Accepted Manuscript

The role of somatosensory input in target localization during binocular and monocular viewing while performing a high precision reaching and placement task

Naime Tugac, David Gonzalez, Kimihiro Noguchi, Ewa Niechwiej-Szwedo

PII: S0014-4835(18)30198-2

DOI: 10.1016/j.exer.2018.08.013

Reference: YEXER 7465

To appear in: Experimental Eye Research

Received Date: 16 March 2018
Revised Date: 15 August 2018
Accepted Date: 16 August 2018

Please cite this article as: Tugac, N., Gonzalez, D., Noguchi, K., Niechwiej-Szwedo, E., The role of somatosensory input in target localization during binocular and monocular viewing while performing a high precision reaching and placement task, *Experimental Eye Research* (2018), doi: 10.1016/j.exer.2018.08.013.

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.



The role of somatosensory input in target localization during binocular and monocular viewing while performing a high precision reaching and placement task

¹Naime Tugac, ¹David Gonzalez, ²Kimihiro Noguchi, ¹Ewa Niechwiej-Szwedo

¹Department of Kinesiology, University of Waterloo, Waterloo, CANADA

²Department of Mathematics, Western Washington University, Bellingham, USA

Number of figures: 4

Corresponding author: Ewa Niechwiej-Szwedo Department of Kinesiology University of Waterloo 200 University Ave W Waterloo ON Canada

Phone: 519-888-4567 x 38311 Email: eniechwi@uwaterloo.ca

Abstract

Binocular vision provides the most accurate and precise depth information; however, many people have impairments in binocular visual function. It is possible that other sensory inputs could be used to obtain reliable depth information when binocular vision is not available. However, it is currently unknown whether depth information from another modality improves target localization in depth during action execution. Therefore, the goal of this study was to assess whether somatosensory input improves target localization during the performance of a precision placement task. Visually normal young adults (n=15) performed a bead threading task during binocular and monocular viewing in two experimental conditions where needle location was specified by 1) vision only, or 2) vision and somatosensory input, which was provided by the non-dominant limb. Performance on the task was assessed using spatial and temporal kinematic measures. In accordance with the hypothesis, results showed that the interval spent placing the bead on the needle was significantly shorter during monocular viewing when somatosensory input was available in comparison to a vision only condition. In contrast, results showed no evidence to support that somatosensory input about the needle location affects trajectory control. These findings demonstrate that the central nervous system relies predominately on visual input during reach execution, however, somatosensory input can be used to facilitate the performance of the precision placement task.

1. Introduction

One of the main benefits of having normal binocular vision is improved depth perception. The ability to accurately localize objects in three dimensional (3D) space is of critical importance during the performance of goal-directed reaching and grasping movements. The two binocular cues that contribute to movement planning and execution are ocular vergence and stereopsis. Studies have shown that ocular vergence provides reliable input about object's 3D location, which is important for planning reaching movements (Brenner and van Damme, 1998; Mon-Williams and Dijkerman, 1999; Tresilian et al., 1999). Stereopsis on the other hand provides the most precise information about object features, such as its size and orientation (Howard, 2012), which is important for grasp execution (Jeannerod et al., 1995). Unfortunately, abnormal binocular vision is the hallmark of developmental visual disorders such as amblyopia or strabismus, which affect 2 – 4% of otherwise typically developing children (Birch, 2013). In addition, disorders of binocular vision are also common in older adults (Leat et al., 2013), and following neurological injury (Bridge, 2016). Patients with abnormal binocularity must develop compensatory strategies, which could rely on inputs from the other sensory modalities. For example, somatosensory input could provide information for planning reaching movements, and adjusting grip forces when grasping objects. Although theoretically plausible, the role of somatosensory input in target localization during monocular viewing when performing reaching movements has not been studied in previous literature. It is important to understand whether input from the other modalities can be used to facilitate the performance of goal-directed movements when binocular vision is not available as this information could be used towards developing potential training regimens to improve visuomotor coordination for people with abnormal binocular function. Therefore, the goal of our investigation was to assess the contribution of somatosensory feedback to the performance of a precision placement task during binocular and monocular viewing.

Binocular vision provides unique input for optimal control of upper limb reaching and grasping movements. When planning a reaching movement, visual input specifies the extrinsic object properties,

such as distance and orientation, as well as the intrinsic object properties, such as size and texture (Bradshaw et al., 2004; Jeannerod et al., 1995; Melmoth and Grant, 2006). This sensory information is used to plan the initial reach trajectory and grip application forces, as well as, to fine-tune the trajectory during execution, which is referred to as online control (Elliott et al., 2001; Elliott et al., 2016; Khan et al., 2006). Significant deficits in motor performance have been reported in people with abnormal binocular vision (Grant et al., 2007; Grant and Moseley, 2011; O'Connor et al., 2010a, 2010b; Webber et al., 2008), and in visually-normal observers during monocular viewing (Gnanaseelan et al., 2014; Gonzalez and Niechwiej-Szwedo, 2016; Servos and Goodale, 1994; 1998), or when binocular vision was degraded (Piano and O'Connor, 2013). Importantly, these deficits are more apparent during performance of complex motor actions. For example, the speed and accuracy of aiming movements towards a single target is not significantly affected during monocular viewing (Coull et al., 2000; Niechwiej-Szwedo et al., 2011; Niechwiej-Szwedo et al., 2014). In contrast, prehension movements and action sequences are performed significantly slower and with more errors when binocular vision is not available (Gnanaseelan et al., 2014; Gonzalez and Niechwiej-Szwedo, 2016; Piano and O'Connor, 2013). Specifically, one type of motor task that is disrupted when binocular vision is not available is bead threading, which consists of grasping a small bead and placing it on a vertical needle (Gonzalez and Niechwiej-Szwedo, 2016; O'Connor et al., 2010a; Piano and O'Connor, 2013). Our previous studies have shown that grasp duration was ~20% longer during monocular viewing; however, the greatest deficit was found for the placement component which was ~70% longer in duration during monocular as compared to binocular viewing (Gonzalez and Niechwiej-Szwedo, 2016). These results demonstrate that the ability to localize the needle in 3D space in order to place the bead is severely disrupted when viewing with one eye. This disruption most likely occurs because ocular vergence is an important cue for distance, and this cue is not reliable during monocular viewing due to phoria.

Studies have shown that ocular vergence provides reliable input about the object's 3D location during binocular viewing which is important for planning a reaching movement (Brenner and van Damme, 1998; Mon-Williams and Dijkerman, 1999; Tresilian et al., 1999). For example, Mon Williams & Dijkerman (Mon-Williams and Dijkerman, 1999) used base-in and base-out prisms to manipulate ocular vergence, which affected the perceived target distance, and in turn influenced the kinematics of reaching movements. Specifically, when participants wore base-out prisms the target appeared to be located closer in depth, which led to lower reach peak velocity and acceleration. On the other hand, the target appeared farther away with base-in prisms, which led to higher reach peak velocity and acceleration. Therefore, the results from the studies by Mon-Williams and colleagues showed that the central nervous system (CNS) uses ocular vergence as a distance cue during binocular viewing, which directly affects the planning and execution of upper limb reaching movements.

The ocular vergence signal is disrupted during monocular viewing due to the phoria (Ono and Weber, 1981). Phoria occurs when the occluded eye deviates outward (exophoria) or inward (esophoria). Previous studies have shown that phoria disrupts judgements of visual direction, which is associated with mislocalization of the target object along the azimuth (Khokhotva et al., 2005; Ono and Gonda, 1978; Ono and Weber, 1981). For example, a temporal eye deviation of the right eye (exophoria) results in mislocalization of the target along azimuth such that the target is perceived to the right of its actual physical location. In the case of esophoria, the eye deviates inward and the target appears shifted toward the seeing eye, so if the right eye is occluded, the target will be perceived to the left of where it is actually located. To summarize, ocular vergence does not provide a reliable cue during monocular viewing because phoria of the covered eye leads to localization errors along the azimuth. It is conceivable that the placement of the bead on the needle is longer during monocular viewing due to phoria, which disrupts localization of the needle in 3D space.

When the visual input is less reliable, the CNS could rely on inputs from other modalities. For example, if the target is in contact with a body part, the somatosensory system could provide information about target location. Elegant studies by van Beers and colleagues (van Beers et al., 1996; 1998) compared the precision of somatosensory and visual inputs in localizing one's own unseen hand. Results showed that somatosensory localization was more precise in the radial direction with respect to the shoulder, whereas visual localization was more precise along the azimuth. In addition, localization was most precise in an experimental condition when the visual and somatosensory inputs were both present, which indicates that multisensory integration improves performance. Relatively few studies examined the kinematics of reaching movements to visual and somatosensory targets (Cameron and Lopez-Moliner, 2015; Monaco et al., 2009). Nonetheless, the main findings from these studies support the idea that the presence of somatosensory input improves the planning and execution of reaching movements.

To summarize, binocular vision provides an important sensory input regarding object location in 3D space, which is critical for the performance of goal-directed movements. One aspect of performance that is impaired when one eye is occluded is target localization. Previous research has shown that presence of somatosensory input regarding target location is associated with better reach endpoint precision during binocular viewing. Therefore, the goal of the current study was to assess the contribution of somatosensory input specifying target location to the performance of a precision reach and placement task during monocular viewing. It was hypothesized that the presence of somatosensory input will be associated with significantly better performance as indicated by limb kinematics. It was also expected that the improvement in motor performance with somatosensory input will be greater during monocular compared to binocular viewing.

Methods

2.1 Participants

Fifteen adults (10 females, 5 males; mean age= 22.4 ± 3.16 years) with normal, or corrected-to-normal vision were recruited. Participants had no history of visual, or ocular abnormalities, and no neuromuscular deficits. All participants were right handed, which was established using the Waterloo Handedness Questionnaire. The Porta test was used to determine eye dominance, which showed that 12 participants were right eye dominant. Distance visual acuity was assessed binocularly and monocularly using the Bailey Lovie vision chart. All participants had best visual acuity of 0 logMAR or better in each eye. Stereoacuity was measured using the Randot Stereoacuity Test (Randot SO-002 test), and all participants achieved at least 40 seconds of arc. All the experimental procedures were approved by the ethics committee at the University of Waterloo. Participants signed an informed consent prior to participating in the study.

1.2 Apparatus

Figure 1 shows the apparatus used in the experiment. A board consisting of two hooks, which were aligned in azimuth and separated vertically by 6 cm, was positioned directly in front of participant's midline. Two beads (diameter 1.6 cm, bead hole 0.48 cm) were placed on the hooks. A vertical needle (16.2 cm long and 0.2 cm in diameter) was placed 10 cm away (in depth) from the bottom side of the board holding the beads. The needle was aligned in azimuth with the two central beads, and the tip of the needle was aligned vertically with the top bead. In order to ensure comfortable reaching distance, the distance from the chin rest to the needle was half the participant's arm length (Mean Arm Length= 69.8 cm, SD=4.1 cm).

Upper limb kinematics were recorded using an Optotrak 3D Investigator motion capture system (Northern Digital, Waterloo, Canada). Two infrared emitting diodes (Ireds) were placed on the proximal

base of the thumb and index finger. Although both fingers were recorded, only the index finger was used for the kinematic analysis. Grip aperture was not a measured in this study because the Ireds were not placed at the tip of the fingers as this could potentially interfere with the participant's grasping behavior. Prior to beginning data collection, the Optotrak system was calibrated using a three-marker digitizing probe.

Eye movements were recorded using a head-mounted binocular eye tracker (Eyelink II, SR Research, Ottawa, Canada). Calibration for the eye tracker was performed under binocular viewing using a standard 9-point grid. Validation was performed to ensure the reliability of the calibration was <1° error. Calibration targets were presented on a 19-inch CRT monitor (Viewsonic P95f+, 1024x768) at a viewing distance of 80 cm. Eye movement recordings were done under binocular and monocular viewing. Monocular viewing was accomplished using an infrared long-pass filter (Edmund Optics, Barrington, NJ, USA), which was placed in front of one eye. The filter blocked all visible light while passing near infrared wavelengths such that the eye tracker was able to record the position the covered eye.. Both limb and eye movement recordings were sampled at a rate of 250 Hz. MotionMonitor software (Innovative Sports Technology, Chicago, USA) was used to temporally synchronize the recordings limb and eye position data, and to integrate the limb and eye position data into a common 3D reference frame. A common Cartesian coordinate system was defined with an origin located at the bottom left corner of the workspace (to the left of the apparatus). The 3D reference frame was defined with respect to the observer: horizontal plane (azimuth) as the x-axis; vertical plane (elevation) as the y-axis; median plane (depth) as the z-axis.

1.3 Experimental Procedure

At the initiation of each trial participants had their eyes closed, and placed the right index finger and thumb of the dominant hand at the tip of the needle. At this time, the researcher placed two beads on the

hooks on the board. Participants were instructed to open their eyes and fixate on the tip of the needle, which was followed by a verbal "Go" signal, and initiation of the reaching movement. Participants were instructed to use their right hand to grasp one bead at-a-time, starting with the bottom bead, and to place it on the needle as fast as possible without dropping. The trial was completed when both beads were placed on the needle. Collection duration was variable as each trial collection was terminated when the participant finished the task. The task was performed under three viewing conditions: binocular, and monocular with the right and left eye. Viewing conditions were randomized and counterbalanced between participants. There were ten trials for each viewing condition.

The main experimental manipulation was the presence of somatosensory feedback on half of the trials. Thus, in each viewing condition there were 5 trials with vision only, and 5 trials with somatosensory feedback and vision. These trials were randomized within each viewing condition using the excel RAND function. Participants received somatosensory feedback regarding the 3D location of the needle by using their own left hand to hold the needle. Specifically, the left thumb and index finger were placed on the needle in a standardized position, 3.5 cm from the bottom. This position was also labeled on the needle to ensure that each participant held the needle at the same location during the experiment. Participants held the needle closer to the bottom rather than at the needle's tip because placing the hand the tip obstructed the view of the beads so participants could not perform the task. Trials with somatosensory feedback were randomly interspersed with vision only trials (i.e., control condition), where the left hand was resting on the table 10 cm to the left of the needle's position.

1.4 Data Analysis

2.4.1 Optotrak Data Reduction

The beads were dropped on 5.3% of trials (BE: 0.7% right eye: 1.3%; left eye: 3.3%), and these data were excluded from the kinematic analysis. Trials with missing data due to loss of finger tracking

were also excluded from the kinematic analysis (4%). Raw position data were filtered using a dual-pass Butterworth filter with a low cut-off frequency of 20 Hz, and instantaneous velocities were calculated using adjacent points (Matlab, Mathworks, Natick, USA). The main analysis focused on two kinematic phases: reaching towards the needle and bead placement on the needle. Figure 2 shows a typical velocity trajectory during binocular and monocular viewing where the two kinematic phases of interest were identified using velocity criteria. Specifically, the start of the reaching phase was defined as a time when finger velocity in the z-axis reached at least 20 mm/s for 20 consecutive milliseconds, with the end of the reach defined as velocity falling under 100 mm/s for 20 consecutive milliseconds after peak velocity. The placement phase was defined as a time when velocity in the z-axis fell under 100 mm/s, and the end of the placement was defined as a time when the hand was moving in the opposite direction and finger velocity in the z-axis exceeded 20 mm/s for 20 consecutive milliseconds. Although not the focus of the current investigation, grasp duration was also calculated using the same velocity criteria. These criteria are consistent with the aiming literature (Elliott et al., 1999; Glazebrook et al., 2009; Grierson and Elliott, 2009), and our previous work on prehension (Gnanaseelan et al., 2014; Gonzalez and Niechwiej-Szwedo, 2016).

2.4.2 Eyelink Data Reduction

Eye tracking data from one participant were excluded due to excessive noise. All trials without a corresponding limb data (i.e., due to dropped beads or loss of Ired tracking) were also excluded from the analysis. All eye position traces were inspected visually by one of the authors, and fixation on the needle was determined using a velocity criterion: fixation was defined as stable when the eye velocity <20 deg/s. Mean eye position of the left and right eye during the fixation interval was used to calculate the vergence angle by subtracting the position of the left eye from the right eye (Howard and Rogers 2002).

2.4.3 Statistical Analysis

2.4.3.1 Mean Limb and Eye Kinematic Analysis

The main dependent measures used to examine the effect of somatosensory feedback on limb kinematics during the performance of a precision placement task were reach peak velocity, reach movement time, and placement duration. Two measures obtained from eyetracking were also examined: fixation duration and vergence angle during the placement task. A repeated-measures analysis of variance (ANOVA) with two within-subject factors: modality (somatosensory, vision only) and viewing conditions (binocular, left eye, right eye) was used to test the main hypothesis. Post-hoc testing was performed using the Tukey-Kramer test. The significance level was set at p < 0.05. Statistical analyses were conducted using the Statistical Analysis System (SAS) Studio, ver. 3.5 Enterprise Edition (SAS Institute Inc., Cary, NC, USA). Descriptive statistics are reported as the mean and corresponding standard deviation.

2.4.3.2 Reach Trajectory Analysis

A multivariate normal-based parametric bootstrap approach was used to examine reach trajectory deviation in azimuth and depth across the experimental conditions. This procedure provides simultaneous pairwise adjusted p-values for comparing time varying continuous data series (for details see: https://cran.r-project.org/web/packages/curvecomp/index.html). The advantage of using this procedure is that it can reliably detect the time points for which the trajectory deviation effect sizes from movement initiation to termination are statistically significant as opposed to using a single point in time (e.g., assessing trajectory deviation at a single kinematic event, such as peak velocity). In particular, the familywise error rate is controlled properly even when multiple experimental conditions are present. In addition to the adjusted p-value at each time point of the trajectory deviations, Cohen's *d* effect size (Cohen, 1992) was calculated to understand the practical significance of the deviation.

A requisite for using this approach is that the movement trajectory must be normalized in time, which requires rescaling of the original range because movement duration is different across trials and participants. In other words, the normalization process involves rescaling the data such that each trial consists of equal number of samples. In our approach, normalization was performed separately for the acceleration interval, which was defined as the time from reach initiation to reach peak velocity, and the deceleration interval, which was defined as the time from reach peak velocity to the end of movement. First, the maximum duration of the acceleration and deceleration interval was determined across all trials and participants, and this value was used to rescale the remaining data. The maximum duration of acceleration interval was 185 frames, and the maximum deceleration interval duration was 123 frames. A custom Matlab script was used to rescale the raw data using interpolation (Pchip matlab function). Next, because each trial consisted of a sequence of two reaching movements to the needle (i.e., each trial involved placing 2 beads on the needle), the reach trajectory for these two movements was averaged. Finally, the multivariate parametric bootstrap analysis was performed, using R version 3.3.3, to assess reach trajectory deviation across viewing conditions (i.e., binocular vs. right eye; binocular vs. left eye; right eye vs. left eye) and modality conditions (i.e., somatosensory vs. vision only). The interaction between viewing and modality conditions was also assessed by comparing reach trajectory using the following three contrasts: 1) somatosensory vs. vision only during binocular vs. left eye viewing; 2) somatosensory vs. vision only during binocular vs. right eye viewing; and 3) somatosensory vs. vision only during right vs. left eye viewing.

3 Results

3.1 Eye Movements

Fixation Duration: There was a significant main effect of viewing condition (F(2,26)=15.72, p<0.0001). Post hoc testing showed that fixation duration on the needle was shorter during binocular viewing

regardless of modality condition (somatosensory: 965±163 ms; vision only: 946±160 ms) as compared to right eye viewing (somatosensory: 1055±123 ms; vision only: 1135±157 ms), and left eye viewing (somatosensory: 1233±181 ms; vision only: 1229±232 ms). No other effects were significant.

Vergence Angle: There was a significant main effect of viewing condition (F(2,26)=21.12, p<0.0001). During binocular viewing the mean vergence angle when fixating on the needle during the placement task was 10.8±2.3°, and during monocular viewing vergence angle was reduced (right eye viewing: 8.1±1.8°, left eye viewing: 8.3±2.1°). No other effects were significant.

3.2 Mean Limb Kinematics

Reaching Phase: There was a main effect of viewing condition for reach movement time (F(2,28)=4.67,p=0.018), and peak velocity (F(2,28)=4.15, p=0.026). Post-hoc test showed that movement time was significantly shorter during binocular (530±84 ms) and monocular right eye viewing (538±91 ms) as compared to left eye viewing (558±104 ms). Peak velocity was higher during binocular (0.450±0.118 m/s) as compared to monocular viewing (right eye: 0.416±0.105 m/s, left eye: 0.425±0.117 m/s). In contrast to the hypothesis, the effect of modality was not statistically significant for movement time (F(1,14)=0.83, p=0.378), or peak velocity (F(1,14)=3.25, p=0.093). The interaction was also not significant for movement time (F(2,28)=0.95, p=0.398) or peak velocity (F(2,28)=0.14, p=0.867). Placement Phase: There was a significant main effect of viewing condition (F(2,28)=30.53, p<0.0001), and modality (F(1,14)=34.21, p<0.0001). In accordance with the hypothesis, the interaction was significant (F(2,28)=4.41, p<0.022; Figure 3). Post hoc testing showed that placement duration was significantly shorter during monocular viewing when somatosensory feedback was present (left eye: 920±232 ms; right eye: 894±171 ms) as compared to vision only condition (left eye: 1102±242 ms; right eye: 1065±158 ms). In contrast, post hoc testing showed that somatosensory feedback did not significantly reduce placement duration during binocular viewing (somatosensory: 711±143 ms; vision only: 748±186 ms).

Grasp Phase: There was a significant main effect of viewing condition (F(2,28)=17.31, p<0.0001), however, the effects of modality (F(1,14)=0.14, p=0.713), and modality by viewing condition were not significant (F(2,28)=0.92, p=0.411).

3.3 Reach Trajectory

Figure 4a shows the mean reach trajectories and their pointwise 95% confidence intervals for each frame during the acceleration interval across the three viewing conditions, and Figure 4b shows the first fifty frames. The adjusted p-values of the pairwise comparisons that control the familywise error rate are shown in Figure 4c. Results show a larger deviation along azimuth when viewing with the left eye (red curves) as compared to right eye viewing (green curves). Statistical analysis, which controlled for the familywise error rate, confirmed that the difference in trajectory when viewing with the left versus the right eye was significant (p=0.030, Cohen's *d* effect size 1.0), and persisted from movement initiation up to 19% of the acceleration interval. After that time, reach trajectories were not statistically different across the viewing conditions. There was no significant difference between trajectories when viewing binocularly compared to left or right eye viewing. Analysis of the deceleration interval showed no significant differences in trajectory across viewing conditions or modality conditions.

4. Discussion

We sought to examine the contribution of somatosensory feedback to the performance of a precision placement task during binocular and monocular viewing. It was hypothesized that the presence of somatosensory input will be associated with a significantly better performance as indicated by limb kinematics. Our hypothesis was only partially supported: when somatosensory feedback was present during monocular viewing placement duration was shorter by ~20% in comparison to a vision only condition. In contrast, reach peak velocity, movement time, and trajectory control were not significantly

influenced by somatosensory feedback, which indicates that target location provided via somatosensory input from the contralateral limb had a limited contribution to the execution of a precision reaching movement. A secondary, important and novel result from our study is the finding that phoria has a significant effect on the initial reach trajectory direction.

Numerous studies have shown significant advantages for the performance of upper limb movements when viewing with both eyes, supporting the idea that binocular vision provides the most accurate and reliable input for motor performance (Bradshaw and Elliott, 2003; Bradshaw et al., 2004; Gnanaseelan et al., 2014; Gonzalez and Niechwiej-Szwedo, 2016; Grant, 2015; Grant et al., 2007; Grant and Moseley, 2011; Jackson et al., 1991; Jackson et al., 2002; Melmoth and Grant, 2006; Melmoth et al., 2007; O'Connor et al., 2010a; Piano and O'Connor, 2013; Servos and Goodale, 1994, , 1998; Watt and Bradshaw, 2000; Webber et al., 2008). In general, previous studies found greater deficits for more complex tasks (i.e., prehension, movement sequences) during monocular viewing; therefore, a complex sequencing task was examined in this study. Although the bead threading task consists of four movement components (i.e., reach-to-bead, grasp, reach-to-needle, place), our analysis focused only on the latter two because the experimental manipulation was most relevant for the planning and execution of these two movements. In order to successfully place the bead on the needle, the tip had to be localized in 3D space. The CNS relies on multiple cues to recover depth information, for example, monocular pictorial cues, motion parallax, accommodation, ocular vergence, and stereopsis for relative depth (Howard and Rogers, 2002; Welchman, 2016). Our task was performed in a well-lit room so participants could have used monocular depth cues, however, motion parallax was not available because head movement was restrained using a chin rest. Our results clearly show that binocular viewing provided a very important input for the performance of the placement task because the duration was 45% longer during monocular viewing. Even when somatosensory input was available, the placement task was performed significantly slower during monocular in comparison to binocular viewing, further

demonstrating the superiority of binocular depth cues. Viewing with both eyes provides the CNS with horizontal and vertical disparities, which are not available when input is restricted to one eye (Blake and Wilson, 2011; Gonzalez and Perez, 1998; Poggio, 1995). In addition, ocular vergence provides a less reliable depth cue during monocular viewing due to phoria (Ono and Gonda, 1978; Ono and Weber, 1981). Our data does not allow us to assess the individual contribution of disparity or vergence to placement task performance; however, placement involves aligning a small bead with the tip of the needle, therefore, horizontal disparities could have provided critical input. Overall, our results are consistent with studies which showed that the CNS can use binocular depth cues faster than monocular cues to correct reaching trajectory in response to a perturbation (Greenwald et al., 2005; Hu and Knill, 2011).

Our study is the first to show that somatosensory feedback about target location specified via the contralateral limb provides a significant benefit for a precision placement task performance during monocular viewing. The unique contribution of somatosensory input to bead placement is also highlighted by the fact that grasping performance was not influenced by the presence of somatosensory information. This was expected because there was no somatosensory input regarding the bead's location. The somatosensory input most likely involves the integration of responses from hand SAI tactile afferents and limb proprioceptors that encode joint angles and arm posture (Badde et al., 2015). These inputs are first processed in the somatosensory specific cortices (S1 and S2), and subsequently in parietal association area, where neurons have multisensory responses involved in visual and somatosensory integration (Duhamel et al., 1998; Gazzaniga et al., 1995). For example, bimodal neurons in the parietal cortex have overlapping receptive fields, and their responses are modulated by eye and limb position. It has been proposed that these multisensory neurons might be involved in coding of extrapersonal visual space (Graziano and Gross, 1993). At the behavioral level, multisensory integration is an important process that improves the accuracy, precision, and speed of perceptual and motor

responses (Angelaki et al., 2009; Lalanne and Lorenceau, 2004). In general, congruent sensory inputs are weighted based on their reliability and previous experience (Ernst and Banks, 2002). In the context of our study, binocular vision provided the most reliable input for the placement task, but when this input became less reliable during monocular viewing, the contribution of the somatosensory input to task performance became more significant. To summarize, during monocular viewing placement duration was shorter with somatosensory input specifying needle location, which can be explained by multisensory integration – a highly adaptable and flexible process fine-tuned to the observer's sensory status and task demands.

It was expected that the CNS will integrate visual and somatosensory inputs about the target location to facilitate reach execution. In contrast to our hypothesis, reaching towards the needle was not influenced by the presence of somatosensory input specifying needle location in either viewing condition. This is supported by the lack of significant difference between the modality conditions for peak velocity, movement time, or trajectory control. Although these results may seem surprising, there are several explanations that may account for the lack of effect. First, when a target's location is provided by two sensory modalities, the initial sensory input is encoded in different frames of reference. Specifically, visual information is encoded in gaze centered coordinates, while somatosensory input is encoded in intrinsic body coordinates (Sarlegna and Sainburg, 2009). Therefore, the tip of the needle was registered in a different frame of reference. Prior to integrating information from different modalities, these inputs must be transformed into a common coordinate frame. As suggested by Sober and Sabes (Sober and Sabes, 2003), sensory integration depends on the sensory inputs and task demands. In general, the CNS relies less on signals that have to be transformed between different reference frames because transforming sensory input into a different coordinate frame is computationally taxing and susceptible to errors (McGuire and Sabes, 2009). The task used in this study was highly visual: after grasping a small bead, participants had to align the bead's hole with the tip of

the needle. Therefore, it is possible that the task was completed using a predominantly visual frame of reference. Second, while participants were holding the needle, they could also see the configuration of the arm and the hand that was holding the needle, which may have led to visual capture – a well-known phenomenon that describes the increased reliance on visual input over other modalities (Holmes et al., 2004; Pavani et al., 2000). Finally, due to experimental limitations described in the methods, the reliability of the somatosensory input could have been reduced because participants held the needle 13 cm below the tip, therefore, the visual and somatosensory inputs were not precisely co-localized along the vertical axis. Previous studies have shown that multisensory integration is optimal when the sensory inputs are spatially and temporally coincident (Avillac et al., 2007; Stevenson et al., 2012), therefore, the vertical offset between the visual and somatosensory information may have reduced the potential for integration. More specifically, it is possible that the somatosensory and visual encoding of the spatial position of the needle's location was outside of the area where these inputs can be optimally integrated or summated. Future research is required to determine the limits of spatial and temporal integration of inputs from different modalities across different tasks, such as localization. To summarize, our study found no evidence to support that the CNS uses somatosensory input specifying needle location to facilitate reach execution. This may be due to increased computational cost and noise that could arise when transforming the somatosensory input into a visual coordinate frame, visual capture, or the vertical offset in hand position specifying needle's location.

In general, results from this study are consistent with previous literature which shows a binocular advantage for reach execution. A novel and interesting finding from our study is the effect of phoria on reach control trajectory. As reviewed in the introduction, phoria is a horizontal eye deviation which occurs naturally during monocular viewing in visually-normal observers (Hrynchak et al., 2010; Ono and Weber, 1981). Previous studies have clearly demonstrated that phoria affects the perceived target location along azimuth when observers point to a visual target without visual feedback of the limb

(Khokhotva et al., 2005; Ono and Weber, 1981). These phoria-induced localization errors indicate that CNS uses an extraretinal eye position signal when planning the direction of a reaching movement. Our study extends this literature by examining the control of reach trajectory during monocular viewing while visual feedback of the reaching limb is present during movement execution. Using this experimental paradigm, and a continuous measure of reach trajectory obtained from the motion capture system provides insight into the temporal dynamics of online trajectory regulation, and the error correction processes. Specifically, phoria induced localization error should affect the initial planning process, however, if visual feedback is available these errors should be amended because the CNS uses online feedback control during movement execution to ensure endpoint accuracy and precision (Elliott et al., 2010; Gaveau et al., 2014; Grierson and Elliott, 2008; Khan et al., 2003; Proteau et al., 2009). Our study provides evidence that errors in motor planning due to phoria are corrected relatively quickly. The initial trajectory direction was shifted towards the covered eye during monocular viewing, however, this shift was only significant within the first 20% of the acceleration interval, and there was no significant difference in trajectories across viewing conditions after that time. Our findings are consistent with a recent study which found that visual feedback during the early acceleration phase provides important input for regulating reach trajectory (Tremblay et al., 2016). In summary, our study adds to the previous literature by providing insight into the dynamics of online control in a situation where the trajectory deviation is due to an eye position error signal rather than an external target perturbation..

Our study has several limitations that should be acknowledged. First, a clinical measure of phoria was not obtained from individual participants. Instead, the presence of phoria was inferred from eye tracking data, which confirmed that the vergence angle was reduced during monocular viewing. A clinical measure of phoria could provide additional insight and explain individual variability in task performance. Another potential limitation maybe the lack of spatial coincidence between the visual and somatosensory inputs along the vertical axis. As discussed previously, it is possible that this factor

contributed to the lack of significant effects associated with the presence of somatosensory input during

reach planning and execution. Finally, future studies should examine the role of visual feedback of the

limb specifying target location. It is possible that removing visual feedback will reduce visual capture,

and increase the contribution of somatosensory input to reach planning and execution.

5. Conclusion

In conclusion, our study demonstrates that somatosensory input specifying target location via the

contralateral limb facilitates the performance of a precision placement task during monocular viewing.

However, the kinematics of the reaching movement were not significantly influenced by the presence of

additional somatosensory input, suggesting that visual input provides adequate information for reach

execution in visually normal participants. It remains to be determined whether these findings can be

generalized to people with abnormal binocular vision, such as patients with amblyopia or strabismus.

Previous studies have shown that patients have significant difficulty when performing the bead threading

task (O'Connor et al., 2010a), therefore, it is possible that adding the somatosensory input could provide

a significant improvement during the performance of a precision reaching and placement task.

Acknowledgments: Banting Research Foundation

20

References

Angelaki, D.E., Gu, Y., DeAngelis, G.C., 2009. Multisensory integration: psychophysics, neurophysiology, and computation. Curr Opin Neurobiol 19, 452-458.

Avillac, M., Hamed, S.B., Duhamel, J.R., 2007. Multisensory integration in the ventral intraparietal area of the macaque monkey. Journal of Neuroscience 27, 1922-1932.

Badde, S., Röder, B., Heed, T., 2015. Flexibly weighted integration of tactile reference frames. Neuropsychologia 70, 367-374.

Birch, E.E., 2013. Amblyopia and binocular vision. Prog Retin Eye Res 33, 67-84.

Blake, R., Wilson, H.R., 2011. Binocular vision. Vision Res. 51, 754–770.

Bradshaw, M.F., Elliott, K.M., 2003. The role of binocular information in the 'on-line' control of prehension. Spat Vis 16, 295-309.

Bradshaw, M.F., Elliott, K.M., Watt, S.J., Hibbard, P.B., Davies, I.R., Simpson, P.J., 2004. Binocular cues and the control of prehension. Spat Vis 17, 95-110.

Brenner, E., van Damme, W.J.M., 1998. Judging distance from ocular convergence. Vis Res 38, 493-498.

Bridge, H., 2016. Effects of cortical damage on binocular depth perception. Philos Trans R Soc Lond B Biol Sci. 371, pii: 20150254.

Cameron, B.D., Lopez-Moliner, J., 2015. Target modality affects visually guided online control of reaching. Vis Res 110, 233-243.

Cohen, J., 1992. A power primer. Quantitative Methods in Psychology 112, 155-159.

Coull, J., Weir, P.L., Tremblay, L., Weeks, D.J., Elliott, D., 2000. Monocular and binocular vision in the control of goal-directed movement. J Mot Behav 32, 347-360.

Duhamel, J.R., Colby, C.L., Goldberg, M.E., 1998. Ventral intraparietal area of the macaque: congruent visual and somatic response properties. J Neurophysiol 79, 126–136.

Elliott, D., Binsted, G., Heath, M., 1999. The control of goal-directed limb movements: correcting errors in the trajectory. Hum Mov Sci 18, 121-136.

Elliott, D., Hansen, S., Grierson, L.E.M., Lyons, J., Bennett, S.J., Hayes, S.J., 2010. Goal-directed aiming: two components but multiple processes. Psychol Bull 136, 1023-1044.

Elliott, D., Helsen, W.F., Chua, R., 2001. A century later: Woodworth's (1899) two-component model of goal-directed aiming. Psychol Bull 127, 342-357.

Elliott, D., Lyons, J., Hayes, S.J., Burkitt, J.J., Roberts, J.W., Grierson, L.E.M., Hansen, S., Bennett, S.J., 2016. The multiple process model of goal-directed reaching revisited. Neurosci Biobehav Rev 72, 95-110.

Ernst, M.O., Banks, M.S., 2002. Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415, 429-433.

Gaveau, V., Pisella, L., Priot, A.E., Fukui, T., Rossetti, Y., Pelisson, D., Prablanc, C., 2014. Automatic online control of motor adjustments in reaching and grasping. Neuropsychologia 55, 25-40.

Gazzaniga, M.S., Graziano, M.S., Gross, C.G., 1995. The representation of extrapersonal space: a possible role for bimodal, visual-tactile neurons, in: Gazzaniga, M.S. (Ed.), The cognitive neurosciences. MIT, Cambridge, MA, pp. 1021–1034.

Glazebrook, C., Gonzalez, D., Hansen, S., Elliott, D., 2009. The role of vision for online control of manual aiming movements in persons with autism spectrum disorders. Autism 13, 411-433.

Gnanaseelan, R., Gonzalez, D.A., Niechwiej-Szwedo, E., 2014. Binocular advantage for prehension movements performed in visually-enriched environments. Frontiers in Human Neuroscience, http://dx.doi.org/10.3389/fnhum.2014.00959

Gonzalez, D.A., Niechwiej-Szwedo, E., 2016. The role of binocular vision in hand-eye coordination during sequential grasping and placing movements. Vision Res 128, 30-38.

Gonzalez, F., Perez, R., 1998. Neural mechanisms underlying stereoscopic vision. Prog Neurobiol 55, 191-224.

Grant, S., 2015. Gaze-grasp coordination in obstacle avoidance: differences between binocular and monocular viewing. Exp Brain Res 233, 3489-3505.

Grant, S., Melmoth, D.R., Morgan, M.J., Finlay, A.L., 2007. Prehension deficits in amblyopia. Invest Ophthalmol Vis Sci 48, 1139-1148.

Grant, S., Moseley, M.J., 2011. Amblyopia and real-world visuomotor tasks. Strabismus 19, 119-128. Graziano, M.S., Gross, C.G. 1993. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. Exp Brain Res 97, 96-109.

Greenwald, H.S., Knill, D.C., Saunders, J.A., 2005. Integrating visual cues for motor control: a matter of time. Vision Res 45, 1975-1989.

Grierson, L.E.M., Elliott, D., 2008. Kinematic analysis of goal-directed aims made against early and late perturbations: an investigation of the relative influence of two online control processes. Hum Mov Sci 27, 839-856.

Grierson, L.E.M., Elliott, D., 2009. Goal-directed aiming and the relative contribution of two online control processes. Am J Psychol 122, 309-324.

Holmes, N.P., Crozier, G., Spence, C., 2004. When mirrors lie: 'Visual capture' of arm position impairs reaching performance. Cogn Affect Behav Neurosci 4, 193-200.

Howard, I.P., 2012. Reaching and moving in 3D space, Perceiving in Depth. Oxford University Press, Oxford, pp. 260-275.

Howard, I.P., Rogers, B., 2002. Seeing in Depth. Porteus, Toronto.

Hrynchak, P.K., Herriot, C., Irving, E.L., 2010. Comparison of alternate cover test reliability at near in non-strabismus between experienced and novice examiners. Ophthalmic Physiol Opt 30, 304-309.

Hu, B., Knill, D.C., 2011. Binocular and monocular depth cues in online feedback control of 3D pointing movement. J Vis 11(7).pii.23. doi: 10.1167/11.7.23.

Jackson, S.R., Jones, C.A., Newport, R., Pritchard, C., 1991. A kinematic analysis of goal-directed prehension movements executed under binocular, monocular and memory-guided viewing conditions. Visual Cognition 4, 113-142.

Jackson, S.R., Newport, R., Shaw, A., 2002. Monocular vision leads to a dissociation between grip force and grip aperture scaling during reach-to-grasp movements. Curr Biol 12, 237-240.

Jeannerod, M., Arbib, M.A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. Trends Neurosci 18, 314-320.

Khan, M.A., Franks, I.M., Elliott, D., Lawrence, G.P., Chua, R., Bernier, P.M., Hansen, S., Weeks, D.J., 2006. Inferring online and offline processing of visual feedback in target-directed movements from kinematic data. Neurosci Biobehav Rev 30, 1106-1121.

Khan, M.A., Lawrence, G., Fourkas, A., Franks, I.M., Elliott, D., Pembroke, S., 2003. Online versus offline processing of visual feedback in the control of movement amplitude. Acta Psychol (Amst) 113, 83-97.

Khokhotva, M., Ono, H., Mapp, A.P., 2005. The cyclopean eye is relevant for predicting visual direction. Vis Res 45, 2339-2345.

Lalanne, C., Lorenceau, J., 2004. Crossmodal integration for perception and action. J Physiol Paris 98, 265-279.

Leat, S.J., Chan, L.L., Maharaj, P.D., Hrynchak, P.K., Mittelstaedt, A., Machan, C.M., Irving, E.L., 2013. Binocular vision and eye movement disorders in older adults. Invest Ophthalmol Vis Sci 54, 3798-3805.

McGuire, L.M., Sabes, P.N., 2009. Sensory transformations and the use of multiple reference frames for reach planning. Nat Neurosci 12, 1056-1061.

Melmoth, D.R., Grant, S., 2006. Advantages of binocular vision for the control of reaching and grasping. Exp Brain Res 171, 371-388.

Melmoth, D.R., Storoni, M., Todd, G., Finlay, A.L., Grant, S., 2007. Dissociation between vergence and binocular disparity cues in the control of prehension. Exp Brain Res 183, 283-298.

Mon-Williams, M., Dijkerman, H.C., 1999. The use of vergence information in the programming of prehension. Exp Brain Res 128, 578-582.

Monaco, S., Kroliczak, G., Quinlan, D.J., Fattori, P., Galletti, C., Goodale, M.A., Culham, J.C., 2009. Contribution of visual and proprioceptive information to the precision of reaching movements. Exp Brain Res 202, 15-32.

Niechwiej-Szwedo, E., Goltz, H., Chandrakumar, M., Hirji, Z.A., Crawford, J.D., Wong, A.M., 2011. Effects of Anisometropic Amblyopia on Visuomotor Behaviour: II. Visually-Guided Reaching. Invest Ophthalmol Vis Sci 52, 795-803.

Niechwiej-Szwedo, E., Goltz, H., Chandrakumar, M., Wong, A.M.F., 2014. Effects of strabismic amblyopia on visuomotor behaviour: Part 2. Visually guided reaching. Invest Ophthalmol Vis Sci 55, 3857-3865.

O'Connor, A.R., Birch, E.E., Anderson, S., Draper, H., 2010a. The functional significance of stereopsis. Invest Ophthalmol Vis Sci 51, 2019-2023.

O'Connor, A.R., Birch, E.E., Anderson, S., Draper, H., 2010b. Relationship between binocular vision, visual acuity, and fine motor skills. Optom Vis Sci 87, 942-947.

Ono, H., Gonda, G., 1978. Apparent movement, eye movements and phoria when two eyes alternate in viewing a stimulus. Perception 7, 75-83.

Ono, H., Weber, E.U., 1981. Nonveridical visual direction produced by monocular viewing. J Exp Psychol Hum Percept Perform 7, 937-947.

Pavani, F., Spence, C., Driver, J., 2000. Visual capture of touch: Out-of-the-body experiences with rubber gloves. Psychological Science 11, 353-359.

Piano, M.E., O'Connor, A.R., 2013. The effect of degrading binocular single vision on fine visuomotor skill task performance. Invest Ophthalmol Vis Sci 54, 8204-8213.

Poggio, G.E., 1995. Mechanisms of stereopsis in monkey visual cortex. Cereb Cortex. 5, 193-204.

Proteau, L., Roujoula, A., Messier, J., 2009. Evidence for continuous processing of visual information in a manual video-aiming task. J Mot Behav 41, 219-231.

Sarlegna, F.R., Sainburg, R.L., 2009. The roles of vision and proprioception in the planning of reaching movements. Adv Exp Med Biol 629, 317-335.

Servos, P., Goodale, M.A., 1994. Binocular vision and the on-line control of human prehension. Exp Brain Res 98, 119-127.

Servos, P., Goodale, M.A., 1998. Monocular and binocular control of human interceptive movements. Exp Brain Res 119, 92-102.

Sober, S.J., Sabes, P.N., 2003. Multisensory integration during motor planning. J Neurosci 23, 6982-6992.

Stevenson, R.A., Krueger Fister, J., Barnett, Z.P., Nidiffer, A.R., Wallace, M.T., 2012. Interactions between the spatial and temporal stimulus factors that influence multisensory integration in human performance. Exp Brain Res 219, 121-137.

Tremblay, L., Crainic, V.A., de Grosbois, J., Bhattacharjee, A., Kennedy, A., Hansen, S., Welsh, T.N., 2016. An optimal velocity for online limb-target regulation process? Exp Brain Res 235, 29-40.

Tresilian, J.R., Mon-Williams, M., Kelly, B.M., 1999. Increasing confidence in vergence as a cue to distance. Proceedings Royal Society of London, B 266, 39-44.

van Beers, R.J., Sittig, A.C., Denier van der Gon, J.J., 1996. How humans combine simultaneous proprioceptive and visual position information. Exp Brain Res 111, 253-261.

van Beers, R.J., Sittig, A.C., Denier van der Gon, J.J., 1998. The precision of proprioceptive position sense. Exp Brain Res 122, 367-377.

Watt, S.J., Bradshaw, M.F., 2000. Binocular cues are important in controlling the grasp but not the reach in natural prehension movements. Neuropsychologia 38, 1473-1481.

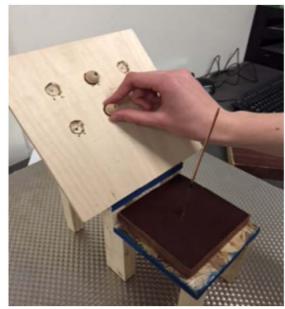
Webber, A.L., Wood, J.M., Gole, G.A., Brown, B., 2008. The effect of amblyopia on fine motor skills in children. Invest Ophthalmol Vis Sci 49, 594-603.

Welchman, A.E., 2016. The human brain in depth: How we see in 3D. Annu Rev Vis Sci. 2, 345-376.

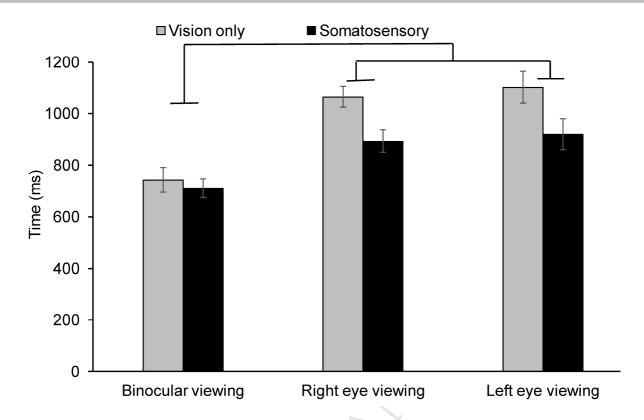
List of Figures

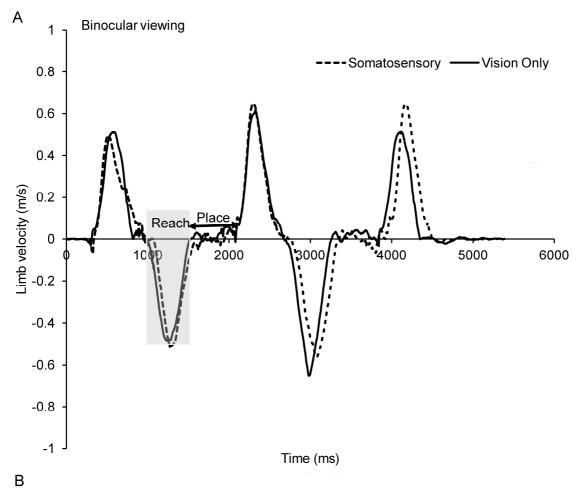
- Figure 1: Experimental setup: vision only condition (A), and somatosensory condition (B).
- Figure 2: Typical velocity trajectory obtained on a single trial during binocular (A), and monocular (B) viewing (solid line is the vision only condition, dotted line is the somatosensory condition). The grey box highlights the duration of reach interval, and the arrow indicates placement duration (reach and placement duration were defined using velocity criteria, please see text for details).
- Figure 3: Average duration of placement across the experimental conditions (error bars are standard error of the mean). Placement time was shorter during binocular viewing in comparison to all monocular conditions (p<0.05). Somatosensory feedback during monocular viewing was associated with shorter placement time in comparison to a vision only condition (p<0.05).
- Figure 4: Comparison of the reach trajectory across viewing conditions. Mean reach trajectories and their pointwise 95% confidence intervals for each frame during the acceleration interval across binocular, right and left eye viewing (A). The first fifty frames (i.e., 30% of the acceleration trajectory, which is highlighted by the rectangle in A) are replotted in Figure B. There was a significant difference during the initial 19% of the acceleration trajectory between left and right eye viewing (p<0.05). The adjusted p-values of the pairwise comparisons that control the familywise error rate are shown in Figure C. The dotted horizontal lines indicate the typical statistical cut-off levels (i.e., 0.01, 0.05, and 0.10).

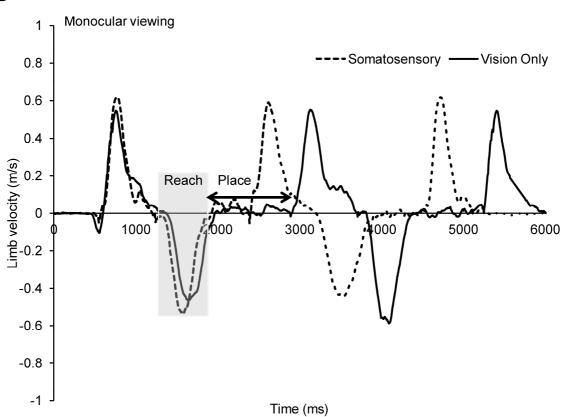
A B

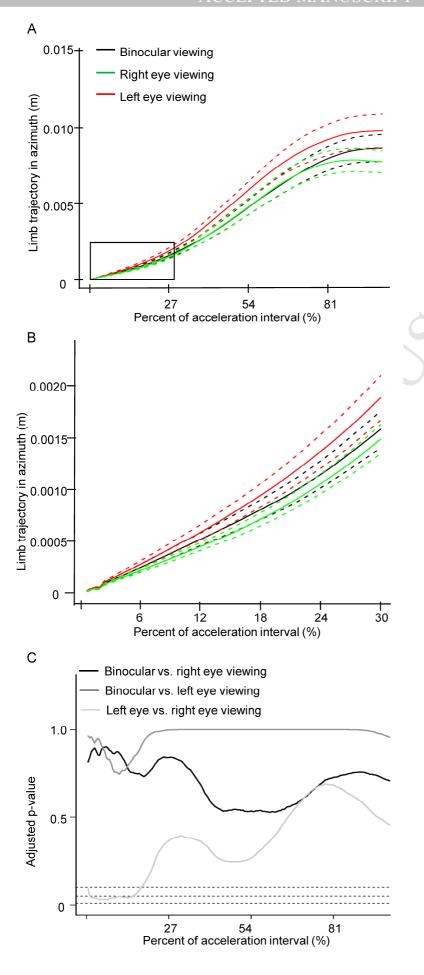












Highlights

- Somatosensory input improves the performance of a high precision placement task during monocular viewing
- Somatosensory input from the contralateral arm specifying target location does not influence arm trajectory when reaching towards a target