RESEARCH ARTICLE

Temporal integration limits of stereovision in reaching and grasping

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Abstract Even though there have been extensive investigations of the temporal integration limits of binocular vision in perceptual tasks, relatively little is known about temporal integration limits during the completion of visuomotor tasks. To assess the temporal integration limits of binocular disparity within the action domain, accuracy of reach kinematics in a reaching and grasping task under continuous binocular and monocular viewing conditions were compared with those obtained under alternating monocular viewing conditions with interocular delays ranging from 14 to 58 ms. Even the shortest of the interocular delays resulted in larger grip apertures than those in the continuous monocular and binocular viewing conditions. The short temporal integration interval of stereovision obtained in this study cannot be accounted for by differential visual feedback in the binocular and interocular delay conditions, nor is it likely to be a consequence of visual disruption due to the interocular delays. Our findings suggest that the visuomotor system has little tolerance to interocular delay.

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Temporal integration limits of stereovision in reaching and grasping

It has been suggested that the visual system performs two distinct but equally crucial tasks: vision for perception and vision for the control of action. Goodale and Milner (1992) have proposed that these two 'streams' of vision map onto separate cortical pathways (also see Goodale et al. 1991; Goodale and Milner, 2004; Faillenot et al. 1997; Milner and Goodale 1995; Parker 2007; Ungerleider and Mishkin 1982): a ventral ("perception") stream, which sends its projections from the primary visual cortex to the temporal lobe, and a dorsal ("action") stream, which sends its projections from the primary visual cortex to the posterior parietal cortex. Both streams clearly employ information about an object's size and location. However, each stream uses this information in different ways and may perform different computations to determine these object properties (see Goodale and Westwood 2004; Parker 2007 for reviews).

Accurate perceptual judgments require an allocentric frame of reference (independent of the viewer), so that object properties, such as size, can be recognized regardless of the observer's perspective. These types of properties play a critical role in learning and identification by producing durable representations of the world. Given that object properties calculated from an allocentric frame of reference rarely change, the perceptual stream may not require updated representations of targets. Consistent with this idea, the perceptual stream has been shown to temporally integrate information across a relatively long period of time (Coltheart 1980) and the integration of information

between the two eyes necessary for binocular depth perception occurs for periods of 45–100 ms (Cogan et al. 1993; Efron 1957; Engel 1970; Julesz and White 1969; Ludwig et al. 2007; Ogle 1963; Wist and Gogel 1966; although see Gheorghui and Erkelens 2005).

In contrast, guiding one's arm towards an object during a reach requires that calculations of object characteristics, such as distance, shape and size, be completed from an egocentric (viewer-centered) perspective. While our previous experience with an object may predispose us to act upon it in a certain way (Desanghere and Marotta 2008; Goodale and Haffenden 2003; Hartung et al. 2005; Haffenden and Goodale 2000), these computations are largely carried out each time a reach is made towards the object of interest (Westwood and Goodale 2003). Since the egocentric frame of reference changes from one moment to the next, representations underlying depth computations are not likely to be enduring and the temporal integration of information about objects and between the two eyes might be expected to be absent or very limited in duration. Although many studies have examined the temporal integration limits of binocular depth perception, we are only aware of one study that assessed temporal integration of information between the two eyes in a visuomotor task (Bennett et al. 2006). In this study, in which participants had to catch a ball under binocular, continuous, or alternating monocular viewing conditions, no evidence of temporal integration of information between the two eyes was obtained. This suggests that the temporal integration limit was less than 20 ms. However, binocular disparity information may not influence performance in such interceptive tasks (Bennett et al. 2006; Servos and Goodale 1998; but see DeLucia 2005). Moreover, the impairments associated with alternating monocular viewing in this task were also obtained relative to continuous monocular viewing suggesting that it may be the introduction of no-vision periods that accounts for their finding. For both of these reasons, it is not clear whether the estimates obtained reflect the temporal integration limits of stereovision in a visuomotor task (see Bennett et al. 2006 and the "Discussion" for further information on this possibility). The aim of our study was to assess the temporal integration of stereovision in a reaching and grasping task.

Experiment 1

We sought to characterize the temporal integration limits of binocular vision in a visually guided task in which binocular vision has clearly been shown to have an effect on performance. The role of binocular vision on the visuomotor system is clearly evident in the differences seen in movement kinematics produced under monocular and binocular viewing (Knill 2005; Marotta and Goodale 1998; Marotta et al. 1997; Watt et al. 2007). For example, maximum grip

aperture and maximum lift of the foot have been shown to be smaller under binocular than monocular viewing (Bennett et al. 2003b; Chajka et al. 2007; Loftus et al. 2004; Marotta et al. 1997; Melmoth and Grant 2006; Patla et al. 2002; Watt and Bradshaw 2000, 2003: although see Jackson et al. 1997; Servos et al. 1992; Servos 2000) and movement velocity has been shown to be higher under binocular than monocular viewing (Chajka et al. 2007; Melmoth and Grant 2006; Servos et al. 1992; Servos and Goodale 1994; but see Watt and Bradshaw 2000).

To investigate the temporal integration of binocular disparity information in a reaching and grasping task, we have adopted a method commonly employed in previous perceptual studies of temporal integration of visual information: assessment of the influence of delays between the input to the two eyes. Ogle (1963) proposed that if an image is presented to the second eye before the information in the first eye dissipates, stereovision will be achieved. Therefore, the longest interocular delay for which binocular vision is evidenced is taken to be a measure of the interval over which information from the two eyes is integrated. In our study, we assessed the influence of interocular delays ranging from 14 to 58 ms on participants' reaching and grasping movements.

Methods

Participants

Forty-four right-handed subjects (29 female, 15 males; age range 18–31 years old; mean age = 20.6 years) with normal or corrected-to-normal vision were recruited from the University of Manitoba Undergraduate Subject Pool. Participants were given partial course credit for their time and provided written informed consent. All participants were strongly right-hand dominant, as determined by a modified Edinburgh Handedness Inventory (Oldfield 1971), and had normal stereoscopic vision (40' of arc or better), as determined by the RANDOT stereogram acuity test (Stereo Optical, Chicago).

Apparatus

Reaching and grasping data were recorded at a sample rate of 200 Hz using the OPTOTRAK Certus 3d motion tracking system to monitor the position of infrared light emitting diodes (IREDs) affixed to participants in the following configuration: 2 placed on the index finger of the right hand near the base of the left side of the cuticle, 2 placed on the right thumb near the base of the right side of the cuticle, and 2 placed on the left side of the wrist, directly in front of the top of the ulna bone. Data were filtered using a 7 Hz second order Butterworth filter.

Three blocks of varying sizes were used as targets. The width and length of the blocks were 53 × 44, 63 × 39, and 73 × 33 mm. Participants were asked to grasp these blocks from front to back. The approximate retinal disparities of these blocks, at a distance of 35 cm were 9.1, 8.1, and 6.8 arcmin, respectively. However, there would have been intra-participant variation in the actual amount of binocular disparity produced by the blocks.

Procedure

Reaching and grasping kinematics were assessed in separate blocks of trials for each of the five viewing conditions: continuous monocular, continuous binocular, and three interocular delay conditions. In all interocular delay conditions, stimulus-viewing times and stimulus presentation were as follows: approximately 50 ms presentation to one eye followed by an interocular delay during which both lenses of the goggles were closed and then approximately 50 ms presentation to the other eye. Participants viewed the blocks through liquid crystal shutter glasses (PLATO, Translucent Technologies, Toronto; transmittance of the open glass: 90%; effective response time is 1 ms to open and 3–5 ms to close; see Milgram 1987). Given the effective response times of the goggles, the durations of the 3 interocular delays in this experiment were 14 ± 1, 30 ± 1 and 58 ± 1 ms.

During this closed-loop task, participants began each trial with both goggle lenses closed and hence could not see the form or location of the block. They were instructed to rest their thumb and index finger on a start button at the midline and to reach for the block quickly but naturally, using their index finger and thumb to grasp the object (from front to back), when each trial began. Participants were further instructed to bring the block about half way back to the start button, put the block down, and return their hand to the start button. On each trial, participants reached for one of three blocks placed on a matte black table at one of three distances (25, 35 or 45 cm from the start button). For each of the viewing conditions, participants completed five practice trials, after which they completed 42 trials. The 42 trials consisted of 12 distractor reaches (6 at a distance of 25 cm and 6 at a distance of 45 cm) and 10 reaches to the target distance of 35 cm for each of the three blocks. Reaching and grasping data were recorded via the OPTOTRAK for 5 s on each trial. The average duration of a reach was 1.02 s (SD = 0.37 s).

Results

Kinematic data were derived from reaches made to a 35 cm distance with the other reaches serving as distractors to prevent trial-to-trial predictability. The influence of viewing condition on maximum limb velocity and maximum grip aperture was assessed using a repeated measures MANOVA and the Tukey correction model was used for multiple pairwise comparisons.

Maximum velocity of the reach was computed using the time and distance data from the wrist IREDs (Jeannerod 1981, 1984). Since block size did not significantly influence the pattern of results obtained across the viewing conditions, the data were collapsed across block size. Velocity was not significantly influenced by viewing condition $F(4,40) = 2.29$, $P = 0.076$, and there was no difference between continuous binocular viewing and continuous monocular viewing, $t(43) = -0.98$, $P = 0.33$, or between continuous binocular viewing and any of the interocular delay conditions, $t(43) < 2.4$, $P > 0.02$ (see Fig. 1).

Maximum grip aperture was calculated using the location difference between paired IREDs on the thumb and index finger (Jeannerod 1981, 1984). As was the case for maximum velocity, block size did not significantly influence the pattern of results obtained across the viewing conditions and the data were collapsed across block size. Average grip aperture was found to be significantly affected by viewing condition, $F(4,40) = 7.73$, $P = 0.0001$. As shown in Fig. 2, grip apertures in the binocular viewing condition were smaller than those in all other conditions, $t(43) > 3.16$, $P < 0.005$. The 58 ms interocular delay also produced larger grip apertures than the monocular viewing condition, $t(43) = 2.96$, $P = 0.001$.

Discussion

Although there was a non-significant trend towards decreased peak velocity with increasing interocular delay, it
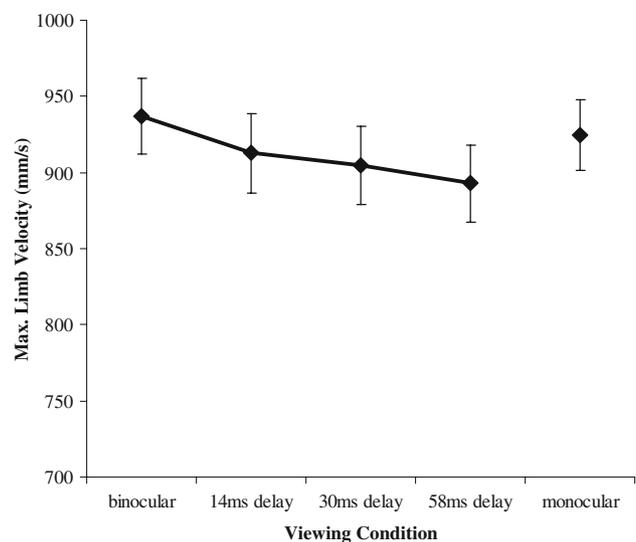
Fig. 1 Maximum limb velocities are shown as a function of viewing condition (*error bars* represent SEM)
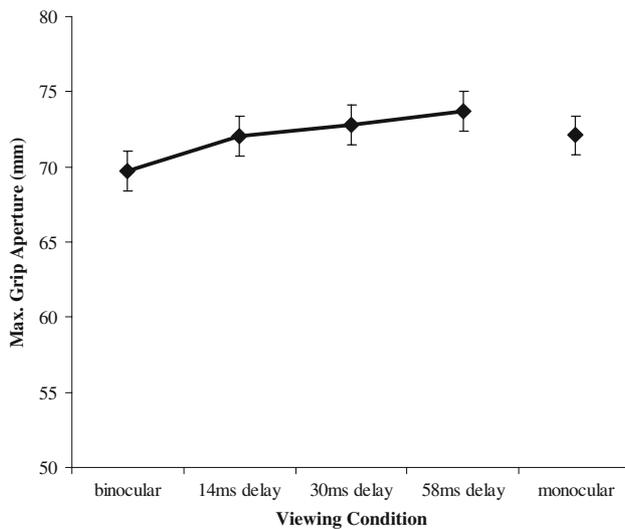
Fig. 2 Maximum grip apertures in each of the viewing conditions are illustrated (*error bars* represent SEM)

is important to note that maximum velocity under continuous monocular and binocular viewing conditions were not significantly different. Hence, any differences as a function of interocular delay were relative to both binocular and monocular vision. Therefore, the trend evident in the peak velocity data may suggest that an introduction of a period of no vision during the reach increases uncertainty and has a tendency to slow peak velocity.

The absence of differential peak velocity under monocular and binocular viewing is consistent with research that reports that kinematics of the reach such as peak velocity, which rely on accurate distance estimations, may be influenced more by vergence and/or monocular cues to depth than by binocular disparity (Hillis et al. 2004; Melmoth and Grant 2006; Melmoth et al. 2007; Mon-Williams et al. 2001; Tresilian et al. 1999; Watt and Bradshaw 2000, 2003). Vergence has been shown to supply veridical information about an object's location (Mon-Williams et al. 2001). Thus, the results may be an indication that vergence was tolerant to even the longest interocular delays used in our study. However, it has been reported that when multiple cues to depth are available, distance is estimated based on a computation which weights vergence and other depth cues based on their reliability (Knill and Saunders 2003; Knill 2005, 2007; Marotta et al. 1997; Tresilian et al. 1999). Therefore, the present finding that neither continuous monocular nor alternating monocular presentation affected peak reach velocity, suggests that regardless of the cue(s) used (vergence or monocular), information sufficient for the programming of reaching was available across all our viewing conditions (Marotta et al. 1997). Future research in artificial environments in which cues to depth can be independently manipulated are necessary to determine the relative weight-

ing of these distance cues in the programming of reach kinematics under alternating monocular presentations with varying interocular delays.

In contrast to peak velocity, maximum grip aperture was affected by viewing condition: grip apertures were smaller under continuous binocular viewing than in any of the other viewing conditions, including continuous monocular viewing. This is consistent with the results of previous studies that have reported smaller grip apertures for reaching tasks performed under binocular viewing conditions than those performed under monocular viewing conditions (Melmoth and Grant 2006; Melmoth et al. 2007; Watt and Bradshaw 2000, 2003). Our results indicate that an interocular delay as short as 14 ms was sufficient to affect visuomotor performance, suggesting that the temporal integration limits for binocular disparity in reaching and grasping tasks may be very short. It is interesting to note that, despite the differences in task requirements for an interceptive ball catching task and reaching for a static object (Bennett et al. 2006; Servos and Goodale 1998), the present estimate of the temporal integration limit of stereovision in reaching and grasping is very similar to that reported in a ball catching task (Bennett et al. 2006).

Experiment 2

Although our current results suggest that the visuomotor system may not tolerate even small interocular delays, it is also possible that this intolerance was due to visual feedback about the position of the hand relative to the target throughout the reach. The change in the position of the hand relative to the stimulus over the course of the reach also means that successive monocular views differ. It may be the case that when the input to the two eyes differs by a sufficient amount temporal integration simply does not occur. Such a possibility is contraindicated by the finding that neurons in the dorsal stream sensitive to binocular disparity respond even then the monocular inputs are opposite in polarity (see Parker 2007). If the monocular views are being temporally integrated, it is unclear what information the integrated representation would be providing given the differences between the monocular inputs and what influence it may have on reaching and grasping. If these temporally separated monocular images are being integrated over time, then changes in maximum grip aperture and reach velocity observed would reflect inaccurately integrated binocular information rather than the absence of any binocular integration over interocular delays. To explore whether the results in "Experiment 1" were a consequence of view of the hand relative to the object, we measured the influence of interocular delay on reaching and grasping when a visual occluder prevented participants from seeing their hand for the majority of the reach.

Methods

Participants

Forty participants (30 female, 10 male; age range 19–46, mean age = 29.4 years) were recruited from the University of Manitoba Undergraduate Subject Pool. Inclusion criteria and remuneration were identical to that described for "Experiment 1".

Procedure

All participants completed the task under conditions identical to those described in "Experiment 1", with the following exceptions: a chin rest was added to maintain viewing position and distance; and all 12 distractor reaches were made to a distance of 45 cm.[1] Half of the participants completed their reaches under closed-loop conditions identical to those described for "Experiment 1", whereas the remaining half completed their reaches under open-loop conditions in which participants were restricted from seeing their hand until it was within a few centimeters of the nearest object via an occluder (i.e. they were unable to see their hand until at least 80% of the reach was completed). Although it has been suggested that information is integrated continuously over the course of the movement (Churchill et al. 2000; Servos and Goodale 1994; Saunders and Knill 2003, 2004, 2005), both maximum grip aperture and velocity occur prior to completion of 70% of the reach (Jakobson and Goodale 1991; Jeannerod 1984). Therefore, the occluder should have reduced the influence of being able to see the hand throughout the reach on maximum grip aperture and velocity (although see "Discussion").

Results

No differences were found between the occluded and non-occluded groups for either limb velocity, $F(1,38) = 0.38$, $P = 0.54$, or grip apertures, $F(1,38) = 2.25$, $P = 0.14$. Given this, the data for all participants were analyzed within a single MANOVA in which open/closed loop was not included as an independent variable. The Tukey correction method was used for error rate control in the pairwise comparisons.

The results replicate those obtained in "Experiment 1". Maximum velocity was not significantly influenced by viewing condition, $F(4,39) = 2.52$, $P = 0.06$ (see Fig. 3). Nor was maximum limb velocity under binocular viewing significantly different from that under monocular viewing, $t(39) = 0.1$, $P = 0.926$. In contrast, maximum grip aperture
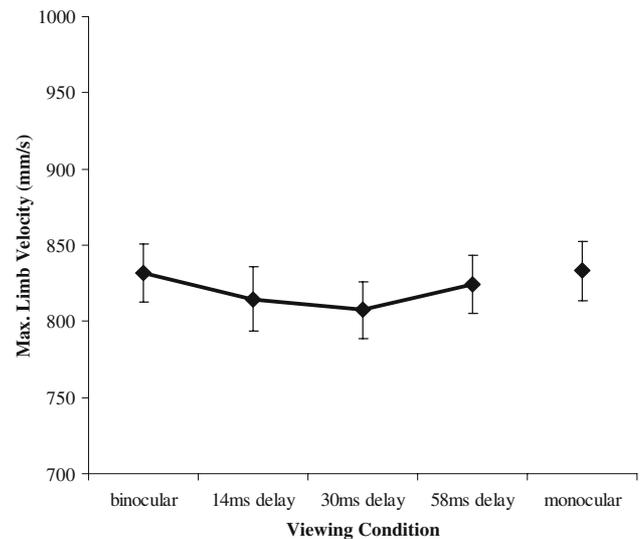
Fig. 3 Maximum limb velocities in each of the viewing conditions are shown. Results shown are the average of the open and closed loop conditions (*error bars* represent SEM)
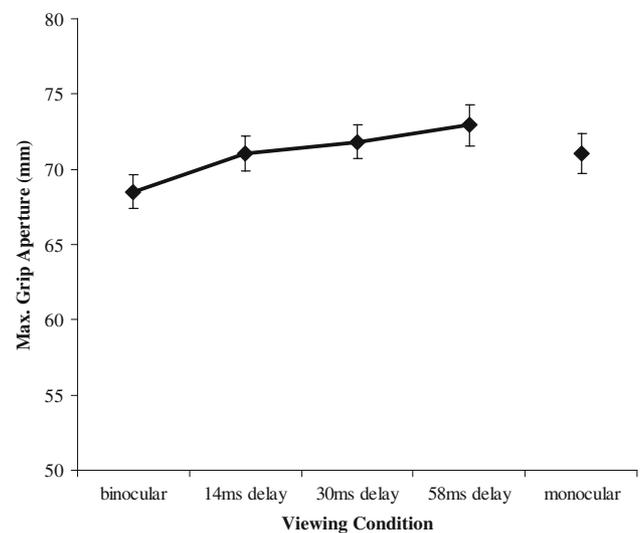
Fig. 4 Maximum grip apertures are shown as a function of viewing condition (*error bars* represent SEM)

was found to be significantly affected by viewing condition, $F(4,39) = 13.5$, $P < .0001$. As shown in Fig. 4, grip apertures in the binocular viewing condition were smaller than those in all other conditions, $t(39) > 3.16$, $P < 0.005$. The 58 ms interocular delay produced larger grip apertures than the both the monocular viewing condition, $t(39) = 2.81$, $P = 0.008$, and the 30 ms interocular delay, $t(39) = 6$, $P = 0.0000001$.

Discussion

As in "Experiment 1", interocular delays of 14 ms influenced grip aperture, but not maximum velocity of reach.

The addition of a chin rest which prevented the use of retinal motion as a cue to depth did not significantly alter the tolerance to interocular delay in reaching and grasping. Therefore, participants in the first study appear not to have been using head movements to improve distance perception when binocular cues were unavailable (cf. Marotta et al. 1997).

The main purpose of Experiment 2 was to explore whether having a view of the hand throughout the reach could account for the intolerance of the visuomotor system to interocular delays observed in "Experiment 1". That limiting participants' view of the hand did not influence reach kinematics is consistent with previous results from Connolly and Goodale (1999). Under continuous binocular viewing, maximum limb velocity and maximum grip aperture were not affected by being able to see the hand in relation to the target. Similarly, Knill (2005) reported that reaching was not significantly altered by whether the object being manipulated was visible or not during the task. Moreover, Knill has previously argued that when the object appears "in view during the last 240–340 ms of the movement, (so) there was little time, given delays in the sensorimotor loop, for special-purpose visual feedback control processes to affect the outcome of the movement." (pg. 110, Knill 2005). These results are consistent with the idea that reach kinematics, including both peak velocity and grip aperture, are largely programmed before the reach begins (see review by Jeannerod 1988; but also see Churchill et al. 2000; Jackson et al. 1997; Jakobson and Goodale 1991). If this is the case, critical information about both object distance and size are derived prior to changes in limb position and the putative visual input critical for these calculations is static.

We attempted to reduce feedback regarding the position of the hand relative to the target prior to the point in the reach when maximum grip aperture and maximum velocity occurs while still maintaining a view of the object. Thus, our second experiment was completed under conditions where the view of the hand was occluded for the majority of the reach (i.e. at least 80%), but not a completely open loop. It should be noted, however, that some studies have reported that binocular vision may contribute to online corrections as the hand makes its final approach to the object (Greenwald et al. 2005; Melmoth and Grant 2006). Given that the occluder was employed on all trials for a given participant, it could be argued that the views of the hand relative to the target during the final part of the reach may have provided information that could have influenced maximum reach velocity and grip aperture on subsequent trials within the block. That being said, given that reaches to different distances and different block sizes were random in order, it seems unlikely that information from previous trials would have been used to program reaches on subsequent trials.

However, future studies in artificial viewing environments in which the view of the hand and the object can be independently manipulated are required for a more definitive conclusion on the role of the view of the hand on temporal integration limits of stereovision in reaching and grasping.

Discussion

We found that reaching and grasping is generally intolerant to interocular delay. Relative to performance with continuous binocular vision, an interocular delay as small as 14 ms significantly affected grip apertures. Were the larger grip apertures observed under interocular delay conditions a consequence of the introduction of a no-vision period and the increased uncertainty that would accompany a period of no vision? Evidence of the effects of a no-vision period on visuomotor performance has been obtained in a few studies. Jakobson and Goodale (1991) found that long no-vision intervals (447 ms) produced larger grip apertures in a reaching and grasping task. Similarly, Bennett et al. (2003b) found that no-vision intervals of 60 and 120 ms impaired reach kinematics relative to continuous monocular performance and studies of ball catching have revealed that no-vision intervals as short as 20 ms impaired ball catching relative to continuous monocular performance (Bennett et al. 2003a, 2006; Olivier et al. 1998). Examination of our results reveals that, with 14 and 30 ms interocular delays, grip apertures were not different than those obtained under continuous monocular viewing. Thus, the observed increases in grip aperture in the 14 and 30 ms delay conditions relative to continuous binocular viewing are not adequately explained by the introduction of no-vision intervals. Finally, a pilot investigation in which the alteration rate between the eyes was manipulated, with no interocular delay, showed the same pattern of results as our current investigation, further refuting the notion that a no-vision interval can wholly account for the current findings.

The results of our study clearly indicate that interocular delays as short as 14 ms significantly influence reaching and grasping kinematics. Using a similar methodology to that employed in this study, the perception of depth has been shown to be tolerant to interocular delays as long as 45–100 ms (Cogan et al. 1993; Coltheart 1980; Efron 1957; Engel 1970; Julesz 1960; Ludwig et al. 2007; Ogle 1963; Wist and Gogel 1966; although see Gheorghiu and Erklens 2005a, b). What these results imply about the temporal integration limits of stereovision within the dorsal pathway requires further study. There are several hypotheses that might adequately explain the discrepancy in the estimates obtained in perceptual and visuomotor studies. First, the differential estimates of temporal integration limits of binocular vision may be a direct consequence of differences in

the dependent variables (i.e. perception of depth versus grip aperture). Second, it is possible, although unlikely (see "Experiment 2"), that the results of the present study are a consequence of temporal integration across changing monocular views rather than a consequence of limited temporal integration in reaching and grasping. Finally, it may be the case that these differential estimates reflect the unique requirements of the ventral and dorsal streams (Goodale and Milner 1992, 2004; Goodale et al. 1991; Faillenot et al. 1997; Milner and Goodale 1995; Parker 2007; Ungerleider and Mishkin 1982). Whereas the dorsal stream requires flexible and transient representations of the world to allow for online corrections, the ventral stream does not. Thus, it may be that the two streams have differential limits on temporal integration of stereovision. Consistent with differential computations and underlying mechanisms of stereovision, physiological responses neurons responsive to binocular disparity within dorsal and ventral stream mechanisms have been shown to differ (for a review see Parker 2007). An alternative interpretation is suggested by the work of Gheorghui and Erkelens (2005), who report that tolerance to interocular delays within the perceptual system may reflect a two stage process that involves the "monocular temporal integration of luminance followed by a cross-correlation-like operation between simultaneous monocular inputs that have each been subjected to the temporal integration of luminance" (p. 1218). When the contribution of monocular temporal integration of luminance is minimized estimates of temporal integration within the stereoscopic mechanism are similar to those obtained in the present study. Thus, the temporal integration limits of stereovision may be the same in the dorsal and ventral pathways and differential estimates of temporal integration limits in stereovision may arise from longer temporal integration of luminance within the ventral pathway. The suggestion that dorsal stream neurons sensitive to binocular disparity may not receive input from an earlier mechanism that temporally integrates luminance information across the eyes is supported by the finding that, unlike neurons in the ventral stream, neurons in the dorsal stream respond to polarity reversed binocular stimuli (see Parker 2007). Further research is necessary to determine which of these intriguing possibilities best describes the temporal integration of stereovision in the dorsal pathway.

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