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RESEARCH ARTICLE

The influence of the Sander parallelogram illusion and early, middle and late vision on goal-directed reaching and grasping

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Abstract

Vision is one of the most robust sensory inputs used for the execution of goal-directed actions. Despite a history of extensive visuomotor research, how individuals process visual context for the execution of movements continues to be debated. This experiment examines how early, middle and late visuomotor control is impacted by illusory characteristics in a reaching and grasping task. Participants either manually estimated or reached out and picked up a three-dimensional target bar resting on a two-dimensional picture of the Sander parallelogram illusion. Participants performed their grasps within a predefined time movement window based on their own average grasp time, allowing for the manipulation of visual feedback. On some trials, vision was only available before the response cue (an auditory tone), while on others vision was occluded until the response cue, becoming available for either the full, early, middle or late portions of the movement. While results showed that the effect of the illusion was stronger on manual estimations than on grasping, maximum grip apertures in the occluded vision and early vision grasping conditions were also consistent to a lesser extent with the illusion. The late vision condition showed longer movement time, wrist deceleration period, time to maximum grip aperture and lower maximum velocity. These findings indicate that visual context affects visuomotor control distinctly depending on when vision is available, and supports the notion that human vision is comprised of two functionally and anatomically distinct systems.

Keywords Visual illusion · Sander parallelogram · Visuomotor control · Action · Perception

Introduction

Over the last couple of decades, there has been considerable controversy regarding how the visual system uses incoming visual information to complete various perceptual and motor tasks. Arguably, the most influential position has been Milner and Goodale's two-visual-systems hypothesis (TVSH), which suggests a dissociation between 'vision-for-action' and 'vision-for-perception' (Goodale and Milner 1992; Milner and Goodale 1995). The basis of the TVSH is that perceptual judgments are associated with a ventral visual pathway that travels from the primary visual cortex to the inferior temporal region of the brain, while goal-directed action movements rely on a dorsal visual pathway originating in the primary visual cortex and extending to the superior parietal area of the brain. Although much of the support for the TVSH comes from animal studies and clinical studies of humans with brain deficits (Milner and Goodale 1995), studies using visual illusions such as the Ebbinghaus and Müller-Lyer illusions have also been used to investigate this dissociation in intact humans.

Since the seminal work of Aglioti et al. (1995), in which they showed that grip apertures were relatively immune to the effects of the Ebbinghaus illusion, some of the most informative and controversial evidence for the TVSH has come to light from studies involving visual illusions. Studies supporting the TVSH have shown that perceptual judgments are affected by the visual context associated with the illusory configurations, while goal-directed action movements tend to be immune to these perceptual biases. Typically, a grasping or aiming movement toward a target presented in

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the context of a visual illusion where full vision is available throughout the entirety of the movement will show that grasping and aiming movements are unaffected or less affected by the illusion compared to perceptual judgments about the same stimuli (e.g., Bridgeman et al. 1981; Mack et al. 1985; Aglioti et al. 1995; Brenner and Smeets 1996; Daprati and Gentilucci 1997; Gentilucci et al. 1996; Haffenden and Goodale 1998). This notion that the ventral stream is affected by illusory visual context while the dorsal stream remains immune is thought to rely on the way each of the streams code visual–spatial information. Specifically, the ventral stream is involved with the allocentric coding of space, incorporating visual information about the target's relationship to its surroundings, while the dorsal stream is involved with the egocentric coding of space, relying on a body-based frame of reference (Haffenden and Goodale 1998).

However, other studies have shown that actions are not immune to illusory context. When vision is withdrawn before movement onset, the outcome reflects the perceptual bias of the illusion, showing shorter aiming movements in pointing studies (Elliot and Lee 1995) and peak grip apertures consistent with the perceived size of the illusion in reaching and grasping studies (Bruno and Franz 2009; Franz et al. 2009; Westwood and Goodale 2003; Whitwell et al. 2018). These differences in illusory susceptibility suggest that object-directed action operates under two systems of control: an 'offline' (memory-guided) system that depends on ventrally based perceptual mechanisms and an 'online' (real-time) system that does not (Goodale et al. 1994; Milner et al. 2001). As such, perceptual mechanisms have been argued as critical for controlling memory-guided actions because the visuomotor mechanisms underlying the dorsal steam require direct visual input and, as a result, only have a brief memory (Goodale et al. 1994). Visual information processed by the dorsal stream generates a precise and accurate movement program when the target is first viewed, but if the target is subsequently occluded, the program decays quickly. In the case of memory-guided tasks, the motor system relies on the stored representation of the target to generate a new movement program, and this less accurate representation is maintained by the perceptual mechanisms in the ventral stream (Westwood and Goodale 2003). This assumes that the dorsal stream is engaged when the target is identified. However, previous research by Westwood and Goodale (2003) demonstrates that real-time, visuomotor mechanisms are not recruited for the control of action unless the target is visible when the response is cued. When participants were shown a target in the context of a size-contrast illusion and then cued by an auditory tone to grasp the target, they found that peak grip aperture was not affect by the illusion when the target was visible between the response cue and movement onset. But, when the target was occluded once the response was cued, peak grip aperture was more consistent with the illusion, suggesting that dorsal mechanisms are not engaged until an action is required (i.e., at the response cue)—and only if the target is visible at the same time. Since the egocentric position of a target can change quickly and in an unpredictable way, it is more efficient for the dorsal stream to generate a movement plan once an action is required as opposed to when the target is first identified, which would ultimately result in the continuous updating of the plan in response to egocentric position changes. Taken together, these studies suggest that visually guided, object-directed actions are largely unaffected by scene-based perceptual information extracted by the ventral stream, but rather rely heavily on the absolute metrics of the target, which are extracted in real time from the dorsal stream to guide the fingers, hands and limbs.

Contradictory evidence for the dissociation between 'vision-for-perception' and 'vision-for-action' stems from the notion that comparisons of grasping and perceptual judgments are confounded by differences in attention, sensory feedback, obstacle avoidance, metric sensitivity and priming. However, a recent study by Whitwell et al. (2018) addressed and eliminated each of these issues using the Sander parallelogram illusion. Participants either reached out to grasp three-dimensional target bars placed on a two-dimensional picture of the Sander parallelogram illusion or made explicit estimates of the length of the target bars. Grasps were performed without visual feedback, and participants were allowed to grasp the targets after making their size estimates in order to reduce illusory error with haptic feedback. Consistent with previous research, the Sander parallelogram illusion influenced both perception and grasps performed without visual feedback. More importantly, their results showed that illusion effects were more robust for perceptual judgments than grasps, supporting the notion that human vision is comprised of functionally and anatomically dissociable systems.

While it has been well established that there is a clear dissociation between 'vision-for-action' and 'vision-for-perception,' recent studies have proposed that there are multiple processes involved in visual online control. Specifically, Elliott et al. (2010) proposed that there are two processes involved in visual online regulation: a process early in the movement concerned with comparisons between actual and expected sensory consequences, and another process late in the movement involved in providing information about the relative positions of the limb and target. Although this notion is supported by previous studies (Grierson and Elliott 2009; Kennedy et al. 2015; Roberts et al. 2013), they are limited to pointing and aiming tasks to examine the overall functioning of these underlying visuomotor processes and as such it is unclear how online control may differ when the outcome diverges from pointing to, for example, grasping the target. Regardless, this divergence from a dichotomous set of visual coding processes emphasizes an emerging issue in the study of perception and visuomotor control related to the time course in which the visuomotor system is affected by perceptual information.

To better understand how online visual processes are influenced by visual context, this study builds off of previous research using aiming tasks in the context of the Müller–Lyer illusion by examining the processes involved in online regulation using a reaching and grasping task involving the remarkably powerful Sander parallelogram illusion. Similar to previous studies involving aiming tasks (Elliott et al. 2010; Grierson and Elliott 2009; Kennedy et al. 2015; Roberts et al. 2013), we manipulated the presence and absence of visual feedback over the entire movement as well as occluded vision during various points along the movement trajectory. While previous studies have focused on the early and late portions of the movement trajectory (Elliott et al. 2010; Grierson and Elliott 2009; Roberts et al. 2013) as well as limb velocity to designate time course windows (Kennedy et al. 2015), here we isolated early, middle and late portions of the movement trajectory using predefined time windows based on each participant's own natural movements to gain a better understanding of how online control is influenced by the context in which the target is presented. Since illusion susceptibility relies on allocentric cues from the ventral stream of visual processing, we expected to see more pronounced perceptual biases in the early vision condition compared to conditions in which visual information was only available in the latter parts of the reach or during the full duration of the reach. We also expected that providing vision during the middle or late windows would yield reach characteristics reflective of uncertainty within the reach, specifically, lower maximum velocities and longer reach durations, time to maximum grip aperture and wrist deceleration periods compared to conditions in which vision is available for the full or early parts of the reach. To ensure illusion susceptibility, and to test the extent to which participants were susceptible to the illusion, we also included a perceptual task in which participants were asked to manually estimate the length of the target bar and a grasping condition in which vision was only available until the movement was cued by an auditory tone (occluded vision condition). Consistent with previous research (i.e., Whitwell et al. 2018; Westwood and Goodale 2003), we expected participants to show susceptibility to the illusion in both conditions, albeit to a lesser extent in the occluded vision condition compared to the manual estimation condition, supporting the notion that there is a clear dissociation between 'vision-for-action' and 'vision-for-perception.'

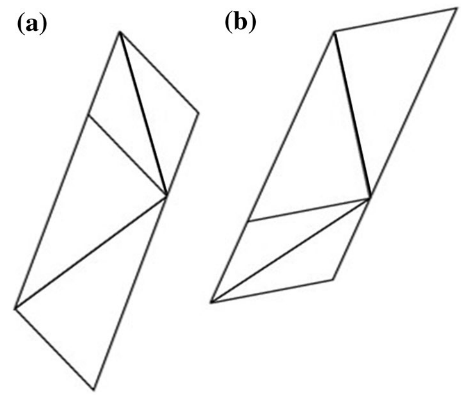

Fig. 1 Sander parallelogram illusion. The bold line in **a** denotes the perceptually shorter of the two diagonal lines, while the bold line in **b** denotes the perceptually longer of the two diagonal lines. Blocks were laid along these bold lines to ensure comfortable grasping and similar placement of the blocks on each trial

Methods

Participants

Thirty-five undergraduate psychology students were recruited for this study and received research credits for their participation. Of these participants, three were excluded from data analysis due to an inability to properly perform the study tasks, two were excluded due to technical difficulties, and five were excluded due to reach durations that exceeded the time window required to perform the reach as determined prior to the experimental trials. In total, twenty-five participants (8 males) between ages 18 and 35 (*M* 22.92, SD 4.84) were included in the study. All participants had normal or corrected-to-normal vision and were right-hand dominant, as determined by a modified version of the Edinburgh Handedness Questionnaire (Oldfield 1971). This experiment was approved by the Psychology/Sociology Research Ethics Board (PSREB) of the University of Manitoba.

Materials/apparatus

The Sander parallelogram illusion was used to examine illusory effects on reaching and grasping when visual information is only available at certain points along the reach trajectory. The illusion underlying the Sander parallelogram is that the diagonal line bisecting the larger parallelogram appears to be considerably longer than the line bisecting the smaller parallelogram, even though both lines are of the same length. Each trial consisted of a single two-dimensional Sander parallelogram, printed in black on a white background. The target was a three-dimensional black rectangular bar made of aluminum that was physically placed on top of the two-dimensional display by the experimenter such that it either bisected the perceived smaller (Fig. 1a) or perceived longer (Fig. 1b) configurations of the illusion. The target bar was 6 cm × 0.3 cm × 0.3 cm, and a single target was placed within one of the parallelograms on each trial. The illusion was rotated so that participants could grasp the block comfortably, and to ensure that participants were reaching and viewing the block at the same angle and distance for each trial.

PLATO goggles (Translucent Technologies, Toronto, ON, Canada) were worn by participants to ensure that they were not able to see the stimuli before the trial began and to vary the amount of vision provided to the participant over the time course of the reach. Six infrared light-emitting diodes (IREDs) were placed on the participant's right hand (2 IREDs on each index finger, thumb and wrist), which were situated in the 'starting position' on the desk in front of them. The three-dimensional positions of the IREDs were recorded using an Optotrak Certus 3D motion tracking system (130 Hz sampling rate, spatial accuracy up to 0.01 mm; Northern digital Inc., Waterloo, Ontario, Canada). MotionMonitor software (Innovative Sports Training Inc., Chicago, IL, USA) was also used to control the time intervals at which the PLATO shutter goggles became transparent or opaque, as well as to generate the auditory tone (350 Hz) that served as a response cue for the participants to perform the grasping or estimation tasks. This software was run on an Inspiron 545 Dell computer (Duo Core 3.16 GHz).

Procedure

All participants performed a manual estimation task and a reaching and grasping task. These tasks were presented in separate blocks of trials and were counterbalanced across participants. After completion of the consent and demographics forms, participants were outfitted with IREDs on their right hand and asked to wear the PLATO goggles for the duration of the experiment. Participants stood in front of a tabletop on which the illusory display and target stimuli were always centered at the same position along the individual's sagittal plane. Participants were asked to rest their index finger and thumb together in a pinched position at a designated starting spot located 10 cm from the edge of the table and 30 cm from the stimulus display.

At the start of each trial, the goggles cleared to permit the participant a full view of the display. Participants were instructed to keep their thumb and index finger pinched together at the start location, and an auditory tone (350 Hz) indicated to participants to begin the estimation or reaching and grasping task. In the manual estimation task, participants were instructed to look at the target bar and adjust their thumb and index finger to match the perceived length of the bar. They were also instructed to keep their hand on the table at the location of the start position to minimize any movement toward the target. Once participants were satisfied with their estimation, they gave a verbal 'ok' to the experimenter, who then ended the trial and the participant resumed the start position. All manual estimation trials were completed with full vision available to the participant for two main reasons. First, we wanted participants to have enough time to be confident and satisfied with their estimates. Second, since manual estimation is driven by the perceptual system, this condition served as a control to ensure that participants were susceptible to the illusion at a perceptual level. As such, we wanted the illusion effect to be as strong as possible, and it has been well established in previous studies that the most robust effects of illusion susceptibility are found when participants are provided with visual feedback for the duration of the estimation (Fabre and Vishton 2003).

In the reaching and grasping task, following the auditory tone, participants were instructed to reach out and pick up the target bar along its length using their right index finger and thumb. Participants were told at the beginning of the block of trials that on some trials vision would be available for the full duration of the reach, while on others the goggles would close during certain portions of the ongoing movement such that vision would only be available for the early, middle or late parts of the reach or not at all. In all, there were five visual conditions: full vision, early vision, middle vision, late vision and occluded vision (Fig. 2). In each condition, except for the occluded vision condition, participants were cued to the beginning of the trial with a short beep from the computer. During this time, the goggles remained opaque, and after approximately 75 ms, an auditory tone cued the participant to begin the reach (the response cue). For the occluded vision trials, visual feedback was available for the 75 ms before the tone in order to ensure participants had some visual context of where to reach their hand, which was particularly important given the size of the small target bar and the precision required to grasp it. Following the auditory tone, vision was either made available for the full duration of the reach (full vision condition), the first 'third' of the reach (early vision condition), the second 'third' of the reach (middle vision condition) or the last 'third' of the reach (late vision condition). For each participant, early, middle and late time windows were determined based on a series of 12 reaching trials performed by each participant prior to the experimental phase. In these trials, participants were asked to reach out and grasp the target bar in the exact same context as the experimental trials, but without the two-dimensional illusory background. Reach duration was then averaged for these 12 trials and divided by 3 to determine early, middle and late time windows based on the participants own natural reach rather than using standardized time windows or limb velocity as has been reported in previous studies (Roberts et al. 2013; Kennedy et al. 2015). Since the manipulation of vision

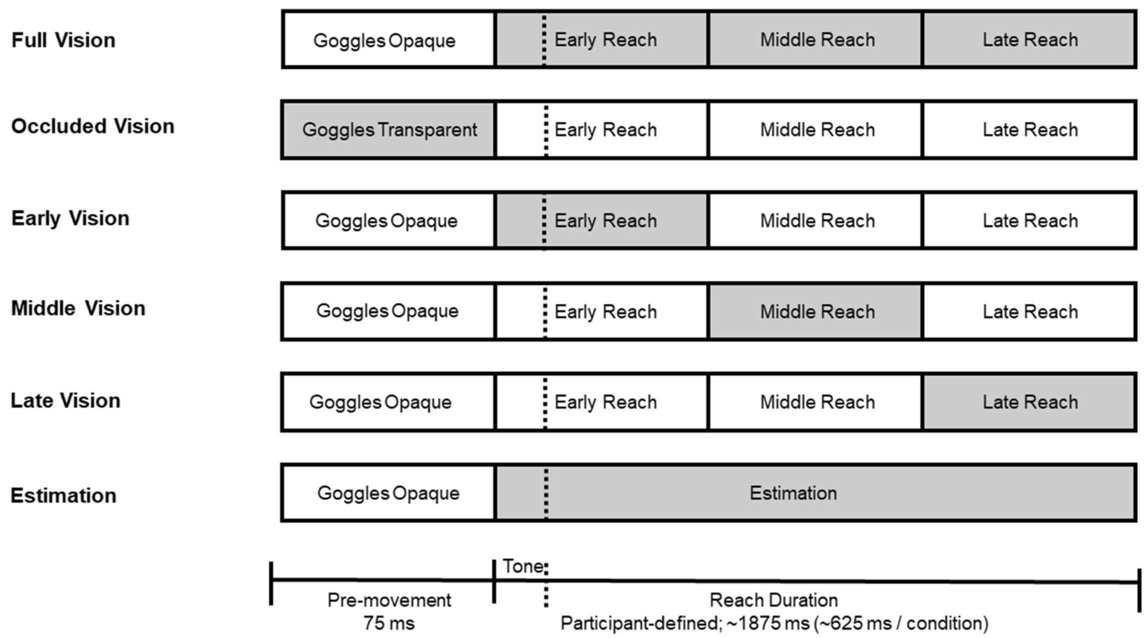

Fig. 2 Procedural timing used in the experiment. The grey color refers to when vision of the target was made available. At the beginning of each trial, the goggles were either opaque (full, early, middle, late and estimation conditions) or transparent (occluded vision condition) for 75 ms. A brief, 350 Hz tone indicated participants to begin the reach, and vision was manipulated such that it was either available for the full duration of the reach, early, middle or late part of the reach, or not available at all. The amount of time vision that was available in each of the early, middle and late conditions was defined for each participant based on a set of 12 reaching trials performed before the experiment itself, and each participants' average reach time was divided by 3 to determine the amount of time the goggles would be transparent in each condition. In order to ensure participants were able to make contact with the target in late trials, visual feedback was available until wrist movement was slowed to 5 cm/s, even if it meant vision was available for longer in the late condition. On average, the reach duration was 1875 ms, with approximately 625 ms allotted to each of the early, middle and late conditions

was based on each individual's average reach time, it was important to only include participants who were close to achieving their average movement time criterion. To this end, we removed participants ($N=5$) failing to reach a mean movement time within 120 ms of their average movement time, a boundary that was based on the visual feedback processing time window (see Carlton 1992 for a review). On average, vision was provided for 1875 ms in the full vision condition, and 625 ms for each of the early, middle and late vision conditions.

In total, each participant performed 84 trials. Before the experimental trials, participants completed the 12 trials used to determine the early, middle and late time windows. Participants then completed the experimental trials. The experimental block for grasping consisted of five exposure conditions (occluded vision, early, middle, late vision and full vision) and two background conditions presented in two dimensions (looks smaller and looks larger) for a total of 10 conditions. Each condition was repeated six times, for a total of 60 trials of reaching and grasping. The experimental block for perceptual estimation was completed with full vision, and the same two background conditions for a total of two conditions. Each condition was repeated six times, for a total of 12 trials of manual estimation.

Data analysis

The primary dependent measure for the manual estimation trials was the final grip aperture (FGA). As per the experimenter's instructions, the final grip aperture represented the participant's perceptual estimation of the target block as measured by the distance between the IREDs on the thumb and index finger at the final frame of the trial. The primary dependent measure for the reaching and grasping task was the maximum grip aperture (MGA). This measure was extracted using a velocity-based search window, where only frames during which the hand was moving toward the target were included in the analysis. Reaching movement onset and offset were defined as the first frame that the wrist IRED exceeded 5 cm/s or fell below 5 cm/s. The MGA was defined as the maximum vector distance between the IREDs on the thumb and index fingers within this search window. Other variables analyzed to characterize the reach included time to MGA, movement time (MT), wrist deceleration period (WDP) and maximum velocity (MV). Time to MGA was defined as the duration of time from movement onset until MGA. MT was defined as the time from movement onset until movement offset (i.e., the velocity-based search window). MV was defined as the frame at which velocity peaked during the velocity-based search window and served as an indicator of the effect of the illusion on pre-movement planning, and WDP was defined as the duration of time from MV until movement offset, allowing for inferences to be made regarding uncertainties in the grasping movement.

Condition means were computed for each participant and for each of the dependent measures. Using the FGA means from the manual estimation trials and the MGA means from the grasping trials, the unadjusted effect of the illusion was also calculated for each participant by subtracting their mean measure from the responses directed at the illusory 'short' conditions from their mean measure from responses directed at the illusory 'long' conditions. Thus, positive values are consistent with the direction of the illusion. The unadjusted effect of the illusion was tested using one-sample t tests against zero to determine which conditions participants were actually susceptible to the illusion as well as paired-sample t tests to determine whether conditions differed from each other. A grip aperture analysis was also conducted using a repeated-measures ANOVA with Condition (Estimation (Est), Grasp—full vision (GFV), Grasp—occluded vision (GOV), Grasp—early vision (GEV), Grasp—middle vision (GMV), Grasp—late vision(GLV)) and Illusion (perceived 'long,' perceived 'short') as the factors to further dissociate the differences between conditions found in the one-sample t tests. The remainder of the variables representing the reach kinematics (time to MGA, MT, RT, MV, WDP) were analyzed using separate two (Illusion: perceived 'long,' perceived 'short') × 5 (Condition: Est, GFV, GOV, GEV, GMV, GLV) repeated-measure ANOVAs. All analyses were carried out using alpha = 0.05, and post hoc analyses were performed using Bonferroni correction.

Table 1 Unadjusted effects of the illusion (in cm)

Task	*N*	Mean	SEM	Tests against zero
Manual estimation	25	0.6252	0.107	$t^* = 5.867$, $p < 0.001$
Early vision	25	0.2912	0.076	$t^* = 3.812$, $p = 0.001$
Middle vision	25	0.1183	0.092	$t = 1.293$, $p = 0.208$
Late vision	25	− 0.0377	0.078	$t = -0.481$, $p = 0.635$
Full vision	25	0.0343	0.0699	$t = 0.490$, $p = 0.629$
Occluded vision	21	0.2759	0.1	$t^* = 2.759$, $p = 0.012$

As the table shows, the mean slopes for manual estimation, occluded vision and early vision conditions differed significantly from zero. The asterisk (*) denotes the significant tests using the Holm (1979) multiple comparisons procedure

Results

Grip aperture analysis

The Sander parallelogram illusion showed a significant influence on manual estimations, as well as grasps, when no visual feedback was available during reaching or visual feedback was allowed only for the early part of the reach (Table 1). A significant main effect of Condition, $F(5, 100) = 10.87$, $p < 0.001$, $\eta_p^2 = 0.352$, showed that manual estimations resulted in significantly smaller final grip apertures (6.4 cm) than the maximum grip apertures produced in conditions where participants had occluded vision (7.6 cm, $p = 0.009$), or early vision (7.4 cm, $p = 0.037$), of the block. Significantly larger peak apertures were found in the occluded vision condition than the middle (7.2 cm, $p = 0.012$), late (7.2 cm, $p = 0.003$) or full (7 cm, $p < 0.001$) vision conditions. The full vision condition also resulted in smaller peak apertures than early ($p < 0.001$) or middle ($p = 0.012$) conditions. A significant main effect of Illusion, $F(1, 20) = 23.656$, $p < 0.001$, $\eta_p^2 = 0.542$, showed that peak apertures were larger in the 'long' condition (7.3 cm) than the 'short' condition (7 cm, $p < 0.001$). The Condition x Illusion interaction was also significant, $F(5, 100) = 7.627$, $p < 0.001$, $\eta_p^2 = 0.276$, showing an effect of the illusion in manual estimation, occluded vision and early vision conditions (Fig. 3), consistent with the results in Table 1.

To examine the extent to which there was a dissociation between 'vision-for-perception' and 'vision-for-action,' paired-sample t tests were performed to assess whether illusory effects found in grasping conditions differed significantly from those of the estimation condition. Results showed that the effect of the illusion was stronger in the estimation condition compared to all grasping conditions, even if the grasping condition also showed a significant effect of the illusion (Table 2). Crucially, the early and occluded vision conditions, in which a significant effect of the illusion was found, both differed significantly from the estimation condition. Within the grasping conditions, only the early vision condition differed significantly from the late vision condition, suggesting that there are multiple processes involved in online visuomotor control.

Time to maximum grip aperture

A significant main effect of Condition, $F(4, 80) = 14.657$, $p < 0.001$, $\eta_p^2 = 0.423$, revealed that the time to maximum grip aperture was longer in the late condition (1268.144 ms) than in the early (1053.291 ms, $p < 0.001$), middle (1073.764 ms, $p < 0.001$), full vision (1046.453 ms, $p < 0.001$) or occluded vision (1074.957 ms, $p = 0.003$) conditions (Fig. 4a). The main effect of Illusion, $F(1, 20) = 0.802$, $p = 0.381$, $\eta_p^2 = 0.039$, and the Condition × Illusion interaction, $F(4, 80) = 0.992$, $p = 0.417$, $\eta_p^2 = 0.047$, was null.

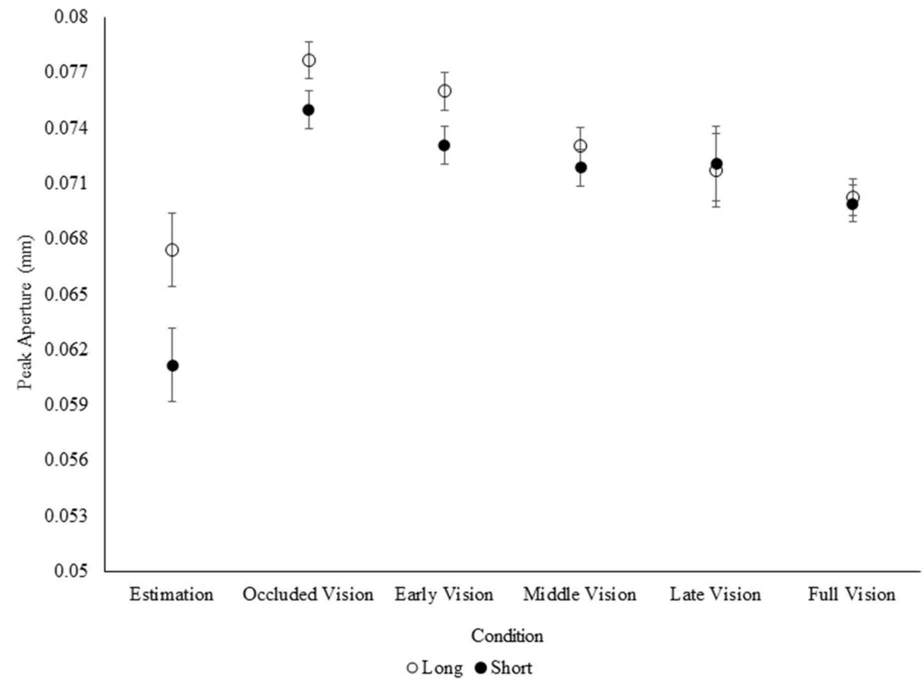

Fig. 3 Mean peak aperture for each of the illusion conditions (long = perceived longer; short = perceived shorter) across the manual estimation task and the five visual conditions of the grasping task. Error bars show standard errors

Table 2 Paired sample t-tests on the illusion effects across visual conditions (in cm)

Pairwise comparisons	Mean	SEM	Paired samples test
Estimation—full	0.475	0.111	$t^* = 4.265$, $p < 0.001$
Estimation—occluded	0.333	0.139	$t^* = 2.391$, $p = 0.003$
Estimation—early	0.297	0.104	$t^* = 2.864$, $p = 0.001$
Estimation—middle	0.406	0.150	$t^* = 2.705$, $p = 0.004$
Estimation—late	0.586	0.120	$t^* = 4.896$, $p < 0.001$
Full—occluded	− 0.151	0.142	$t = -1.061$, $p = 0.305$
Full—early	− 0.178	0.112	$t = -1.588$, $p = 0.129$
Full—middle	− 0.069	0.128	$t = -0.541$, $p = 0.595$
Full—late	0.110	0.122	$t = 0.907$, $p = 0.376$
Occluded—early	− 0.019	0.134	$t = -0.145$, $p = 0.887$
Occluded—middle	0.134	0.147	$t = 0.914$, $p = 0.375$
Occluded—late	0.256	0.148	$t = 1.730$, $p = 0.103$
Early—middle	0.108	0.104	$t = 1.043$, $p = 0.310$
Early—late	0.288	0.088	$t^* = 3.294$, $p = 0.004$
Middle—late	0.180	0.113	$t = 1.597$, $p = 0.127$

As the table shows, significant differences were found between manual estimations and all grasping conditions, as well as between early vision and late vision conditions. The asterisk (*) denotes significant tests using the Holm (1979) multiple comparisons procedure

Movement time analysis

A significant main effect of Condition, $F(4, 80) = 23.787$, $p < 0.001$, $\eta_p^2 = 0.543$, showed that participants completed the reach significantly slower in the late condition (1565.592 ms) than the early (1323.309 ms, $p < 0.001$), middle (1343.022 ms, $p < 0.001$), full vision (1290.632 ms, $p < 0.001$) or occluded vision (1338.071 ms, $p = 0.006$) conditions (Fig. 4b). The main effect of Illusion, $F(1, 20) = 0.022$, $p = 0.883$, $\eta_p^2 = 0.001$, and the Condition × Illusion interaction, $F(4, 80) = 2.154$, $p = 0.082$, $\eta_p^2 = 0.097$, was null. Thus, the time it took for participants to reach out and grasp the block was primarily influenced by the point at which they received vision to perform the reach.

Maximum velocity and wrist deceleration period

For maximum velocity, a significant main effect of Condition, $F(4, 80) = 5.219$, $p = 0.001$, $\eta_p^2 = 0.207$, and the Condition × Illusion interaction, $F(4, 80) = 2.626$, $p = 0.041$, $\eta_p^2 = 0.116$, was found (Fig. 4c). The main effect of Illusion, $F(1, 20) = 1.697$, $p = 0.208$, $\eta_p^2 = 0.078$, was null. Follow-up tests showed that maximum velocity was significantly lower for the late condition (663.089 mm/s) than the early (720.326 mm/s, $p = 0.03$), full vision (714.041 mm/s, $p = 0.031$) or occluded vision (720.248 mm/s, $p = 0.026$) conditions. There was no significant difference between the late condition and the middle (712.678 mm/s, $p = 0.140$) condition. For the interaction, it was found that maximum velocity was lower for trials in which the stimuli was perceived as longer (697.160 mm/s) than shorter (743.337 mm/s) in the occluded vision condition, $p = 0.026$.

As with maximum velocity, analysis of the wrist deceleration period revealed a significant main effect of Condition, $F(4, 80) = 15.850$, $p < 0.001$, $\eta_p^2 = 0.442$ (Fig. 4d). The main effect of Illusion, $F(1, 20) = 0.376$, $p = 0.547$, $\eta_p^2 = 0.018$, and the Condition × Illusion interaction, $F(4, 80) = 0.802$, $p = 0.528$, $\eta_p^2 = 0.039$, was also null. Follow-up tests showed

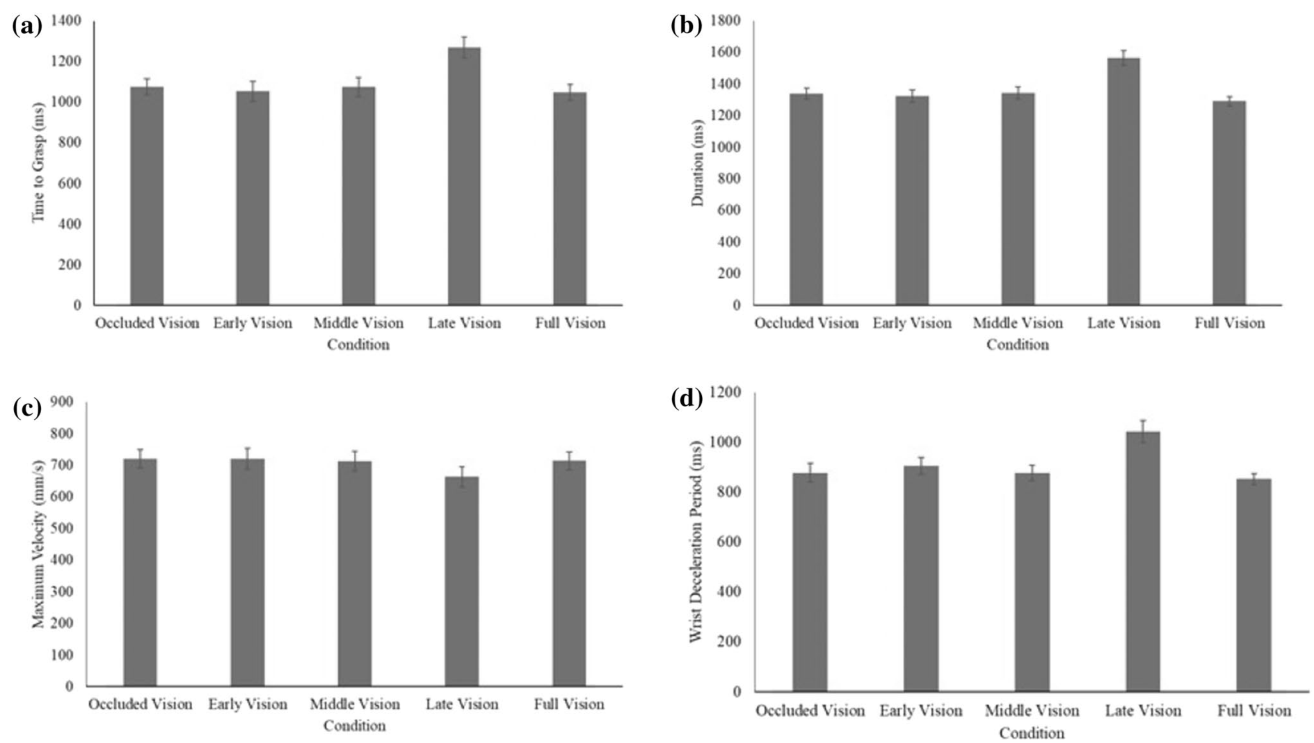

Fig. 4 The main effect of Condition in each analysis showed a longer time to reach MGA (**a**), longer overall reach duration (**b**), lower maximum velocity (**c**) and a longer wrist deceleration period (**d**) in the late condition compared to the other conditions. All bars represent condition means, and error bars represent standard errors

that wrist deceleration period was significantly longer for the late condition (1042.292 ms) than it was for the early (906.078 ms, $p = 0.002$), middle (876.981 ms, $p < 0.001$), occluded vision (877.299 ms, $p = 0.003$) or full vision (852.981 ms, $p < 0.001$) conditions.

Discussion

The purpose of this study was to examine how online visuomotor processing is influenced by the surrounding context in which a target is presented when vision is manipulated at varying points along the movement trajectory. Extending prior research using the Müller–Lyer illusion and aiming tasks (Elliott et al. 2010; Grierson and Elliott 2009; Kennedy et al. 2015; Roberts et al. 2013), participants performed a perception-based manual estimation task and an action-based reaching and grasping task in the context of the Sander parallelogram illusion. Our results showed a robust illusion effect in the manual estimation condition, confirming that participants were susceptible to the illusion and ruling out this methodological consideration as a potential confound to the results of the grasping analysis. Results of the grasping analysis showed that when grasps were performed with visual feedback (closed loop), the illusion did not influence maximum grip aperture (MGA), consistent with previous research (Aglioti et al. 1995; Gentilucci et al. 1996). Grasps performed without visual feedback for the duration of the reaching movement (open loop) showed that MGA reflected a susceptibility to the illusion, also consistent with the previous literature (Westwood and Goodale 2003; Gentilucci et al. 1996; Haffenden and Goodale 1998). Interestingly, grasps were also influenced by the illusion when visual information was only available for the early part of the reach, similar to the results of the manual estimation task albeit less robust. No bias toward the illusion was found when vision was provided for the middle or late parts of the reach. From these results, two major points emerge. First, the Sander parallelogram illusion was found to influence both manual estimations and grasps performed when vision was occluded for the duration of the reach or with vision only available for the early part of the reach. Second, compared to the manual estimations, pairwise comparisons showed that grasps were influenced significantly less by the illusion (Whitwell et al. 2018; Aglioti et al. 1995; Gentilucci et al. 1996; Haffenden and Goodale 1998). As such, these results are consistent with Milner and Goodale's (1992) TVSH that action and perception are part of two dissociable streams, while also supporting the notion that goal-directed movement involves multiple processes.

Previous research has established that the extent to which actions are immune to illusions is partially reliant on the amount of visual information available to the participants before movement onset. In the current study, our occluded vision condition was designed such that participants were able to view the target until the auditory tone (response cue), after which vision was occluded for the duration of the reach. Importantly, no visual feedback was available between the response cue and movement onset, which prior research has shown leads to a reduction in the illusory response (Westwood and Goodale 2003). MGAs were found to be consistent with an illusion-based response, suggesting that ventrally driven information was used to influence the outcome and in line with previous research supports the argument that dorsal visuomotor mechanisms are only engaged when the response is cued *and* the target is visible (Westwood and Goodale 2003; Elliot and Lee 1995; Bruno and Franz 2009; Franz et al. 2009; Haffenden and Goodale 1998). In the full vision condition, there were no illusion-based differences, suggesting that dorsally driven information was used to process the outcome. That is, the availability of vision during the whole duration of the reach allowed the visual system to correct for errors resulting in unbiased hand position by the end of the reach. However, when vision was only available during early, middle or late parts of the reach, results showed that only middle and late vision conditions showed MGAs consistent with those of the full vision condition. When vision was presented at the beginning of the reach, the MGA was consistent with the illusion such that participants had larger grip apertures for stimuli perceived as longer than shorter. Critically, pairwise comparisons revealed that illusion effects in the early vision condition differed significantly from those of the late vision condition, suggesting that visuomotor processing includes two online control processes, consistent with the notion that goal-directed movement involves multiple processes (Elliott et al. 2010).

Although MGA in the early vision condition was influenced by the illusion, it is important to note that the illusory configuration did not influence movement time, time to MGA, maximum velocity or wrist deceleration period for any of the five visual conditions. However, these reach kinematics were impacted by the point at which visual feedback was provided, showing differences for the late condition compared to the other conditions. While participants were able to complete the reaching and grasping task successfully and within their pre-defined average movement time window regardless of the point at which they received visual feedback, movement duration in the late condition still took significantly longer than the other conditions overall. Longer movement durations in the late condition are likely a by-product of the lower maximum velocity and longer wrist deceleration period also found in this condition (Handlovsky et al. 2004), which is typically associated with error-reducing online processes as a result of a speed/accuracy trade-off. This notion of a speed/accuracy trade-off is consistent with Elliott et al.'s (2010) multiple-process model of limb control, which suggests that aimed movements function under the guidance of two visually dependent modes of online control: a process of impulse regulation and a process of late discrete control. Specifically, impulse control early on in the movement is more involved in bringing the limb as close to the target area as possible without overshooting it, while late discrete control involves error estimation and small submovements designed to correct any aiming error (Elliott et al. 2001; Meyer et al. 1988). In the current study, when vision was only provided for the early part of the reach, a quick ballistic movement would have propelled the limb toward the target, but with vision occluded for the latter part of the movement there would be no opportunity for error correction. That is, MGA must reflect the initial motor plan associated with the perceived size of the target block. However, when vision was available for the late part of the reach, corrective processes were available to reduce discrepancies between limb and target position. Vision was also provided in the late condition until target contact to ensure that trials in this condition were accurately reflecting the kinematics associated with the latter part of the reach.

One of the limitations to this design is that while participants were instructed to naturally reach out to grasp the block as they did in the pre-experimental trials used to derive their movement time window, they may have become aware that vision was available in late trials until the movement was completed and inadvertently taken longer to complete the trial once vision came online. However, time to MGA, which involves the duration from movement onset until MGA, was also longer for late trials. Since MGA occurs during the latter part of the reach and time to MGA includes the early and middle parts of the reach when vision was not available, longer durations in the late condition likely also reflect a degree of uncertainty associated with starting the reach without any visual feedback. As such, longer reach durations in the late condition may be due to participants inadvertently moving their hand more slowly than expected by the participants standard reach profile, resulting in more time to correctly grasp the target and a decrease in illusion susceptibility. Yet, the anomalous movement time in the late condition is not enough to explain why participants did not fall for the illusion in this condition since a reduced effect of the illusion was found on grasps overall, and a similarly null effect of the illusion was found in middle vision and full vision conditions, both of which had durations that did not differ significantly from the participants standard reach profile. It is likely, then, that decreased illusion susceptibility in the late condition is due to the recruitment of corrective processes and the availability of online, real-time visual feedback until target contact to make corrections as opposed to a longer duration of time to complete the reach in this condition.

Another limitation concerns the sensitivity of different responses to target size. Due to the number of conditions tested in this study, we only included one target size, which has the potential to lead to biased estimates in both manual estimation and grasping conditions (Franz et al. 2001; Whitwell et al. 2018). However, since our study design follows closely with that of Whitwell et al. (2018), who found that task differences in response sensitivity to a difference in the length of the target stimuli did not affect their overall findings, it is unlikely that an adjustment in the current study would end up equating the effect of the illusion on the manual estimates and grip apertures in the grasping conditions.

While results from this study suggest that there are two types of processing involved in visuomotor control, the mechanisms by which the early part of the reach operates under remains unclear. Elliott et al. (2010) posit that before a movement is initiated, both motor and sensory representations of the expected consequences of the movement are formed. This motor representation, or efferent copy, provides a reference against which incoming visual and proprioceptive feedback can be compared. It should follow then that in the occluded vision condition in which visual information was only available before the response was cued the efferent copy reflects the perceived size of the target block since the recruitment of dorsal mechanisms requires the response to be cued and vision of the target. Without visual feedback, there is nothing to compare to the efferent copy to, and without vision to facilitate online corrective processes in the latter part of the reach, resulting MGAs should reflect the perceived size of the target bar. In the full vision condition, the efferent copy would have been formed at the beginning of the reach once the response was cued and the target became visible. Visual and proprioceptive feedback would have then been compared to this efferent copy, and corrective processes applied in the latter part of the reach producing MGA sun biased by the illusion. Results showing that MGAs in the early vision condition were susceptible to the illusion just as they were in the occluded vision condition suggest that the initial efferent copy represents the perceived size of the target. However, since the response cue occurred at the same time the target became visible; this would suggest that dorsal visuomotor mechanisms were engaged at the beginning of the reach. Since dorsal mechanisms rely on online, real-time information, it is likely that the efferent copy generated at the beginning of the movement decayed once vision was occluded, causing the motor system to generate a new movement program using the somewhat less accurate stored representation of the target, which was then maintained by the perceptual mechanisms of the ventral stream. While this could likely be elaborated on in future studies using eye tracking technology, our current results suggest that perceptual mechanisms are easily accessible when dorsal mechanisms are taken 'offline,' supporting the notion that visuomotor control involves multiple online control processes.

Conclusion

People typically organize their reaching and grasping movements to achieve a precise, efficient movement while optimizing movement speed. When unexpected changes to the visual environment occur, people are quite adept at making adjustments to their movement trajectories to accommodate the new visual constraints. In the current study, we showed that part of this accommodation process may be due to the recruitment of multiple processes during the reaching movement. The results indicated that grasps were influenced by the Sander parallelogram illusion in occluded vision and early vision conditions, indicating that the perceptual system influences online motor control to some extent. Late vision conditions were characterized by longer movement durations, time to MGA, wrist deceleration period and lower maximum velocities compared to other vision conditions, indicating a temporal cost associated with online trajectory amendments. While these results point to the idea of multiple online control processes involved in voluntary movement, it is also important to note that manual estimations were more robustly affected by the illusion compared to grasps, supporting Milner and Goodale's (1992,1995) important work on the differential roles of ventral and dorsal stream processing. As such, the current study moves beyond a single dichotomous model to examine the extent to which visuomotor control involves multiple online processes, providing support for a two-component model: an initial movement impulse that relies heavily on perceptual processes and a late feedback-based control process that provides online corrections consistent with a traditional view of dorsal processing in action.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Declaration of Helsinki and its later amendments or comparable ethical standards.

Consent to participate Informed consent was obtained from all individual participants included in the study.

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