclusions

As described above, it is difficult to determine behaviourally whether gaze movements were triggered or delayed because of imprecision in the timing of predicted events; the time course of many of the gaze movements in *Experiment 2* could feasibly indicate either option. However, the catch trials in *Experiment 2* display a variability that is at least inconsistent with reactively programmed movements. Although the catch trials were delayed relative to correct contacts, they were not consistently timed across conditions and therefore do not provide clear evidence that gaze movements were triggered based on tactile inputs. Still, the role of tactile inputs in organizing visually guided manual behaviour may prove to be an important area of research. While the role of gaze in directing the hand to future sites of action has been well documented (Ballard et al., 1992; Epelboim et al., 1995; Johansson et al., 2001; Land et al., 1999), the influence of tactile feedback in such tasks has been less considered. The data here may be a start: Monitoring the result of the just-completed action by assessing visual and non-visual markers of task success might be a viable proxy for maintaining sensorimotor correlations when visual markers are removed.

Few studies have directly examined the contributions of tactile feedback in determining the control of coordinated eye and hand movements toward to-be-contacted targets (e.g., Akerfeldt et al., 2006; Amlot et al., 2003; Groh and Sparks, 1996) and fewer still have examined this question using sequential movements (Bowman et al., 2009; Epelboim et al., 1997). Even in the current paradigm tactile information was limited in its scope. Contact was brief and provided relatively little information when compared to the continuously available visual feedback. Nevertheless behavioural changes linked to the
availability of tactile information were observed across several of the conditions in
*Experiment 1* and *Experiment 2*. It is therefore reasonable to ask whether increasing the
required manipulation (and therefore the amount of sensory information) at each object
might influence accuracy or the timing of coordinated gaze and hand movements. Our
results demonstrate that gaze movement timing relative to the hand is not an immutable
characteristic of motor control, and is instead contextually influenced depending on task
pressures. Testing the parameters of the relationship between these two systems will
further the understanding of how concomitant sensory feedback registered from key
sites of action is integrated to yield greater coordination between these separable motor
systems.
Chapter 5
The roles of hand and gaze during simple object manipulation

Effectively planning visually guided manual action requires generating and maintaining correlations between the gaze and hand controllers that relate to successfully completing a desired action (Flanagan et al., 2006). In performing such tasks gaze is often positioned upon key points where multisensory inputs are provided—also known as control points—to facilitate sensorimotor integration and intermodal alignment related to planning purposeful motor commands (Johansson et al., 2001; Flanagan et al., 2006; Johansson & Flanagan, 2007). Recently we described how gaze is sometimes positioned to register, in central vision, non-visual sensory feedback related to predicted sensorimotor events (Bowman et al., 2009). Interestingly, when studying eye hand coordination most experiments involve pointing movements (e.g., Desmurget et al., 2004; Neggers & Bekkering, 2000; Neggers & Bekkering 2001; Neggers & Bekkering 2002; Pellison et al., 1986; Prablanc et al., 1986; van Donkelaar, 1997), or involve singular reach and grasp motions (Winges, Weber, & Santello, 2003), but do not actively measure the sensory inputs to the hand following reaches (for examples see, Land 1992; Land and MacLeod 2000; Land et al., 1999; Hayhoe et al., 2003; Aivar et al., 2005; Mennie et al., 2007). As such, in manipulation tasks the potential contribution of touch and other sensory feedback (e.g., auditory) in relation to visual information is less well understood than it might be if both systems were measured and compared.

Because gaze persists at keys sites until action has been completed, a clear question remains: what might gaze be registering beyond confirming the location of action?
During manipulation somatosensory feedback significantly contributes to maintaining control (Flanagan et al., 2006; Johansson & Westling, 1984; Nowak, Glasauer, & Hermsdörfer, 2003; Nowak & Hermsdörfer, 2003; Nowak & Hermsdörfer, 2006). My colleagues and I have recently provided evidence to suggest that tactile feedback can influence gaze positioning and timing control by contributing to predictions of the timing of key events, and may even stop gaze movements following the unexpected removal of tactile information in a sequential object contact task (Bowman et al., 2009). Yet despite providing a benefit, gaze-related signals may not always be required for sequenced action phases involving manual response, as when additional phases occur well after the hand reaches a location. For example, when pressing a power switch on a television gaze might guide the hand to the switch but may not be required for control as the switch is depressed and released. In our other work participants exhibited such behaviour when using a hand held block to manipulate a simple switch: gaze timing was associated with a mechanical signal, (i.e., switch release) signaling task completion (Johansson et al., 2001). Participants consistently direct gaze to points of mechanical contact between the hand (or object-in-hand) and the objects (Bowman et al., 2009; Flanagan & Johansson, 2003; Johansson et al., 2001). It is possible that this behaviour results from a desire to monitor, at control points, visual and tactile information that might influence future planning.

It has been submitted that monitoring and comparing actual feedback to predicted consequences can help to determine errors used in refining sensorimotor representations and, where needed, help launch corrective actions (Wolpert & Flanagan, 2001; Wolpert & Ghaharamani 2000; Wolpert et al., 2001). Thus gaze hand coupling
may arise from a dual strategy in which gaze is controlled to facilitate directing the hand to a target in addition to registering, at control points, multiple sources of sensory feedback related to planning future components of sequenced action. We have previously reported that gaze is used to capture key events involving the hand, even when those events cannot be seen (Bowman et al., 2009; Chapter 4). Moreover, gaze may be directed to these sites of action irrespective of whether the hand is seen (Neggers & Bekkering, 2001). Indeed, Neggers and Bekkering (2001) have suggested that eye-hand coordination might arise as a function of a common motor plan directing action to a single locus; gaze movements may be bound to the goal of the hand (Neggers & Bekkering, 2002) and gaze may be required to wait for the hand to complete one movement before a new motor plan can be initiated (Neggers & Bekkering, 2001). Although the two systems are coordinated in directing the hand to a location, it remains unclear whether gaze will continue to remain at a site of action when longer manipulation is required and the contribution of gaze to manipulation is limited.

Gaze might remain at a site of action to monitor multisensory signals that relate to the ongoing action. We therefore hypothesize that gaze should remain longer upon control points with greater manipulation times in order to capture continuing sensory events at the site of manual action. With longer manipulation time and greater number of mechanical events, there may also be a greater amount of sensory information with which representations of the workspace and predictions of action can be refined. Such gaze maintenance might also improve accuracy by gathering a greater sample of information related to key components of the task. If gaze is not used in this manner we might instead expect to see gaze forging ahead when manual action at a visually guided
location takes longer as well as seeing little difference in performance relative to viewing time.

Manipulating a switch might involve additional discrete mechanical events, that can theoretically provide a greater opportunity for learning and adapting multimodal sensorimotor correlations through additional control points used in integrating and aligning afferent and efferent signals related to gaze and hand positions. We have previously reported that gaze is positioned at key sites of mechanical consequence (Flanagan & Johansson, 2003; Johansson et al., 2001) and that the timing of gaze movement is influenced by the accuracy of contact (i.e., successful contact) and the consequences of contact upon the objects (Bowman et al., 2009; Chapter 4). Because future action depends on coordinating multiple effectors relative to viewed locations in the task, gaze may be controlled such that planned visual and non-visual consequences of sequenced action can be registered in central vision and used to maintain and adapt the ongoing motor plan. Looking to these sites of prolonged manual action (which are typically visible) might be helpful in controlling the involved effectors and aligning incoming sensory information to viewed locations.

Using our sequential object contact task (Bowman et al., 2009), we introduced several phases of manipulation to the goal of contacting a series of 5 virtual objects. Here participants could contact either static objects or more complex objects with push buttons attached to their front (i.e., switches). The switches involved discrete mechanical events corresponding to the “on” and “off” positions signaled by visual, tactile, and auditory feedback that may comprise additional control points within the task. Using both visible and invisible cursor conditions, we could directly test whether gaze movement
timing was linked to visual signals (e.g. cursor-object contact) or a non-visual signals (e.g., tactile feedback at the visible object location) arising from manipulation. Gaze and hand path measures were quantified and compared to detect differences in movement accuracy, hand approach, and gaze-hand coupling across the experimental conditions.

5.1 Methods

5.1.1 Participants
We tested eight participants (18-24 y). All participants had normal or corrected-to-normal vision and each provided informed consent prior to testing. The experimental protocol complied with Queen’s University General Research Ethics Board’s guidelines and the Declaration of Helsinki and the participants were compensated for their time.

5.1.2 Apparatus and stimuli
The experimental setup was the same virtual set up described in Bowman and colleagues’ (2009) work with the amendment of upgrading the projection unit to a faster CRT projector (Marquis 8500, VDC Display Systems) with a refresh rate of 120 Hz with a fixed computer-to-screen delay of 1 ms resulting in an average delay of 8 ms.

Eye movements were recorded on each trial. An infrared video-based eye-tracking system (ETL 500 pupil/corneal tracking system, ISCAN Inc. Burlington, MA), recorded the gaze position of the left eye at 240 Hz. The ISCAN software was also upgraded such that the moving average feature previously applied to the raw data was removed allowing raw gaze signal data to be sampled at 240 Hz (c.f. Bowman et al., 2009). As with our previous work a bite-bar was used to stabilize the head. Gaze was
calibrated using a two-step procedure: an initial 5-point calibration using ISCAN’s Line-of-Sight Plane Intersection Software followed by a 25-point calibration routine. During calibration, points (4 mm diameter circles) were projected onto the horizontal plane distributed over a region that incorporated the start location and all possible locations of the objects. Raw gaze signals were converted into the coordinates of the Phantom robot in the horizontal plane. Gaze was calibrated at the start of the experiment, checked following each block of trials (see below), and re-calibrated as necessary. The spatial resolution of gaze, defined as the average standard deviation of all calibration fixations, was 0.36° visual angle. This corresponded to ~3 mm when gaze was directed to the center of the object zone for the middle object. We detected saccadic movements using the same algorithm described in our previous work (Bowman et al., 2009).

Participants moved a handle attached to a lightweight force-reflecting robotic device (Phantom Haptic Interface 3.0L, Sensable Technologies, Woburn MA) with their right hand to contact a series of five visible virtual objects. Two object types were used: static objects and switches. Participants were asked to contact each static object in turn, from left to right, or asked to press each switch to its “on” and then “off” positions (see below). Each object was located randomly within a 4 by 4 cm region subject to the constraint that the lateral distance between any two objects was not less than 1 cm (c.f. Bowman et al., 2009). The start position was located in the participant’s midsagittal plane approximately 35 cm below and 22 cm in front of the participant’s eyes. During these movements we sampled hand and gaze position, hand forces, and sound (see below) at 1000 Hz, over-sampling the data provided by the ISCAN system.
The objects were displayed as rectangles (2 wide by 4 cm long); each object was divided lengthwise into two 2 cm squares of different colour (see Figure 15). All the objects in the scene were the same two colours. The static objects were modeled with slightly compliant sides (all four sides) linked to the center of the object by way of a damped spring with stiffness and viscosity of 1000 N/m and $0.9^{-4}$ Ns/m, respectively. The sides did not visually move when contacted. The front half of each switch was modeled with the same slightly compliant sides as the static objects but was attached, via a non-linear spring (see below), to the center of the rear square, the position of which was fixed. The front square was modeled with a mass of 0.45 Kg and a viscosity of 0.8 Ns/m and as force was applied, it moved toward the rear square. Because the rear square was drawn on top this gave the impression that the front slid into the rear and provided the sensation of depressing a button. Once a switch was turned “on” its resting position changed to indicate its’ “on” status (see below); pressing the switch again returned it to “off” status.

The switches were modeled using a non-linear spring that was effectively a set of 4 damped springs that became active at different points (Figure 15A). Only one spring was engaged at a time allowing us to change, at designated positions, the resistive force applied to the hand and promote the perception of pressing a mechanical switch with the hand. Springs 1,3, and 4 had a stiffness of 0.9 N/mm; spring 2 had a stiffness of 0.3 N/mm. The four springs had the same viscosity of $0.1^{-3}$ Ns/m. Disengagement and engagement of the springs corresponded to the mechanical events signaling “on” and “off” status of the switch. Coincident to the mechanical events auditory feedback was provided (see below).
Figure 15. Switch mechanics and sample static and switch object trials. A. Schematic showing the activation positions of the springs in the switch objects. Force and stiffness are plotted relative to the position of the front of the object in the OFF position (top) and ON position (bottom). The solid coloured lines show the resistive force for each spring, and the dashed coloured lines indicate the resting length. The activation position of each spring (vertical dashed black lines) indicates the potential for a mechanical event. Auditory events (dashed orange lines) indicate auditory feedback. Spring stiffness is plotted during switch depression (thick lines) and release (thin line). B. Individual trials showing hand and gaze position while contacting static (top) or switch objects (bottom). Gaze (black) and hand position (blue) are shown through the entire trial. Targets (green squares) and home position (empty yellow circle) are displayed. Gaze (solid red) and hand (solid yellow) positions while contacting the third object in the sequence show differences in object response. During switch manipulation the front square moved into the rear providing the perception of a moving switch. C. Time varying plots showing 1 s excerpts from trials with static objects (left), switches with a visible cursor (middle), and switches with an invisible cursor (right). Force output from the handle (green), gaze velocity (purple), auditory feedback onset (orange), and gaze (light traces) and hand (dark traces) x (blue) and z (red) positions are shown.

When a switch was “off” spring 1, with resting length of 0 mm, was engaged (Figure 15A). At contact, the resistive force of spring 1 equaled 0 N. When the switch was depressed 2 mm, the resistive force increased to 1.8 N and spring 1 disengaged. Spring 2, with a resting length of -1 mm then engaged producing only half the resistive force (0.9 N). This change in force and stiffness was included to give the perception of beginning to engage the mechanical component of the switch. In pressing the switch to 10 mm a resistive force of 3.3 N was reached; here spring 2 disengaged and spring 3 engaged. At this time spring 3, with a resting length of 8.17 mm, only produced a resistive force of 1.65 N. This lessening in force produced the sensation of overcoming and engaging the switch. When the hand passed 10.5 mm, an audible “click” was triggered signaling the switch was in its “on” position. Continuing to press the switch to 15 mm produced a resistive force of 6.15 N, disengaged spring 3 and engaged spring 4. Spring 4, with a resting length of 8.17 mm, maintained the resistive force generated from spring 3 and eventually produced enough resistive force to simulate a mechanical limit for the switch. When the hand retracted, springs 4, 3 and 2 acted sequentially to return the switch to its “on” position 2 mm in from the initial “off” position. Because the switch
was in its “on” status, spring 1 did not again become active. Auditory feedback did not occur as the switch passed the spring thresholds in reverse.

To turn the switch “off” participants again pressed the switch (Figure 15A). Reaching 10 mm disengaged spring 2 (now with resting length 2 mm and stiffness 0.47 N/mm) and engaged spring 3. An audible “click” corresponded to this mechanical event (drop in force) indicating the first component of pushing the switch into “off” status. Pressing to 15 mm disengaged spring 3 and engaged spring 4. On reaching 15.5 mm an audible “clack” indicated that the switch was now “off”. Thus, as a switch was turned “off” it produced two closely paired auditory events – a “click-clack” disengagement. When the hand retracted, springs 4, 3 and 2 (now with resting length of 0 mm and stiffness 0.3 N/mm) returned the switch to the “off” position of 0 mm.

Recorded auditory sound files confirmed object contact. Audible feedback coincident (within 1 ms) with designated switch depression lengths was provided through a speaker located 90 cm from the floor and 130 cm in front of the participant that produced sounds localized to the vicinity of the objects. The sounds were programmed to trigger following the disengagement of a spring such that multiple sounds could not fire if the hand did not overcome the mechanical limit of a spring. Sounds did not vary with contact force, were edited to be 54 ms long, equivalent amplitude, and were played at a consistent volume. Contacting static objects was paired with a recording of a hand contacting a piece of wood. While in the “off” position the switch issued a single metallic “click” (recorded from pressing the seal on a juice bottle lid) while in the “on” position a two part metallic “click-clack” was issued (recorded from pressing and releasing the seal on a juice lid).
5.1.3 Design
To initiate a trial, participants maintained the handle and gaze within 5 and 60 mm, respectively, from the center of start position. The cursor was always shown during this phase of the trial. After 200 ms, five objects appeared and participants reached out and lightly contacted the near surface of each object moving from the leftmost to the rightmost object before returning to the start position. Feedback on movement speed and correct contact order was displayed using the parameters described in Bowman and colleagues’ (2009) earlier work. However, because switch contacts took an appreciably longer duration participants were told to disregard the feedback about their movement speed during these trials. Participants were not instructed where to look during the task.

Participants first completed 30 trials with static objects and a visible cursor. Ten trials were then performed to learn the correct motion of turning the switches “on” and “off”. These trials were not included in subsequent analyses. After training a block of 20 trials with the switch objects and a visible cursor was performed followed by a similar block with an invisible cursor.

5.1.4 Analyses
We calculated several variables related to hand control including hand path distance, hit interval, hand approach angle, hand velocity at contact, and manipulation time. Hand path distance was defined as the displacement of the hand between contacting the first and fifth objects. Hit interval was defined as the time between contacting the previous object to the time of the current object contact. Hand approach angle was computed based on a vector between the location of the cursor at contact and 3 cm before this contact location. Hand velocity at contact is the resultant of the $x$ and $z$ velocities of the
hand as it contacted each object. Manipulation time is the interval between contacting an object and final force offset when the hand withdrew from an object.

To assess the coupling of gaze to hand movements we calculated the gaze parameters of gaze arrival latency, gaze exit latency, fixation time and gaze path distance. Gaze arrival latency is the interval between the end of a saccade bringing gaze to an object and when the hand contacted the object. Gaze exit latency is the difference in time between the onset of gaze movement away from an object and the time that the cursor contacted the object. Fixation time is the epoch from the end of a saccade that brings gaze to an object to the time of the beginning of a saccade exiting from that object. Gaze path distance is the total displacement of gaze in x and z coordinates during the interval of gaze arriving to an object to when an object is contacted.

We compared the accuracy rates between conditions with 3 planned comparisons among the groups. Because the increase in error associated with these few comparisons was slight, we did not apply a correction. Our dependent measures for the hand were compared across conditions (static objects, visible cursor switches and invisible cursor switches) with repeated measures ANOVAs. We used planned orthogonal comparisons to compare static objects compared to the two switches conditions combined, and to compare between the switch conditions and again did not correct our alpha levels. Our principle interest in this experiment was changes in gaze timing, and as such, we chose to more closely analyze gaze movements throughout the task. Thus, our dependent measures for gaze were compared across conditions (static objects, visible cursor switches and invisible cursor switches) and object number (objects 1-5) using 3 x 5 repeated measures ANOVA. We used planned orthogonal
contrasts to compare gaze movements for static objects to the two switches conditions combined, and then to compare between the switch conditions and did not correct our alpha levels. Bonferroni corrected pair-wise comparisons were used to examine gaze movement timing across object number. Finally we compared the dependent measures for gaze with 2 x 2 repeated measures ANOVAs comparing the switch conditions (visible cursor and invisible cursor) and the accuracy of contacts (correct contacts, erroneous contacts). Our uncorrected alpha was set to 0.05 and the Bonferroni corrected alpha was set to .005.

5.2 Results
As shown in Figure 15B participants moved between the objects in order, fixating upon each one prior to and following contact, and moved the hand between objects in a u-shaped profile as we have previously described (Bowman et al., 2009). However, there were several important changes in the coordination of eye and hand movements that resulted from adding a manipulation component to our sequential target contact task. We report below on accuracy and the temporal and spatial profiles of gaze and hand movements. The mechanical events for the three conditions are shown in detail in Figure 15C. Key mechanical events involving multisensory feedback are demarcated with vertical gray lines. Note that in all cases gaze is positioned at the site of action to capture these events.

5.2.1 Accuracy
We quantified hand movement accuracy in each condition using the same techniques described in our previous work (see Bowman et al., 2009). We intended to code contact
attempts into three categories: correct contacts, erroneous contacts and misses; however, there were no misses in either of the conditions with switches. For static objects, participants correctly contacted the objects 1070 times (89.17%) and participants correctly contacted the switches 624 times (82.10%) when the cursor was visible, and 540 times when the cursor was invisible (71.05%). We performed paired-samples t-tests on the percentage of correct contacts across the conditions (static objects, cursor visible switches, and cursor invisible switches) finding no difference between correct contacts for the static objects and the cursor visible switches, \( t(7) = 1.0, p = .334 \). Participants made fewer correct contacts for cursor invisible switches than either static objects \( t(7) = 3.9, p = .006 \) or cursor visible switches \( t(7) = 2.4, p = .050 \).

5.2.2 Hand trajectories
As required by the task, participants produced u-shaped hand paths between objects across all conditions (c.f., Bowman et al., 2009). Contacting switches resulted in longer manipulation times compared to static objects, \( F(2, 14) = 723.6, p < .001 \). Planned comparisons revealed that the manipulation time for static objects (\( M = 136 \text{ ms} \ SE = 9 \text{ ms} \)) was significantly shorter than for visible cursor switches and invisible cursor switches combined, \( F(1, 7) = 1065.9, p < .001 \). Moreover visible cursor switches (\( M = 543 \text{ ms} \ SE = 16 \text{ ms} \)) and invisible cursor switches (\( M = 525 \text{ ms} \ SE = 20 \text{ ms} \)) did not differ (\( p > .05 \)). Manipulation of the switch required greater hand motion over longer time, producing greater hand path distances and longer hit intervals as compared to the static objects (see Figure 15B). We therefore chose to focus on hand path comparisons between the switch conditions. We computed the median hand path distance for each participant and compared the switch conditions using repeated measures ANOVA. Hand
path distance when the cursor was visible ($M = 83.28 \text{ cm } SE = 7.77 \text{ cm}$) was significantly less, $F(1, 7) = 8.3, p = .024$, than when the cursor was invisible ($M = 95.62 \text{ cm } SE = 15.39 \text{ cm}$). This replicates our earlier finding that hand path distance increases when the cursor is invisible (Bowman et al., 2009). However, we did not find a similar difference for hit interval between the switches conditions, $F(1, 7) = .4, p = .564$. Hit intervals in the cursor visible condition ($M = 898 \text{ ms } SE = 23 \text{ ms}$) took as long as in the invisible condition ($M = 909 \text{ ms } SE = 31 \text{ ms}$). When contacting switches with an invisible cursor, participants may have compensated for the greater hand path distance by moving more quickly through the manipulation phase at the switch.

Comparing median hand velocity at contact, computed for each participant and condition, revealed a main effect across condition, $F(2, 14) = 11.2, p = .01$. Pair-wise contrasts revealed that participants contacted static objects with lower hand velocity ($M = 517.89 \text{ mm/s } SE = 44.53$) than when contacting the combined average of the switches, $F(1, 7) = 12.2, p = .01$. Furthermore the velocity of the hand at contact for visible cursor switches ($M = 683.8 \text{ mm/s } SE = 91.4 \text{ mm/s}$) was less than for invisible cursor switches ($M = 766.7 \text{ mm/s } SE = 136.6 \text{ mm/s}$), $F(1, 7) = 6.8, p = .035$. This hand velocity at contact result is consistent with our earlier findings suggesting that the visible cursor provides cues for scaling hand velocity prior to contact (Chapter 4) and predicting the position of the hand relative to the goal.

To examine potential differences in the approach angle we computed the median value for each participant and condition (static objects, cursor visible switches, cursor invisible switches) and compared these values using repeated measures ANOVA. Here an approach of $90^\circ$ is directly perpendicular to the object base while angles larger than
90° indicate that the cursor approached the object from the left. This analysis yielded a main effect of condition, $F(2, 14) = 56.6$, $p < .001$. Furthermore, planned comparisons revealed that participants approached static objects at less perpendicular or sharper angle ($M = 117.7° SE = 2.6°$) than the combined average of the switches $F(1, 7) = 70.4$, $p < .001$. In comparing the approach angle for visible cursor switches ($M = 90.5° SE = 1.4°$) and invisible cursor switches ($M = 87.2° SE = 2.1°$; where) no difference was detected ($p > .05$). These results replicate our previous results of perpendicularly approaching to-be-contacted objects where precise contact is required (Bowman et al., 2009).

### 5.2.3 Temporal coordination of gaze and hand movements

In our analysis of the temporal coupling of gaze and hand we examined gaze arrival latency, gaze exit latency, and fixation time. For each participant’s correct contacts we calculated the median value of our gaze measures and compared these across the factors of object number (object 1-5), and condition (static object, cursor visible switches, cursor invisible switches) using a 3 x 5 repeated measures ANOVA. Recall that planned comparisons were used to examine differences in conditions while Bonferroni corrected comparisons were used to compare across object number.

Figure 16 shows cumulative frequency distributions of gaze arrival and exit latencies for correct contacts as a function of object location for each condition. Gaze arrival latency did not depend on condition, $F(2, 14) = .2$, $p = .823$, but depended on object number, $F(4, 28) = 31.1$, $p < .001$, and a significant interaction between the factors, $F(8, 56) = 3$, $p = .008$. Overall, gaze arrival latency was similar for static objects ($M = 301$ ms $SE = 16$
ms), cursor visible switches ($M = 301 \text{ ms} \ SE = 15 \text{ ms}$) and cursor invisible switches ($M = 294 \text{ ms} \ SE = 20 \text{ ms}$) and neither planned comparison revealed a difference (both values $p > .05$). In contrast, gaze arrival latency differed among the objects. Gaze arrival latency was greatest for the first object ($M = 434 \text{ ms} \ SE = 25 \text{ ms}$) compared to all the other objects (all four values, $p < .005$), potentially because a larger hand movement is required to reach this object from the start position. Gaze arrival latency to the second ($M = 266 \text{ ms} \ SE = 15 \text{ ms}$), third ($M = 276 \text{ ms} \ SE = 15 \text{ ms}$), fourth ($M = 277 \text{ ms} \ SE = 14 \text{ ms}$) and fifth objects ($M = 239 \text{ ms} \ SE = 27 \text{ ms}$) were not significantly different from each other ($p > .05$ in all 6 cases). The interaction resulted from greater gaze arrival latency to the first object with static objects ($M = 478 \text{ ms} \ SE = 22 \text{ ms}$), than with cursor visible switches ($M = 415 \text{ ms} \ SE = 26 \text{ ms}$) or cursor invisible switches ($M = 409 \text{ ms} \ SE = 42 \text{ ms}$). In addition, gaze arrival latency was shorter for the fifth object with static objects ($M = 201 \text{ ms} \ SE = 37 \text{ ms}$) than cursor visible switches ($M = 272 \text{ ms} \ SE = 20 \text{ ms}$) and cursor invisible switches ($M = 244 \text{ ms} \ SE = 31 \text{ ms}$).
Figure 16. Average gaze arrival and exit latencies by object number. A. Cumulative percentage distributions of gaze arrival latency and gaze exit latency for all participants across object number for the static object condition. B. Cumulative percentage distributions of gaze arrival latency and gaze exit latency for all participants across object number for visible cursor switches. C. Cumulative percentage distributions of gaze arrival and gaze exit latency for all participants across object number for invisible cursor switches.
Gaze exit latency depended on condition, $F(2, 14) = 280.1, p < .001$, object number, $F(4, 28) = 20.7, p < .001$, and an interaction between the factors, $F(8, 56) = 5.8, p < .001$ (Figure 16). Far shorter gaze exit latencies occurred with static objects ($M = 113$ ms $SE = 16$ ms) compared to the combined average for the switches, $F(1, 7) = 485.2, p < .001$. There was no difference between the cursor visible switches ($M = 547$ ms $SE = 16$ ms) and cursor invisible switches ($M = 550$ ms $SE = 21$ ms; $p > .05$). Gaze exit latency from the fifth object was greater than from the other objects (objects 1-3, $p < .005$; object 4, $p = .02$). The interaction resulted from greater gaze exit latencies from the fifth object in relation to the other objects in the invisible cursor switch conditions ($M = 666$ ms $SE = 26$ ms) and cursor visible switches ($M = 615$ ms $SE = 26$ ms) compared to static objects ($M = 148$ ms $SE = 14$ ms). These results might indicate that the timing of gaze exit is linked to the availability of sensory information at a site of sensory consequence. The pressure to continue moving gaze and the hand (or not) would be equivalent across all three of these conditions, yet the mechanical events related to switch manipulation (e.g., visual, tactile, and auditory), particularly at the last object may have provided additional feedback signaling task progress and provided a reason to maintain gaze at the site of action well after contact (see Figure 15B for an example of how gaze remains upon object 5 while the hand continues home during a switch contact).

Fixation times on switches were longer than on the static objects irrespective of cursor visibility. We calculated the median fixation time for each participant across the factors of object number and condition, finding main effects of object number, $F(4, 28) = 13.8, p < .001$, condition, $F(2, 14) = 282.9, p < .001$, and an interaction between the factors, $F(8, 56) = 9.1, p < .001$. Planned comparisons revealed shorter fixation times
with static objects \((M = 406 \text{ ms } SE = 24 \text{ ms})\) compared to the switches conditions combined, \(F(1, 7) = 456.6, p < .001\). When comparing the fixation times for visible cursor switches \((M = 910 \text{ ms } SE = 28 \text{ ms})\) and invisible cursor switches \((M = 900 \text{ ms } SE = 30 \text{ ms})\) no difference was found \((p > .05)\). Participants fixated the first object longer than the second, third and fourth objects \(p < .005\), but not the fifth object. The interaction arose because of differences in the relative fixation durations for the first and last objects between the static objects and the switches. With static objects, participants fixated the first object longest \((M = 572 \text{ ms } SE = 43 \text{ ms})\) and the fifth object least \((M = 339 \text{ ms } SE = 37 \text{ ms})\). In contrast, with cursor visible and invisible switches, respectively, participants fixated the first object longer \((M = 986 \text{ ms } SE = 44 \text{ ms}; M = 960 \text{ ms } SE = 51 \text{ ms})\) than the middle three objects, but fixated the fifth object longest \((M = 991 \text{ ms } SE = 46 \text{ ms}; M = 1003 \text{ ms } SE = 35 \text{ ms})\).

We have previously described how gaze tends to lead hand position in manual tasks (Bowman et al., 2009; Johansson et al., 2001; Sailer et al., 2005). At 4 cm in length, the switch objects were larger than the functional fovea \((\sim 2-3 \text{ cm}, \text{ see Johansson et al., 2001})\) and it is therefore possible that gaze may have been repositioned from the contact point to the latter half of the object in order to capture, in central vision, the mechanical events related to action. To assess this we examined median gaze path distance for each participant across the factors finding a main effect of condition, \(F(2, 14) = 26.5, p < .001\), and object \(F(4, 28) = 14.9, p < .001\), but no interaction \(F(8, 56) = 1.1, p = .386\). Planned contrasts revealed that gaze path distance was shortest for static objects \((M = 26.66 \text{ mm } SE = 2.47 \text{ mm})\), compared to the switches conditions combined, \(F(1, 7) = 34.2, p < .001\). However gaze path distance did not travel further between
cursor visible switches (M = 40.15 mm SE = 1.14 mm) and invisible cursor switches (M = 41.55 mm SE = .74 mm; p > .05). Importantly, these distances are calculated from equivalent durations (see above). Gaze path distance tended to be greater for the first object; however pair-wise comparisons only revealed greater gaze path distances for the first object compared to the second object (p = .002; all other values p > .01). This result is difficult to interpret but may possibly result from participants’ efforts to reposition gaze after the initial saccades bringing gaze to the vicinity of the first object to start each trial (see Figure 15B). Together these findings help instantiate the claim that it is not visual confirmation of contact, *per se*, but the consequences of action at a site that are captured with gaze (c.f., Bowman et al., 2009; *Chapter 4*).

Recall that turning on and off each switch gave rise to several independent mechanical events that could be sensed in the tactile modality as well as the visual and auditory modalities. The events signaled the completion of different phases of the manipulation components of the task. To investigate whether gaze exit times coincided with a particular event, we examined cumulative frequencies of gaze exit latency relative to 4 events (Figure 17A-D). For all three conditions gaze exit latency was calculated relative to contact, the time of force onset, and the time of the first sound, (corresponding to contact with static objects and turning on the switch with switches; see methods). For the two switch conditions, gaze exit latencies were also calculated relative to the second sound (corresponding the first component of turning “off” a switch) and the third sound (corresponding to the final switch disengagement). Figure 17C and 17D show gaze exit latency was most closely associated with events that signal completing the interaction with the switch (i.e., second or third sound, produced when disengaging the switch).
Figure 17. Gaze movement profiles relative to task events. Graphs A-D show cumulative percentages of gaze exit latency for all participants pooled across condition (static object, cursor visible switches, cursor invisible switches). Each plot shows gaze exit relative to a different event. A. Gaze exit latency relative to initial contact. B. Gaze exit latency relative to sound 1—the sound corresponding with contacting a static object or activating a switch from its “off” position. C. Gaze exit latency relative to sound 2—the sound corresponding with the first component of deactivating the switch from its “on” position. D. Gaze exit latency relative to sound 3—the sound corresponding to the final manipulation of a switch object. Note: Contact time and sound correspond when contacting static objects and thus the data are identical. Because static objects did not provide a sound 2 or sound 3 event the data for sound 1 were superimposed onto the graph as a visual reference.
We performed one final test of whether gaze placement reflected a control strategy by which key events could be captured in central vision. To do this median fixation times for switches were compared, post hoc, between the factors of accuracy (correct contacts and incorrect contacts) and condition (visible cursor and invisible cursor) in a 2 x 2 repeated measures ANOVA. We found a main effect of accuracy, $F(1, 7) = 77.3, p < .001$, but not condition, $F(1, 7) = 3.0, p = .125$, nor an interaction, $F(1, 7) = 2.5, p = .158$. These results suggest that the length of fixation may also be influenced by a desire to capture expected sensory information following errors. Fixation times were longer for erroneous contacts ($M = 1286 \text{ ms} SE = 49 \text{ ms}$) than for correct contacts ($M = 886 \text{ ms} SE = 26 \text{ ms}$) indicating that gaze remained longer, perhaps to continue monitoring a site of action. Longer fixations occurred irrespective of cursor visibility. When comparing the averaged fixation time of correct and erroneous contacts in the cursor visible condition ($M = 1119 \text{ ms} SE = 45 \text{ ms}$), they were not different than the cursor invisible condition ($M = 1053 \text{ ms} SE = 27 \text{ ms}$). These results are consistent with the idea that gaze control can be influenced by a non-visual signal (perhaps related to task-relevant mechanical events) independent of visual confirmation of a goal. When contacting switches—with and without a visible cursor—sensory information related to errors could feasibly be used to modify gaze movement plans before gaze is repositioned to a new site of action.

### 5.3 Discussion

In this sequential manipulation task we used objects that did not necessarily require vision or gaze related signals to complete the manipulation of the switch. The results
support our proposed hypothesis that gaze is controlled so as to register visual and non-visual information related to the goals of action at control points (Bowman et al., 2009; Flanagan et al., 2006; Johansson & Flanagan, 2007). Consistent with Johansson and colleagues’ (2001) work with block manipulation gaze exit latency appeared to be associated with predictions of when key events would be completed rather than when the hand arrived to a site (c.f. Neggers & Bekkering, 2000; 2001). The maintenance of gaze until action was completed is also compatible with our hypothesis that such control may be important for integrating multisensory inputs related to completing action goals and for aligning related inputs to a common position (e.g., a seen, felt, and heard location). For switches gaze exit latencies were greater than 545 ms, a sufficiently long enough period to generate reactive gaze movements based on confirmation of contact (Groh & Sparks, 1996). Yet we report that gaze movements were more closely associated with the completion of manipulation than contact. That is, once a switch was contacted gaze could have been free to locate the next object but instead remained positioned at the site of action until the hand was also finished.

Several researchers have suggested that determining control parameters for a given motor task is limited by the availability of task-specific sensory information (e.g., Bresciani et al., 2006; Ernst & Banks, 2002; Vaziri, Diederichsen, & Shadmehr, 2006; Wolpert and Flanagan, 2001; Wolpert and Gharahmani, 2000; Wolpert et al., 2001; Wolpert and Harris, 1998). When parameters that influence predictions of actions such as the position of the cursor are limited or removed the accuracy of the prediction related to that parameter will also degrade (Wolpert & Flanagan, 2001). However, if another modality can provide crucial information through alternate means (e.g. tactile feedback
from contact), the decrement might be mitigated. During manipulation tactile information provides crucial information about task progress (Flanagan and Johansson, 2003; Johansson et al., 2001) and may influence eye-hand coordination differently than when the hand simply points by determining information that visual feedback is less able to provide (Castiello, 2005, but see also Culham & Valyear, 2006). Tactile feedback can, for example, result in more accurate estimates of predicted stimulus intervals than are achieved with vision; pairing visual and tactile stimuli produce the most accurate estimates (Bresciani et al., 2006). Here, when gaze was positioned at control points, where additional sensory information (e.g., tactile, auditory) was expected, estimates of planned action relative to the actual feedback could be better assessed and contribute to generating appropriate responses in the future.

5.3.1 Accuracy
As we have reported before, an invisible cursor negatively affected hand movement accuracy (Bowman et al., 2009; Chapter 4). However, participants in this experiment did not miss the objects, a result contrasting earlier work in this paradigm. Here, when more sensory information was provided through longer manipulation, participants produced no misses even when the cursor was invisible. By sampling information across several coincident modalities, sensory estimates used in planning can gain precision (Wolpert & Flanagan, 2001; Wolpert & Ghaharamani 2000; Wolpert et al., 2001). While accurate reaches were achieved when the cursor was invisible, it should still be noted that participants’ performance in movements between the switches was still impacted.
5.3.2 Hand measures

Hand path distance and trial duration with switches were differentially influenced by cursor visibility than with static objects. With switches only hand path distance increased with an invisible cursor. This finding may support the notion that these measures reflect discriminate components of hand control (e.g., Saunders and Knill, 2005; Liu, Tubbesing, Aziz, Miall, & Stein, 1999). Hand path distance increased when the cursor was invisible (c.f., Bowman et al., 2009; Chapter 4) suggesting that this information is used in planning how to move the hand between objects; however, participants may have compensated for the longer hand path distance by generally speeding up hand movements during switch manipulations.

Hand approach measures were also differently affected by the experimental manipulations. Hand velocity at contact was scaled down most prior to contacting static objects; with switches, participants scaled hand velocity least with the invisible cursor. Turning on the switches required greater force output and might explain the difference between the static objects and switches while a faster approach when the cursor was invisible would replicate findings in our previous work (Chapter 4); the approach may be less well determined without visibility of the hand. The approach angles differed between conditions more than in our previous work in this paradigm (c.f., Bowman et al., 2009). Participants approached static objects less perpendicularly (on average ~17° from perpendicular), and decreasing the angle of approach may have enabled more rapid and efficient hand movements between objects. In comparison, the approach to switches—irrespective of cursor visibility—was approximately perpendicular to the front surface, presumably to best direct force along the z-axis for a sustained period of time. Here if the
hand moved laterally it would be more likely to slip off the surface during manipulation.
By guiding the fingertips perpendicularly toward an object surface in manipulation such a
pitfall is circumvented (Kleinholdermann et al., 2007). Together these results highlight
the highly contextual control of the hand during manipulation tasks that is benefited by
visually guiding the hand toward an object. It is also likely that these efficiencies in
control are the result of precise predictions of action outcomes.

5.3.3 Gaze hand coordination
In this task gaze appeared to be used to monitor control points well after the hand had
been directed to a site of action. Gaze preceded the hand to the point of contact and was
even repositioned further along the switches to capture the mechanical events (i.e.,
additional control points) resulting from the hand depressing and releasing the switch. It
is possible that this was done to register, with gaze, the non-visual signals related to
switch manipulation and integrate these signals to facilitate planning future components
of the sequence. Several of our earlier findings have also demonstrated that gaze is
controlled so as to capture multisensory signals during visually guided manual tasks
(Bowman et al., 2009; Flanagan & Johansson 2003: Johansson et al., 2001). For
example, when contacting static objects in a sequence with an invisible cursor, even
though no additional information was available following contact gaze remained until
action was completed (Bowman et al., 2009). When contacting moveable objects under
the same circumstances, gaze exit times increased (Chapter 4) potentially indicating that
gaze was used to capture the sensory consequences arising from planned action. Here,
with longer manipulation time, gaze timing was associated with the completion of the
task (i.e., the mechanical event of switch release) rather than its initiation (i.e., object
contact). The longer gaze maintenance even when the hand could not be seen may indicate the importance of determining the location and timing of each planned action relative to an estimated control point. By positioning and maintaining gaze at control points, the estimated and actual sensory information—available in multiple modalities—can be registered and compared. Indeed when information relative to control points is lacking, using gaze to integrate the remaining signals may be even more important. Using this method of gaze positioning as a means of integrating sensory signals might be critical in helping to launch corrective actions.

5.3.4 Summary and future directions

Although participants’ performance was negatively impacted by an invisible cursor it was less so than in previous versions of this paradigm (c.f Bowman et al., 2009; Chapter 4). Here the objects did not change position and participants interacted with them for longer. This may have provided additional information used in predicting the timing and location of sensory consequences as the task unfolded (Mennie et al., 2007). Given that gaze appears to be positioned upon control points to help integrate sensory signals, it might be interesting to examine how gaze is positioned upon these sites when they do not visually respond to manipulation while providing tactile and auditory feedback (e.g., switches that do not visually move). Such an investigation might prove useful for delineating the ongoing contributions that alternate sensory inputs have in planning behaviours.

The present results might also indicate that multisensory integration and sensory alignment are separable benefits of gaze positioning strategy. Aligning multiple signals
to a single viewed location might occur when a common position can be confirmed as when the hand contacts an object. In contrast, because sensory integration requires comparing predicted and actual feedback, this benefit would be best assessed after action has occurred. Given the recurring strategy of gaze maintenance until the final phase of action at an object, the present results beg the question of whether the same gaze behaviour would persist when the source of sensory alignment (i.e., the contacted object) is invisible. This question might be of further interest if removing visual feedback of the hand starting position is found to negatively influence performance—as has previously been reported with pointing movements (Prablanc et al., 1979)—particularly if the objects could still be located by touch. Since gaze might be directed to future sites of sensorimotor consequence, rather than following the hand (Batista et al., 1999; Buneo et al., 2002; Crawford et al., 2004), testing whether gaze continues to lead, and register, hand action when visual information is not present may reveal more about why gaze is used to lead, and follow, planned action.
Chapter 6
General Discussion

This collection of studies sought to investigate how visual and tactile feedback related to the goals of planned movement, indicated at control points, might contribute to retaining control during a sequence of coordinated eye and hand movements involving manipulation. By removing aspects of sensory feedback signaling key events in the task, and measuring resultant changes in behaviour, we tested which sources of feedback may have been needed to accurately plan and execute effective action in our task.

Analyses were focused on three components of movement: the accuracy with which objects were contacted, hand approach, and the timing of gaze movements to and from each object. The results are consistent with a strategy in which sensory consequences linked to estimated goals are preferentially sought after. These registered inputs may aid in confirming just-completed actions as well as facilitating the retention of control in planning future actions. The key finding—evident in all experiments—demonstrates that a tactile component in a sequential pointing task prompted a behavioural organization such that key events, at which tactile feedback was available, were captured with central vision. In the discussion that follows, the significance of the findings in relation to current theories of motor control will be addressed with particular attention paid to the importance of control points as a basis for understanding the coordination of multiple effectors during action.

Based on the reported behaviours, the sensory manipulations included in these experiments may have challenged participants’ ability to determine the hand’s location relative to the to-be-contacted objects. Yet despite myriad attempts to limit what were
thought to be critical features for planning accurate and well-timed movements, participants were nevertheless able to complete the task. Such performance was often achieved with limited visual and tactile feedback related to the goal of movement; even so, it was not clear that participants resorted to reactive movements when sensory information was limited. The present results might reveal a facet of goal-based movement parameterization that occurs during sequenced movements that has been relatively little investigated: when a goal can be confirmed across multiple sensory modalities, a stable sensory modality may serve as a proxy when another modality is unavailable or unreliable. By substituting sensory signals associated with a key event, an individual might still be able to generate predictions of forthcoming consequences necessary to maintaining smooth action sequences in impoverished environments. Sensory substitutions of this nature might also indicate that when a sensory modality can significantly contribute to the execution of a task (e.g., tactile feedback in manipulation). It may be appropriate for the brain to represent the goal of planned action such that the sensory consequences of any of the involved modalities can be used to confirm the success of movements made in an attempt to achieve the goal.

6.1 Control points
Typically reaches involve adjustments to the eyes, head, arm, and body. A reach can be programmed in an infinite number of ways, yet it is defined as the same action so long as the goal remains the same; it is the goal that defines a task’s movements (Binstead et al., 2001; Medendorp et al., 2008; von Hofsten, 2004). In impoverished circumstances (e.g., virtual reality) available sensory information is especially important for measuring the efficacy of executed actions (Bresciani et al., 2005; Flanagan et al., 2006; Gepshtein
et al., 2005). Thus, when appropriate sensory information is lacking, one potential strategy to mitigate this loss might be to recruit another reliable source of information in another modality (Ernst & Banks, 2002; Hillis et al., 2002; Gepshtein et al., 2005). Control points might provide this option because they are often not only sites of multimodal feedback but are acutely related to confirming the success of movements selected for accomplishing a desired goal.

6.1.1 Control points improve detecting sensory consequences

Though we were unable to directly measure whether participants detected the sensory consequences arising from each contact, their behaviour nevertheless indicated that its detection mattered for retaining control during the task. Participants coordinated eye and hand position such that key consequences—rather than just movements—were measured. The most apparent illustration of this is that gaze was commonly directed to, and remained at, the location to which the hand was directed, even when the hand was invisible. Stated differently, participants fixated the objects and virtually never the hand. Fixations upon a site of hand action may aid in visually confirming an event that is also signaled by tactile afferents (Amlot et al., 2003; Johansson & Flanagan 2007; Maravita et al., 2003). When the objects disappeared following contact (as in Chapter 4 Experiment 2) accuracy degraded, suggesting that this information was less accessible for planning movements; the consequences of contacting the object were likely used to orient and direct the hand to the next object. Thus, participants’ behaviours showed signs of being organized to increase the probability of detecting the consequences of goals rather than simply monitoring intervening hand movements or a goal’s location.
As previously described, sensory detection is improved when an event can be registered in more than one modality (Wallace et al., 1993; Wallace et al., 1998). Miall and colleagues have demonstrated that such multimodal enhancement can directly benefit visuospatial processing (Balslev et al., 2007; Miall & Cole, 2007) relative to key points in a motor task that can best supply visuomotor errors for correcting action (Miall & Cole 2007). The reported data here would support a visuomotor interpretation as well; key events in the task were nearly always monitored with gaze. In positioning gaze thus, detecting correspondent stimuli (in time and space) would lend credulity to their association within the task (Flanagan et al., 2006; Maravita et al., 2003) and may have provided greater information for determining visuospatial errors relative to the desired goal (Buneo & Andersen, 2006).

Remember that participants not only fixated sites of contact, they maintained gaze well past this event – and did so in all conditions. In this way performance could be best assessed relative to planned consequences. Recall that gaze released more quickly with the static objects and invisible cursor when no new information was available (Bowman et al., 2009; Chapter 3). In comparison, longer gaze exit latencies occurred when the cursor was invisible and the objects moved (Chapter 4 Experiment 1). Importantly, participants did not follow the moving objects; object position did not seem to be what drew gaze. Lastly, with the disappearing objects, participants maintained fixation long after visual object information was removed, even with disappearing loose-spring objects when the object had moved away from the hand (Chapter 4 Experiment 2). This may have been indicative of participants switching to a reactive strategy or
possibly that participants were less able to determine the control point when it was invisible.

The behaviours surrounding catch trials also support a strategy of improving the detection of sensory consequences. In catch trials the correct action is completed while the desired goal is not, providing a unique perspective on how goal-based feedback might be assessed. The inhibition of saccadic movements following catch trials could be interpreted as evidence that when an error in the predicted sensory event occurs (i.e., the goal) it can halt performance even though an action was correct. The inhibition of gaze exits following the unexpected removal of tactile inputs reported in Chapter 3 and Chapter 4 Experiment 2 are in line with other findings showing that issuing motor commands is influenced by the temporal and spatial contiguity of multisensory inputs during eye-hand tasks (Akerfeldt et al., 2006; Amlot et al., 2003; Balslev et al., 2007; Diederich, 2003; Driver & Spence, 1998; Miall & Cole, 2007; Spence et al., 2001). Here, the absence of expected sensory consequences related to a goal (i.e., contact) influenced whether gaze continued to the next object (c.f. Akerfeldt et al., 2006; Amlot et al., 2003; Diederich et al., 2003). Perhaps owing to this absence—related to the goal of contacting the object, but not necessarily the action required to do, so—saccadic movements in some trials may have been inhibited.

6.1.2 Control points improve sensory estimation

When integrating sensory signals, the detected signals from different senses should not be combined indiscriminately (Gepshtein et al., 2005; Hillis et al., 2002). Recently Gepshtein and colleagues (2005) argued that the CNS avoids such a pitfall by only integrating spatially and temporally proximate signals, increasing the probability that
signals linked to a common point (i.e., one object) are associated (Bresciani, Dammier, & Ernst, 2006; Bresciani et al., 2005). However, while we may use statistical optimality in combining sensory cues to form robust percepts (Ernst & Banks, 2002; Hillis et al., 2002), by their own concession, Ernst and colleagues have recently argued that cue combination is more likely biased toward generating a unified percept (Bresciani et al., 2005; Gepshtein et al., 2005) rather than a weighted combination based on the reliability and availability of sensory information (Ernst & Banks, 2002; Hillis et al., 2002). That is, sensory integration functions best when combined cues (i.e., available information) are used to generate specific features of a percept relevant to a desired action. Sensory integration may not be maximal fusion of cues so much as a synthesis of spatially and temporally dependent signals needed to achieve a specific action (Bresciani et al., 2005; Bresciani et al., 2006; Burges et al., 2008; Gepshtein et al., 2005). It may be that control points are synonymous with the sites of multiple sources of relevant information whereupon information is gleaned that would generate the most useful percept needed for estimating how to achieve a desired goal. If this is the case, estimates of action would stand to directly benefit from such a context dependent percept.

Behaviours in the present experiments support the interpretation that control points are acutely linked to generating the parameter estimates for controlling action. For example, the greater sensory information provided with switches in Chapter 5 may have contributed to improved accuracy rates. In contrast, when sensory information was removed as when the cursor was invisible, participants’ general accuracy degraded (c.f. Beurze et al., 2006; Neely, Heath, & Binstead, 2008a). Unlike in pointing tasks where hand visibility does not produce a difference in movement times (Goodale et al., 1986),
an invisible cursor tended to produce longer trial durations. Cursor invisibility was also associated with a propensity to damp the velocity of the hand prior to contact (e.g., Chapter 4 Experiment 1 and Experiment 2; Chapter 5) and to approach the object more perpendicularly to insure well-controlled contact. These results all likely arise as a result of poorer estimations for controlling the hand relative to the goal and may be directly influenced by the percepts used in planning the action.

6.1.3 Control points improve sensory prediction

To prevent halting, jerky movements the demands necessary to control future action (e.g. moving the hand between upcoming targets) and the sensory consequences that an action will produce (e.g. the force borne out at contact) must be predicted so that compensations can be prepared before they are needed. The present data could be interpreted as demonstrating a break down in this predictive process, though whether restricted sensory information resulted in greater reactivity or more variable and delayed predictions is difficult to say; both behaviours were evidenced. Removing sensory information may increase the variability of estimates needed for action control (Wolpert & Ghahramani, 2000; Ernst & Banks, 2002) and therefore the resolution of predicted consequences. After all, estimates of the timing of expected events can only vary so much before reactivity becomes a possibility, and hence the need for a fluid capacity to switch between the two modes of programming. Flexibility between reactive and predictive modes would provide an economical means of using sensory information—when it is available—to expedite action, while retaining the option of using reactively triggered movements when information is limited or when errors are detected.
Several recent works have begun to demonstrate that the CNS adroitly switches back and forth between predictive and reactive modes based on the sensory errors that it measures at key points in the task (Balslev et al., 2007; Droll et al., 2005; Miall & Cole, 2007; Neely et al., 2008a; Neely et al., 2008b; Zorn et al., 2007). Miall and Cole (2007) have documented such shifts between feedforward and feedback modes of control during a visuomotor task (i.e., mirror tracing). Deafferented Patient IW shows equivalent error rates to normal participants when tracing sharp corners. Errors in the mirror-drawing task were likely assessed through visuospatial processing relative to key points. However, when tracing curved trajectories IW’s performance outstrips his competitors, perhaps because he can visually assess performance based on broader estimates and without proprioceptive interferences. It is possible that IW also shifts between feedforward and feedback based control depending on task requirements. Interestingly, for IW the shifts appear to be associated with measuring feedback related to directional changes at sharp corners (Miall & Cole, 2007) – that is, related to precisely determined progress at key points in the task which are perhaps an example of control points.

6.2 Planning action relative to control points

To plan most reaching movements, visual information must be available in order to parameterize an appropriate metrical response (Medendorp et al., 2008; Neely et al., 2008a; Prablanc et al., 1986). Such planning is accomplished, in part, by generating an estimate of the desired action using available sensory information (Brown et al., 2005; Goodale et al., 2008), while also assessing ongoing action lest corrections need to be administered (Mennie et al., 2007; Neely et al., 2008a; Neely, Tessmer Heath, Binstead, 2008). Control points may be critical components of such movement planning because
they provide distinct visual references—linked to the location of the goal of action—from which estimates related to the goal of action may be launched while also providing a stable location to which ongoing actions can be compared. Removing this information could negatively impact estimates of action and limit the potential for detecting errors in ongoing action.

The importance of visually locating and monitoring the sensory consequences relative to control points has revealed that these key points are critical components of planning and assessing issued eye and hand movements. During pilot testing, without a visible cursor between trials participants were unable to orient themselves, even though the home position was available. Indeed, limiting any means by which the hand position in relation to the object could be determined generally meant that participants were less able to effectively plan action. This decrement in performance is consistent with the notion that control points play a role in determining the accuracy of issued motor commands (here, the hand’s position relative to a viewed location) but may also indicate that the influence of control points extends past visual cues. That is, control points may not simply indicate visually determined future hand positions. Since tactile information became available following the first contact, this information may also have influenced subsequent planning in the movement sequence. One possible influence is that tactile information may be represented in an environmental (i.e., external) reference centered on the actor (Shore et al., 2005). This environmentally based representation of object positions may have influenced how the remaining objects in the sequence were contacted. After all, control points by their very nature often provide information related to an executed action in several related modalities. It seems likely that when an action
can be confirmed by multiple sources of information, the estimates used in planning that action would also make use of these multiple signals.

As discussed earlier, effective action plans must also account for the consequences of action—often signaled at control points. It is possible that action is encoded relative to an internal multisensory representations of the workspace influenced by, but not entirely conceived in, visual coordinates (Medendorp et al., 2008; Neggers & Bekkering, 2002). Such an interpretation coincides with Buneo and Andersen’s (2006) claims of a goal-centered representation that may make use of tactile and proprioceptive inputs when assessing motor errors relative to visual position of action. The present results are also consistent with visually assessed errors since participants reliably fixated sites of sensory consequence (i.e., control points) throughout the task—even when no visual feedback was available—in an effort to capture completed action at a goal site.

With regard to spatial representations used in action Burr and colleagues (2001) have suggested that there are two visual space representations: a plastic perception-based system that, for example, compensates for changes in eye position when making saccades, and a more static action based representation that determines where to direct action. Dual representations such as this reinforce Hayhoe and colleagues’ findings that repeated fixations during action facilitate action planning by increasing the known layout of the workspace in which reaching actions are made (Aivar et al., 2005; Hayhoe & Ballard, 2005; Hayhoe et al., 2003; Mennie et al., 2007; Triesch et al., 2003). Moreover, recent fMRI evidence from Wolbers and colleagues (2008) demonstrated that spatially updating seen objects so as to accurately point to them after a perceived displacement was independently represented in the brain from oculomotor signals produced as the
eyes moved around during the task. These authors contend that such separation in neural representations indicates that the representation of extrapersonal space can be updated and represented independent of eye movements (Wolbers, Hagerty, Büchel, & Loomis, 2008). This finding is particularly interesting because it may indicate that planning sequences of movement in extrapersonal reachable space can be informed by visual feedback while being represented separately from gaze movements within the task. Moreover it begs the question of whether these representations might be differently influenced by other sensory modalities involved in the task.

Taken together, the behaviours we report here indicated a dynamic role for gaze during action. Gaze not only foraged ahead to guide the hand to future locations of action but also remained to register key events that had just been completed. Importantly, as behavioural deficits resulting from removing just-contacted control points indicate, directing the hand may rely on confirming previous hand locations as well as locating forthcoming positions for hand action. The results following catch trials might indicate that confirming tactile consequences of action may have a similar dynamic time course – switching between generating estimates of future contacts while confirming just completed contacts. When omissions of expected feedback occur, behaviour can be modified. That is, these studies are in agreement with several authors’ claims of fluid transitions between feedforward and feedback related planning. The novel addition is that we demonstrate, especially in sequences of movement, that the role of gaze in confirming just-completed actions may be just as important as the function of guiding the hand to future locations. While locating an upcoming control point may benefit estimates of forthcoming action, monitoring that same key event also directly furnishes the CNS
with error-related feedback that can be used to refine future estimates of action. Our findings might also suggest that fluidly changing between feedforward and feedback modes would be particularly useful when sensory information is so limited that estimates of action become unreliable. Visual feedback—related to the goals of movement and determined at control points—may be the primary means of obtaining information that could allow behaviours to move from reactive to predictive, though perhaps the more task-related feedback that is used to inform an estimation related to the planned sensory consequences of an action, the better it will be predicted and the more accurately and efficiently the movement will be made.

6.3 Limitations
As is the case with any virtual reality it is possible that participants’ performances may have changed as a function of our paradigm. To ameliorate the lack of believability associated with our stimuli we engaged in extensive piloting prior to testing. The task was developed such that it was highly intuitive; participants understood it and capably completed it; and little training was required for performance to reach asymptote. The objects were believable enough that several participants commented that they thought they were contacting real objects. In pilot testing some participants unstably grasped and moved the handle. To minimize this effect and control the precision of handle and object contact, we placed the handle in the air-sled to provide stability and to protect the equipment. We found no evidence in participants’ movements that this modification changed performance in the task. Still, arm movements were limited to one plane, which is arguably different than natural reaching-to-grasp movements. Finally, although we were unable to measure 3D vision it is unlikely that this impacted performance because
hand movements were all constrained to the plane in which gaze was originally calibrated. Moreover, there is no literature that I know of that indicates a fundamental reorganization in gaze movements when movements occur in only one plane of motion.

One final limitation in the data is the individual differences, since across these experiments individuals differently responded to the conditions. Similar to the results reported by Neggers & Bekkering (2000), some participants seemed more susceptible to certain manipulations than others. For example, some participants delayed the timing of their gaze exits more in cursor invisible conditions. However, the reported group means still reflect the overall behavioural tendencies. Besides, if Gepshtein and colleagues’ (2005) interpretation is correct that participants differently select and weight sensory information when determining a percept, variability among the participants should be expected. Such variability between the eye and hand has been demonstrated in pointing tasks when some participants show bias toward the hand while others show a gaze-based bias (Beurze et al., 2006). Nevertheless, although variability among participants that is beyond experimental control should be expected, the general trend across the group remains the focus here.

6.4 Future directions

The present experiments open several possibilities for future research in eye-hand coordination tasks. As just mentioned, an examination of individual differences could be a fruitful endeavor. Though it is unfortunately beyond the scope of this dissertation, it would be of value to identify participants biased toward a given sensory modality (e.g. visual) and compare their performance with those who more readily rely upon an alternate source of information (e.g. tactile). This might help identify how some
individuals seemingly vacillate between multimodal representations while others are apparently beholden to a dominant source of feedback. It might also be interesting to more thoroughly compare timing differences across contacts following errors or catch hits when a discrepancy in detected error and predicted feedback occurs. As was speculated in Chapter 3, there is likely a limited time window in which sensory information can be detected and still have an effect on control. A future question of interest stemming from this might be to more carefully catalogue changes in behaviour following detected errors in contact. For example, an examination of the main sequence of saccadic movements in relation to gaze movements following errors might reveal more about the synergistic nature of eye and hand movement programming (see Arvind & Tharion, 2005).

It is also well documented that sex differences regularly influence behaviour in spatial navigation tasks. These gender differences may also exist in sensory integration as well (Berthoz & Viaud-Delmon 1999) especially when related to spatial tasks. Given these potential differences, it might be interesting to investigate whether there are gender differences in how men and women incorporate and make use of visual and tactile information from the workspace. Such an analysis could potentially provide further insights into the individual differences that we observed throughout the testing. This type of investigation might also reveal clues to indicate why one sensory modality becomes preferred by one group of individuals over another.

Finally in future studies it would be beneficial to more precisely examine the location of gaze during dexterous manipulation. Unfortunately, a lack of spatial resolution prohibited testing the exact position of gaze during action. It would be informative to
more carefully discern whether gaze is positioned upon the contact position, just in front of the object, or on the object itself. This might help distinguish the role of gaze placement in assessing predicted sensory consequences related to a goal.

**6.5 Summary**

In sum, the present results shed light on how available sensory information may be used to plan simple interactions with objects in the environment. Central in these observations is the strategy we have characterized demonstrating the dominance of goal-centered planning to register sensory consequences, estimate parameters of control, and predict forthcoming consequences to account for interactions with an object. Importantly, we demonstrate that this strategy is based upon the preferential selection and registration of sensory information arising from key points within a task, and that measured errors relative to these key points can be used to update the ongoing motor plan. Lastly this strategy was influenced by multimodal sources of sensory information that were used in determining the parameters for controlling action.

The representation of the workspace in which we act is largely influenced by visual input; however, when available, additional sensory information can also inform this representation and may also contribute to how action involving these percepts is planned. The present results may help to bridge the gap between pointing and reaching movements and provide a reasonable basis for tactile information to functionally contribute to representations used in planning action toward a goal in the workspace when the hand is used as an agent.
References


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