Experimental Brain Research (2018) 236:1091–1103
https://doi.org/10.1007/s00221-018-5196-4

RESEARCH ARTICLE

Gaze anchoring guides real but not pantomime reach-to-grasp: support for the action–perception theory

Jessica R. Kuntz[1] · Jenni M. Karl[2] · Jon B. Doan[3] · Ian Q. Whishaw[1]

Received: 16 November 2017 / Accepted: 2 February 2018 / Published online: 13 February 2018

Abstract

Reach-to-grasp movements feature the integration of a reach directed by the extrinsic (location) features of a target and a grasp directed by the intrinsic (size, shape) features of a target. The action-perception theory suggests that integration and scaling of a reach-to-grasp movement, including its trajectory and the concurrent digit shaping, are features that depend upon online action pathways of the dorsal visuomotor stream. Scaling is much less accurate for a pantomime reach-to-grasp movement, a pretend reach with the target object absent. Thus, the action-perception theory proposes that pantomime movement is mediated by perceptual pathways of the ventral visuomotor stream. A distinguishing visual feature of a real reach-to-grasp movement is gaze anchoring, in which a participant visually fixates the target throughout the reach and disengages, often by blinking or looking away/averting the head, at about the time that the target is grasped. The present study examined whether gaze anchoring is associated with pantomime reaching. The eye and hand movements of participants were recorded as they reached for a ball of one of three sizes, located on a pedestal at arms' length, or pantomimed the same reach with the ball and pedestal absent. The kinematic measures for real reach-to-grasp movements were coupled to the location and size of the target, whereas the kinematic measures for pantomime reach-to-grasp, although grossly reflecting target features, were significantly altered. Gaze anchoring was also tightly coupled to the target for real reach-to-grasp movements, but there was no systematic focus for gaze, either in relation with the virtual target, the previous location of the target, or the participant's reaching hand, for pantomime reach-to-grasp. The presence of gaze anchoring during real vs. its absence in pantomime reach-to-grasp supports the action–perception theory that real, but not pantomime, reaches are online visuomotor actions and is discussed in relation with the neural control of real and pantomime reach-to-grasp movements.

Keywords Action–perception · Pantomime reaching · Reach-to-grasp · Dorsal stream · Ventral stream · Visually guided reaching · Visual attention

Introduction

A real reach-to-grasp movement to a visual target is different from a pantomime or pretend reach-to-grasp in which the target is absent. A real reach-to-grasp movement features scaling of the hand's trajectory and digit shape in relation with a target, whereas scaling for a pantomime reach-to-grasp is inaccurate relative to the pantomimed target (Goodale et al. 1994; Westwood et al. 2000; Fukui and Inui 2013; Holmes et al. 2013; Kuntz and Whishaw 2016). One interpretation of the kinematic differences is that they support the action–perception theory. The theory proposes that real reach-to-grasp movements are online actions mediated by dorsal stream visuomotor pathways, whereas pantomime reaches are offline actions mediated by ventral stream visuotemporal pathways (Milner and Goodale 2008). The action–perception theory is further corroborated by studies with neurological patients with visual form agnosia (D.F.) and optic ataxia (I.G.). Patient D.F. sustained damage largely to the ventral stream with some bilateral posterior parietal damage (James et al.

✉ Jessica R. Kuntz
Jessica.Kuntz@uleth.ca

1 Department of Neuroscience, Canadian Centre for Behavioral Neuroscience, University of Lethbridge, 4401 University Drive West, Lethbridge AB T1K 3M4, Canada

2 Department of Psychology, Thompson Rivers University, Kamloops, Canada

3 Engineering and Human Performance Lab, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, Canada

2003; Bridge et al. 2013) which hindered her ability to pantomime reach movements, but left intact her ability to grasp real objects (Goodale et al. 1991). In contrast, patient I.G.'s bilateral posterior parietal damage impaired the real reach-to-grasp movement to a real object more severely than the same movement to a remembered object (Milner et al. 2001). Although both behavioral and neurological studies support the action–perception theory's explanation of real and pantomimed movements, a number of lines of research suggest that both real and pantomime actions are perhaps more complex in the form that they take and in their neural substrates. For example, the presence/absence of contextual cues can influence pantomime movements (Gentilucci et al. 1996; Coats et al. 2008; De Stefani et al. 2014; Kuntz and Whishaw 2016) as can the presence/absence of haptic feedback associated with grasping a real object (Bingham et al. 2007; Chan and Heath 2017; Jazi and Heath 2017; Rinsma et al. 2017). With respect to identifying neural pathways, fMRI activation in the dorsal stream occurs for both real and pantomime reaching, but in different hemispheres (Króliczak et al. 2007; Cohen et al. 2009). In addition, Vry et al. (2015) suggest that pantomime movement is mediated by at least two pathways, a dorsoventral pathway that is involved in the representation of the virtual target and a more ventral temporofrontal pathway projecting through the extreme capsule that represents the pantomime action [see also, (Hoeren et al. 2014; Goldenberg 2017)].

A central characteristic of the visual control of real reach-to-grasp that likely contributes to its performance as an online movement is gaze anchoring. At about the time that a reach is initiated, a target is visually fixated and fixation is maintained until about the time that the target is grasped. Visual fixation is disengaged, often with a blink and/or head aversion (Prablanc et al. 1979; Neggers and Bekkering 2000; de Bruin et al. 2008; Sacrey and Whishaw 2012a). Similar gaze anchoring occurs when participants point to a target (Neggers and Bekkering 2000; Prablanc et al. 1979). Because real-reaching features two movements, the reach that directs the hand to the target guided by the extrinsic (location) features of the target, and the grasp that shapes the hand guided by the intrinsic (size and shape) features of the target (Arbib 1981; Jeannerod 1981; Jeannerod et al. 1994), gaze anchoring may be required to integrate these two movements. In the absence of gaze anchoring, as occurs when participants reach without vision or reach into peripheral vision, the reach and grasp dissociate, such that the reach is used to locate the target and the grasp is formed in response to touch cues obtained from the target (Karl et al. 2012; Hall et al. 2014). Similarly, as the contextual cues available during pantomime reaching are reduced, there is a systematic loss of the integration of reach/grasp movements (Kuntz and Whishaw 2016). These findings raise the question of the extent to which the absence of movement scaling featured in pantomime reaching is due to the absence of visual control of the movement provided by gaze anchoring.

The purpose of the present study was to investigate whether a distinguishing feature of real vs. pantomime reach-to-grasp movements is the presence vs. absence of gaze anchoring. For the real reach-to-grasp task, participants reached for three targets, small, medium, and large balls that were located on a pedestal in front of them. For the pantomime task, the target ball and pedestal were absent and participants were briefly shown a ball and instructed to pretend to reach for it. Participants wore scene-based eye-tracking goggles as well as electromagnetic sensors attached to the hand to monitor eye and hand movements. This arrangement documented where participants were looking as they completed both real reaches and pantomime reaches.

Materials and methods

Participants

Participants were 21 right-handed young adults (11 female, 10 male; mean age 19.95 ± 0.9 months) recruited from Thompson Rivers University introductory psychology classes and received class credit for their participation. Each participant gave informed consent, authorized use of photos or videos, and was self-reported as having no history of neurological, sensory, or motor disorders as well as normal, or corrected-to-normal, visual acuity. The University of Lethbridge and Thompson Rivers University, Human Subject Research Ethics Committees approved the study.

Apparatus

Participants were seated in a brightly lit room with a self-standing height-adjustable pedestal placed in front of them. The pedestal was placed at a horizontal reach distance normalized to the participant's arm length (100% of the length of the shoulder to the tip of the index finger with the elbow at 180° flexion) and the height of the pedestal was adjusted to the participant's trunk height, with 100% of height from floor to outstretched arm while seated with the arm–shoulder at 90° flexion (Whishaw et al. 2002). This experimental setup allowed participants to naturally reach with their right hand towards the pedestal to pick up the target object as three measures of reaching behavior were made:

1. *Video recording* Two high-speed video cameras recorded behavior throughout the task. Filming was performed at 30 Hz and 1/1000 shutter speed with cameras placed to capture both frontal and lateral views.

2. *Hand kinematics* Thumb, index, and wrist movements were acquired online at 60 Hz using a trakSTAR® (Ascension Technology Corporation) system. The position of the digits and wrist was calculated from electromagnetic sensors placed on the participant's hand; two on the distal phalanges of the thumb and index finger, and one on the wrist on the anterior aspect of the ulnar styloid, with respect to the transmitter. The transmitter was fastened to the floor beneath the participant's right chair legs, such that the transmitter and the hand's start position were vertically aligned.
3. *Eye movement* Eye movement was recorded using a ViewPoint EyeTracker® (Arrington Research, Inc) a monocular scene-based eye-tracking device. Eye-tracking glasses were worn for the entirety of the experiment and collected data at a sampling rate of 30 Hz. A 16-point eye calibration was performed prior to data collection and was adjusted if necessary during the experiment (when there was a significant drift between gaze point and the target to be fixated).

Reach targets

Participants reached for three targets (spherical balls) each with a different size: small (circumference = 15.5 cm, diameter = 4.9 cm, volume = 19.1 cm^3), medium (circumference = 20.5 cm, diameter = 6.5 cm, volume = 33.4 cm^3), and large (circumference = 22.5 cm, diameter = 7.2 cm, volume = 40.3 cm^3). Balls, rather than other target objects, were selected, because a reach directed towards a ball is not influenced by intrinsic properties other than size. The sizes of the balls were chosen based on preliminary experiments in which participants reliably judged that the balls represented increasingly larger sizes. The small and medium targets had a rougher surface compared to the smoother plastic of the large target. The textual properties and surface colorations were intentionally chosen to be different so as to not distract the participants from the size differences. Targets were placed at the centroid of the pedestal prior to trial initiation.

Procedure

A participant was seated in a comfortable upright position with the feet flat on the floor with their hands placed in the start position. The start position for the right hand was marked on the dorsum of the upper thigh, and participants started with their thumb and index finger in opposition, whereas the left hand was resting in an open and relaxed position on the dorsum of the left upper thigh. Participants were then presented with a set of practice trials, where they reached out and grasped an object and brought it back to their chest. This was done so that participants would not only be accustomed to the task, but to ensure that the equipment would not interfere with their natural reach-to-grasp movement.

Participants adopted the start position between trials and waited for a start prompt which was a verbal "1-2-3-GO" command. The experiment consisted of two tasks:

1. *Real reach* For the real task, participants were instructed to "reach out and grasp the target and bring it back to your chest".
2. *Pantomime reach* For the pantomime reach, a participant was shown a ball for which they should reach, but the ball was not present during the reach. The pedestal was also removed, because preliminary work suggested that if it were present the task would in part comprise a pointing task for which gaze anchoring would be present (Neggers and Bekkering 2000; Prablanc et al. 1979), a feature that would thus confound the objectives of the present study. The instructions for the real reach and the pantomime reach tasks were otherwise similar; the participants were instructed to "reach for the real ball and bring it to your chest", or instructed to "reach out and grasp the (small, medium, or large) ball at the same location as you had for the real condition and bring it to your chest."

All reaches for the real task were completed prior to the pantomime task. This was done to ensure that all participants were familiar with the real task before they performed the pantomime.

Experimental design

The study used a 2 × 3 × 3 repeated-measures within-subjects design. Each participant performed the reach-to-grasp movement under two task conditions (real vs. pantomime), for three different sized targets per task (small, medium, and large), at a rate of three trials (1, 2, and 3) per target per task. Trial number was based on the previous reach-to-grasp studies (Karl et al. 2013). This experimental design allowed for adequate statistical power while ensuring participants remained attentive. Thus, each participant completed a total of 18 reaching trials. Each scenario is illustrated in Fig. 1. Figure 1a–c illustrates the real reach task with a ball of each of the three different sizes, and Fig. 1d–f illustrates the pantomime reach task.

Data analysis

Hand movements

Kinematic events were processed offline using custom-written algorithms created in Matlab® (Version R2016b; The

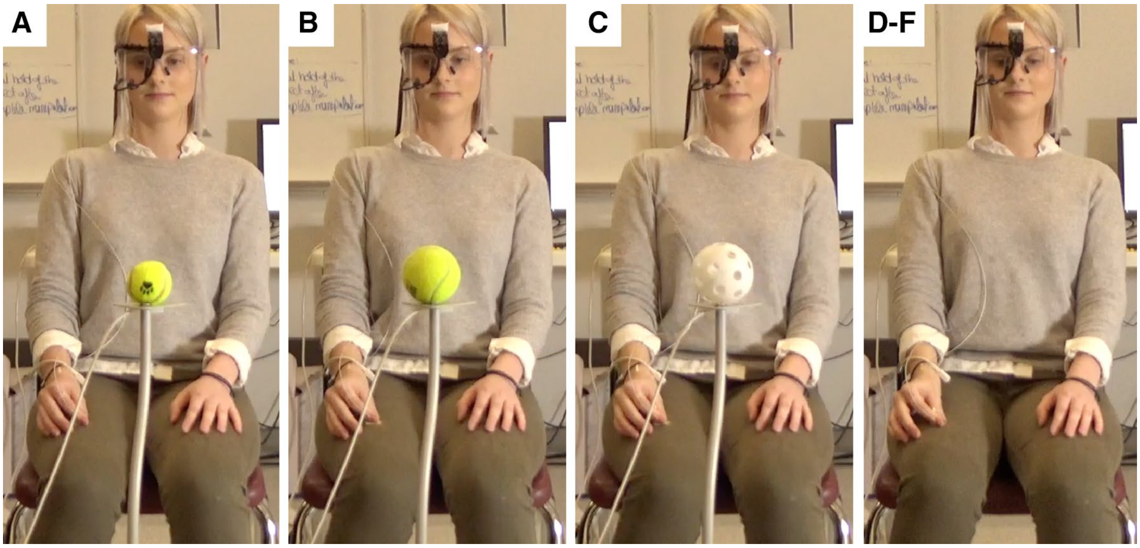

Fig. 1 Real- and pantomime-reaching conditions. **a** Real small, **b** real medium, **c** real large. In the real conditions, the participant reached from their lap for a ball (small, medium, and large) located on a pedestal at arms length and brought the ball back to the chest. **d** Pantomime small, **e** pantomime medium, **f** pantomime large. In the pantomime conditions, neither the ball nor the pedestal were present

Mathworks, Natick, MA, USA). A participant made a lateral movement with the reaching hand before they placed the hand in the start position with the first two digits in opposition. On the kinematic record, this movement was used to separate data into discrete trials. Movement initiation was defined as a minimum wrist velocity threshold of 5 mm/s in the frontal direction after the 1-2-3-GO command. Withdraw was defined as occurring after the grasp and constituted a backwards movement of the hand back to the body. The reach-to-grasp movement then consisted of measures between reach initiations to withdraw. Kinematic measures determined from the data consisted of the following:

1. *Maximum pre-grasp* Maximum pre-grasp was defined as the maximum index-thumb aperture obtained between the movement initiation and grasp.
2. *Grasp* Grasp was defined as the minimal closing aperture between the index finger and thumb, prior to the beginning of the withdraw movement.
3. *Maximum height* Maximum height was defined as the maximal vertical displacement of the index finger prior to the beginning of the withdraw movement and was measured relative to the dorsal surface of the pedestal platform.
4. *Reach duration* Reach duration was defined as the time difference between movement initiation and grasp.

Gaze direction

Participant visual fixations, relative to the visual scene in front of them, were analyzed offline using Point Picker (ImageJ, Natick, MA, USA). In the real reach task, relative gaze measures were calculated from 8 points that were identified by stepping through the visual fixation data frame-by-frame. The 8 points were the tips of the thumb and index finger, the three corners of the pedestal, the fixation point, and the center of the target. For the pantomime reach task, 4 points were identified: tips of the thumb and index finger, the tripod block of the camera positioned in front of the participant, and the fixation point. Sometimes, the eye tracker lost track of the eye, due to blinks, eyelash interference, or other unknown factors. If the eye tracking was lost at an abnormal rate on multiple trials across reach scenarios, data from that participant was discarded; therefore, eye movement results are derived from 17 subjects. The locations of visual fixations were derived from these measures.

Visual distance Measures of visual fixation were taken at three different timepoints during each reaching trial: movement initiation, midpoint of hand transport—defined as 50% of reach duration, and termination of reach signified by a grasp. Three measures of gaze fixation were taken at each timepoint.

Distance of gaze fixation relative to the center of the pedestal. The mean position of the center of the pedestal in the real condition was defined as the location of the "center of the pedestal" in the pantomime condition.

Distance of gaze fixation relative to the midpoint between the thumb and index finger.

Distance of gaze fixation relative to the eventual grasp location as indicated by the midpoint between the tip of the first and second digits at the time of grasp for that trial.

Visual trajectory To calculate the gaze trajectory associated with the real reach-to-grasp movement and the pantomime of the movement, the distance between gaze fixation and the center of the pedestal was measured on each frame, beginning ten frames prior to reach initiation and ending five frames after grasp completion. Data were interpolated to plot average visual trajectory in relation with reach time.

Statistical analysis

All data were analyzed using repeated-measures, analysis of variance (RM-ANOVA), and ANOVAs of the coefficient of variation, when appropriate, using the statistical computer program SPSS (v.24.0.0). A p value of <0.05 was considered significant.

Data for gaze fixation relative to the pedestal, gaze fixation relative to the hand, and gaze fixation relative to grasp location were analyzed using Time (Initiation, Midpoint, and Grasp), Task (Real and Pantomime), Size (SM, MD, and LG), and Trials (1, 2, and 3), as the within-subjects factors. Visual Trajectory data were calculated using Fixation Point (relative to Pedestal, relative to Hand), Task (Real and Pantomime), Size (SM, MD, and LG), Trials (1, 2, and 3), and Frame (1–30) as the within-subjects factors.

Hand movement data were calculated using Task (Real and Pantomime), Size (SM, MD, and LG), and Trials (1, 2, and 3), as the within-subjects factor for the separate dependent variables of Maximum Pre-Grasp, Grasp, Maximum Height, and Reach Duration. Additional tests of variance were calculated for kinematic data for Group (RealSM, RealMD, RealLG, PantSM, PantMD, and PantLG). Post-hoc tests with Bonferroni corrections were completed after statistical significance was determined. Results are reported as mean ± standard error.

Results

Reach duration

Reach-to-grasp movements for both real and pantomime conditions were completed in under 0.8 s, but the time to complete a real reach was significantly longer than the time to complete a pantomime reach, $F(1,16)=6.693$, $p=0.020$. There was a significant main effect of ball size, $F(2,32)=5.259$, $p=0.011$, and post-hoc tests with Bonferroni correction indicated that the average duration was longer for the small ball than for the medium and large balls for both real and pantomime reaches ($p<0.001$). There was no significant main effect of trials, $F(2,32)=0.397$, $p=0.676$, nor a significant interaction of task by size $F(2,32)=0.175$, $p=0.840$.

Maximum pre-grasp aperture and grasp aperture

Figure 2 shows that both maximum pre-grasp aperture and grasp aperture were larger for real reaches than for pantomime reaches, although both measures increased with ball size for both real reaches and pantomime reaches. The difference in maximum pre-grasp aperture between real reaches and pantomime reaches (Fig. 2a) was not significant $F(1,20)=0.041$, $p=0.842$, but there was a significant main effect of ball size [size $F(2,40)=41.58$, $p<0.001$]. Furthermore, there was no significant interaction of task by size, $F(2,40)=1.478$, $p=0.240$. Nevertheless, the boxplots of maximum pre-grasp aperture size in Fig. 2a did suggest that there was greater variance in the maximum pre-grasp aperture size for the pantomime reaches vs. real reaches. This was confirmed by running an ANOVA of the coefficient of variation, $F(5,377)=26.361$, $p<0.001$. Follow-up paired samples t tests revealed significant differences in the scores for real small ($M=0.1362$, SD = 0.1018) and pantomime small ($M=0.1862$, SD = 0.1238) coefficient of variation; $t(62)=-2.228$, $p=0.030$, and real large ($M=0.1041$, SD = 0.0664) and pantomime large ($M=0.1375$, SD = 0.1015) coefficient of variation; $t(62)=-2.055$, $p=0.044$.

An ANOVA of grasp aperture (Fig. 2b) showed that grasp aperture size was larger for real reaches than for pantomime reaches, task, $F(1,20)=12.930$, $p=0.002$. Furthermore, the grasp aperture increased with target size as was confirmed by a significant main effect of size $F(2,40)=63.026$, $p<0.001$. No significant interaction between task by size, $F(2,40)=0.319$, $p=0.729$, was found. Follow-up analyses indicated that the small, medium, and large ball sizes were all significantly different from one another in both tasks. In addition, the boxplots in Fig. 2b suggested that there was greater variance in grasp aperture for pantomime reaches vs. real reaches, which was confirmed by a significant coefficient of variation for task $F(5,377)=6.103$, $p<0.001$.

Maximum reach height

Figure 3 summarizes the results of maximum height of the index finger relative to the surface of the pedestal for the real reach vs. the pantomime reach tasks. Peak height increased with target size as was confirmed by a significant main effect of size, $F(2,40)=21.485$, $p<0.001$. Post-hoc tests with Bonferroni correction revealed significant differences for the small and medium ($p<0.001$) and the small and large target ($p<0.001$), but not for the medium and large target ($p>0.05$). An ANOVA also revealed a significant main effect of task $F(1,20)=18.333$, $p<0.001$. Follow-up post-hoc tests with Bonferroni correction revealed significant differences in the peak height scores for real small ($M=0.0344$, SD = 0.0392) vs. pantomime small ($M=0.0778$, SD = 0.0689) coefficient of variation;

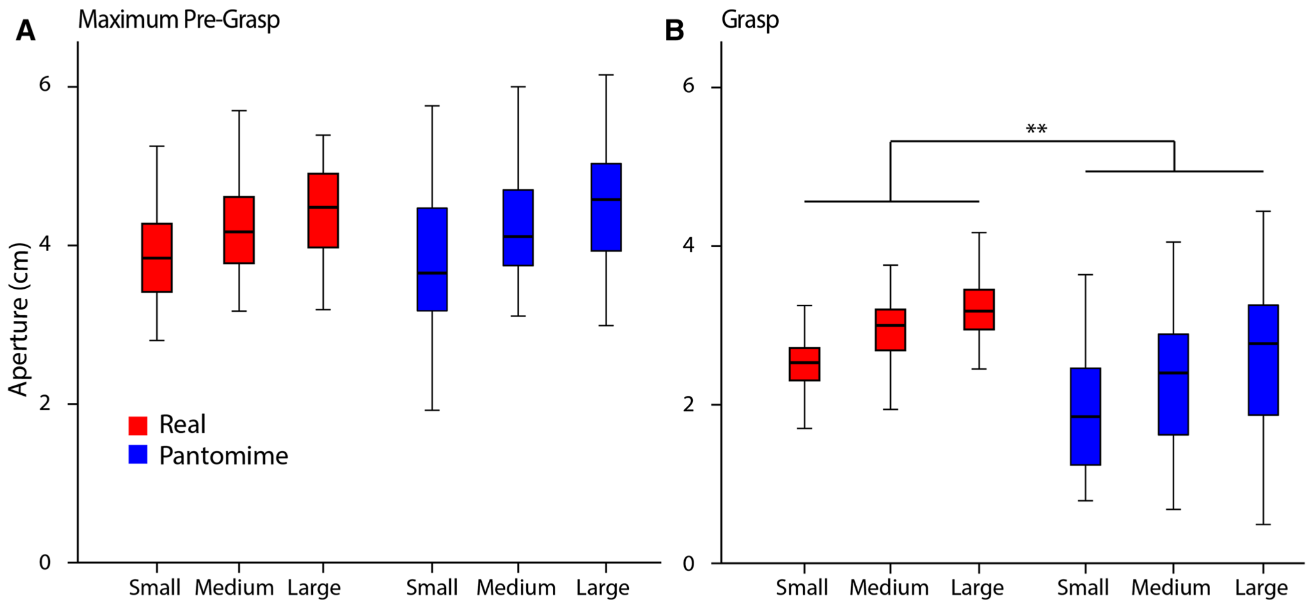

Fig. 2 Maximum pre-grasp and grasp aperture. **a** Box plot of aperture at maximum pre-grasp in real (red) and pantomime (blue) conditions showing the third quartile (Q3) and the first quartile (Q1). **b** Box plot of aperture at grasp in real (red) and pantomime (blue) conditions. (**$p < 0.01$). Aperture variability is high in pantomime conditions

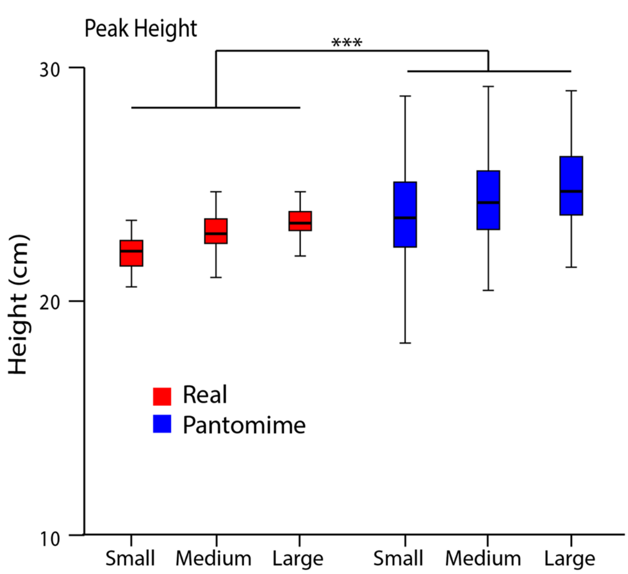

Fig. 3 Box plot of maximum height of the index finger in real (red, left) and pantomime (blue, right) conditions showing the third quartile (Q3) and first quartile (Q1) (***$p < 0.001$). Peak height variability is high in pantomime conditions

$t(62) = -5.842$, $p = 0.000$, real medium ($M = 0.0476$, SD = 0.0611) vs. pantomime medium ($M = 0.0707$, SD = 0.0076) coefficient of variation; $t(62) = -2.940$, $p = 0.005$, and real large ($M = 0.0281$, SD = 0.0342) vs. pantomime large ($M = 0.0710$, SD = 0.0081) coefficient of variation; $t(62) = -4.884$, $p < 0.001$.

Gaze direction

The gaze direction of participants on the real-reaching task was directed to the target from movement initiation to about the time the target was grasped. Figure 4, top shows a typical example of gaze anchoring, in which gaze remained on a target during a participant's real reach. During pantomime, there was no systematic relationship between gaze and the target and Fig. 4, bottom shows an example in which gaze is directed well above the virtual target at initiation, approximately halfway through the reach, gaze is briefly directed towards the participant's hand and then quickly returns to a point above the target. Support for the differences for this general finding is given in the following paragraphs.

Figure 5 shows that the distance between visual fixation and the pedestal at reach initiation, reach midpoint, and grasp was smaller for the real reach task than the pantomime reach task. Figure 5, left shows that gaze distance for the real reaches at reach initiation, the midpoint of the reach, and at the grasp was significantly closer to the platform than it was for pantomime reaches. That the gaze fixation point for real reaches was closer to the platform than that of pantomime reaches was confirmed by an ANOVA that gave a significant main effect of task $F(1,16) = 33.249$, $p < 0.001$. There was a significant main effect of size $F(2,32) = 5.768$ $p = 0.007$ but no significant main effect of time $F(2,32) = 0.666$ $p = 0.521$.

Figure 5, right shows gaze fixation position relative to the pedestal's surface for all ball sizes of each participant. The distance of the gaze fixation points relative to the center of the pedestal surface at reach initiation, reach midpoint, and

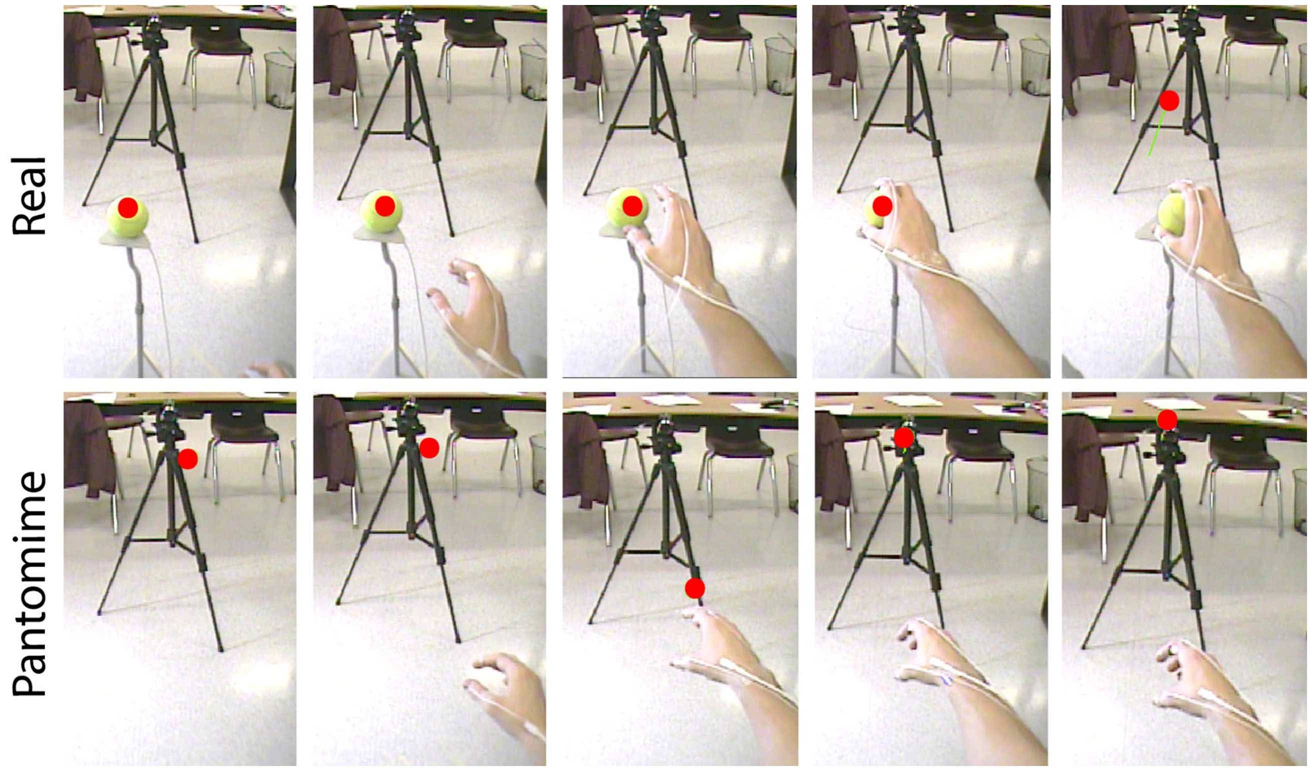

Fig. 4 Still frames of gaze point and reach behavior taken prior to reach initiation until withdraw of the hand for the medium-sized target in the real condition (top) and pantomime condition (bottom). Gaze is anchored to the target in the real condition from reach initiation until disengagement at grasp, whereas in the pantomime condition, gaze is not anchored to the target

grasp for individual participants was smaller for the real vs. the pantomime task. At all three timepoints in the real reach task, most participants fixated the target, as is represented by the dense population of red symbols above the pedestal. Only at reach initiation and grasp was there variation in gaze fixation in the real reach task (when participants initiated gaze anchoring or disengaged gaze anchoring). The fixation points for the pantomime reaches were more frequently displaced from the virtual platform location and were more variable at all points in the reach as is indicated by the more dispersed blue symbols.

Figure 6 illustrates that the absolute distance between the gaze point and the center of the platform of the pedestal was maintained throughout the reach in the real reach task. That is, once the reach was initiated, gaze was directed to, and then anchored on, the target until the target was grasped in the real reach condition. There was no similar gaze anchoring for the pantomime reach task. An ANOVA on gaze location distance relative to the platform confirmed that real reaches were different, in that they were more closely anchored on the target, than pantomime reaches, task, $F(1,16) = 32.090$, $p < 0.001$. There was also a significant main effect of frame of the reach with the gaze fixation point being directed to the target at the beginning of the reach and away from the target at the end of the reach, with maximum fixation on the target occurring around the midpoint of the reach, which was greater for real reaches vs. pantomime reaches, as confirmed by a significant main effect for frame $F(29,464) = 5.249$, $p < 0.001$, and a significant interaction of task x frame $F(29,464) = 2.524$, $p < 0.001$, no significant interaction for task x size $F(2,32) = 0.998$, $p = 0.380$.

In addition, Fig. 7 shows that variance in gaze location relative to the pedestal surface decreased as a real reach was initiated specifically in the latter two-thirds of the reach. Variance during the pantomime condition did not follow this trend and exhibited greater variance with minimal change with reach progression.

Distance of gaze fixation point relative to the hand and virtual target

The finding that gaze is directed to the platform throughout the duration of the real reach task raised the question of whether there was any systematic gaze direction for the pantomime reach task. There were two possibilities, participants in the pantomime task might be looking at their hand, or they might be looking at the virtual target, i.e., the location at which they will make a grasp movement.

Figure 8a shows that during the pantomime task, participants did not fixate on the reaching hand at any of the

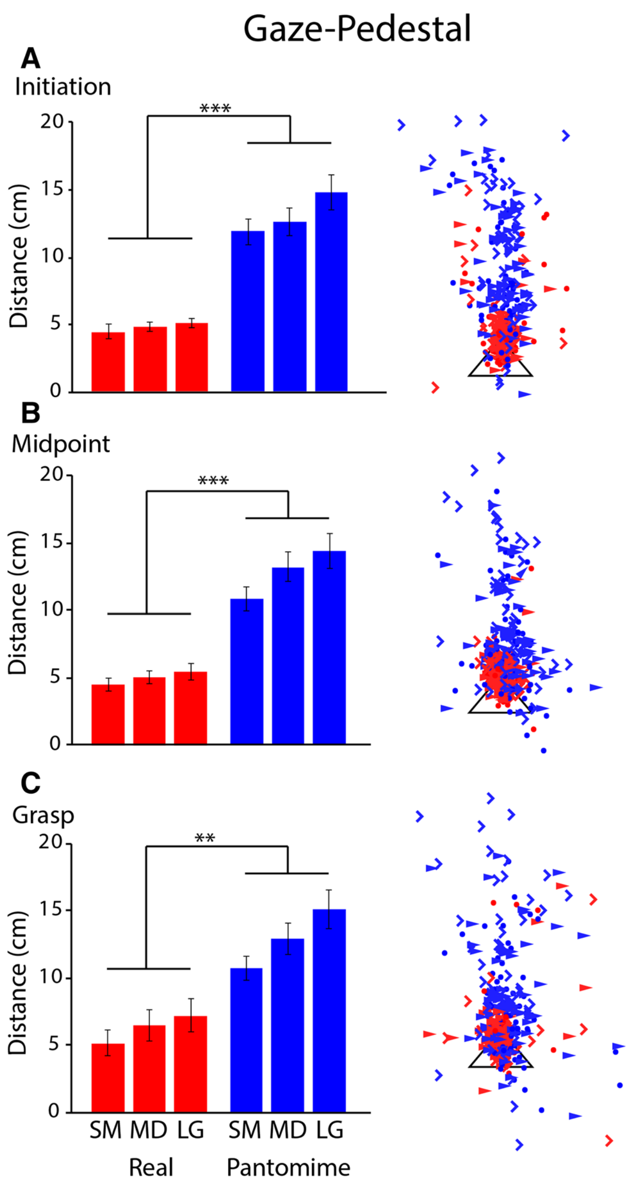

Fig. 5 Visual fixation relative to the pedestal at three timepoints of the reach. Left. Average absolute distance from point-of-gaze to center of the pedestal (mean ± standard error) in the real (red, left) and pantomime (blue, right) conditions at three timepoints: **a** initiation, **b** midpoint, and **c** grasp. (**$p < 0.01$, ***$p < 0.001$). Right: visual fixation points of all participants relative to the pedestal. Average distance from point-of-gaze to the center of pedestal for the entire reach-to-grasp movement in the real and pantomime conditions for three target sizes: small circle, medium right triangle, and large arrow. Visual trajectory is closely linked to the target's location for the real reaches, but is more variable for pantomime reaches

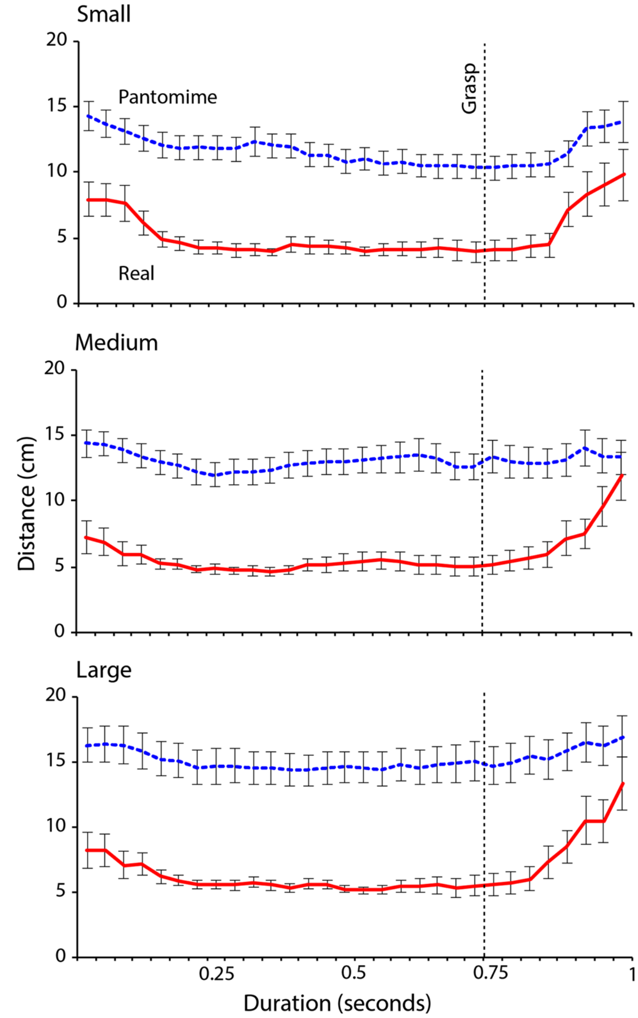

Fig. 6 Visual fixation throughout the reach relative to the center of the platform for real (red) and pantomime (blue) reaches (mean ± standard error). The gaze point is directed towards the pedestal at the beginning of the reach and away from the pedestal at the grasp for real reaches but not for pantomime reaches

timepoints measured: initiation, midpoint, and grasp. Figure 8a shows that as the reaching hand approached the target, the distance between gaze fixation and the hand location for real reaches decreased (because the hand was approaching the gaze fixation point near the pedestal). These differences between the real and the pantomime task were confirmed by an ANOVA that gave significant main effects of task, $F(1,16) = 35.220$, $p < 0.001$, time, $F(2,32) = 210.730$ $p < 0.001$, and an interaction of time × task, $F(2,32) = 0.005$, $p = 0.995$. For pantomime reaches, there was only a slight tendency for participants to direct their gaze towards the reaching hand and then only for the terminal point of the reach and mainly for smaller ball sizes, but this did not reach statistical significance. The ANOVA also gave a significant main effect of ball size, $F(2,32) = 11.665$, $p < 0.001$, and an interaction between task and ball size, $F(2,32) = 5.698$, $p = 0.008$.

Figure 8b shows that during the real task, participants visually fixated on the target at all points during the reach, but there was no similar fixation on the virtual target in the pantomime task. An ANOVA on gaze to target

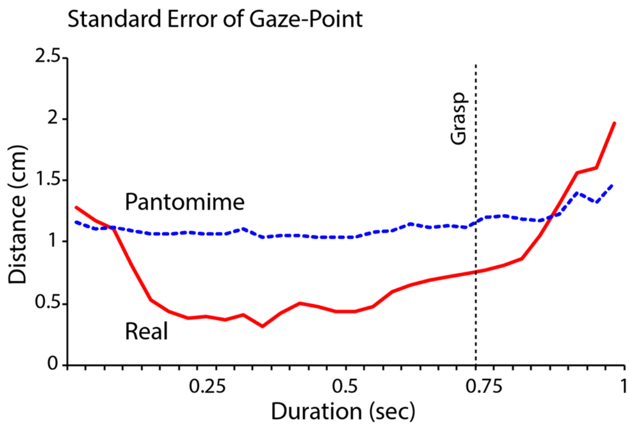

Fig. 7 Average variance for all real and all pantomime reaches relative to the center of the platform on which the target is located (mean). The decrease in variance for real reaches is smallest shortly after the reach is initiated, but there is little change in variance for pantomime reaches

distance confirmed that the distance was smaller for the real reach vs. the pantomime reach task, $F(1,16) = 19.306$, $p < 0.001$. There were also significant main effects of time, $F(2,32) = 1.237$ $p = 0.304$, and size, $F(2,32) = 9.182$, $p = 0.001$. Furthermore, there were significant interactions of time x task $F(2,32) = 12.802$, $p < 0.001$ and task X size $F(2,32) = 5.407$, $p = 0.009$. Pairwise analyses revealed that the fixation to target distance for the small ball was smaller ($p = 0.001$) from the medium ball ($p = 0.002$). Taken together, these results suggest, whereas participants in the real condition were looking at the real target; only some of the participants in the pantomime task, and mainly for the small ball, were directing their gaze towards the virtual location of the target, and then only towards the end of the reach, the point at which participants in the real reach task disengaged.

Discussion

This study compared gaze anchoring and hand shaping movements associated with real reach-to-grasp movements, reaching for a ball of one of the three different sizes located on a pedestal, and pantomime reach-to-grasp movements, pretending to reach for one of the target balls on a pedestal, with the ball and pedestal absent. When making real reaches, participants visually fixated the target as the reaching movement was initiated and disengaged visual fixation of the target at about the point that the target was grasped, a behavior that is referred to as gaze anchoring. Gaze anchoring was absent in the pantomime reach task. Real reach-to-grasp movements also featured kinematic measures of the reach, i.e., maximum height, maximum pre-grasp, and grasp that were proportional to the size of the target. Pantomime reaches featured kinematic measures for the reach in which scaling did not reflect the actual target size. Furthermore, during pantomime movements, gaze was not systematically related to the previous location of the target, the virtual location of the target as defined by the point that a participant made a grasping movement, or the participant's hand. The presence of gaze anchoring during real reach-to-grasp is consistent with the action–perception theory that proposes that real visuomotor action is mediated via dorsal stream online control. The absence of gaze anchoring during pantomime reach-to-grasp is consistent with the action–perception theory proposal that pantomime is mediated by offline control.

The present study supports previous work showing that the reach trajectory and hand shaping movement associated with a pantomime reach is different from that associated with a real reach (Goodale et al. 1994; Westwood et al. 2000; Fukui and Inui 2013; Holmes et al. 2013; Kuntz and Whishaw 2016). Here, we found that a pantomime reach featured a peak height that was larger than that of real reach, a peak aperture (maximum pre-grasp) and minimum aperture (grasp) between the first two digits that was smaller than that of a real reach, and a movement duration that was shorter than that of a real reach. In addition, the variability in the kinematic measure of pantomime reaches was greater than that of real reaches. In general, that there are kinematic differences between real reaches and pantomime reaches is consistent with the original finding of Goodale et al. (1994).

Nevertheless, previous work has also shown that pantomime movements are influenced by visual contextual cues (Gentilucci et al. 1996; Coats et al. 2008; De Stefani et al. 2014; Kuntz and Whishaw 2016). For example, in a task in which participants reach for a food item located on a pedestal, kinematic measures are different depending upon whether the participants pantomime with the pedestal displaced, absent, or pantomime without vision (Kuntz and Whishaw 2016). Therefore, it might be expected that kinematic differences in real and pantomime reaching will vary from experiment to experiment in concert with contextual differences. The pedestal was removed in the present study, because its presence, although requiring a pantomime grasp, would nevertheless provide a target for the reach. In this respect, the task would be a pointing task, in part, and pointing tasks have been shown to feature gaze anchoring (Neggers and Bekkering 2000; Prablanc et al. 1979). All of the other room cues were unchanged for the real and pantomime tasks and the subjects were sighted. Therefore, in general, the test situation and the kinematic results are sufficiently similar to test situations used in previous work to make a rigorous comparison of the gaze activity associated with real and pantomime reaches.

Experimental Brain Research (2018) 236:1091–1103

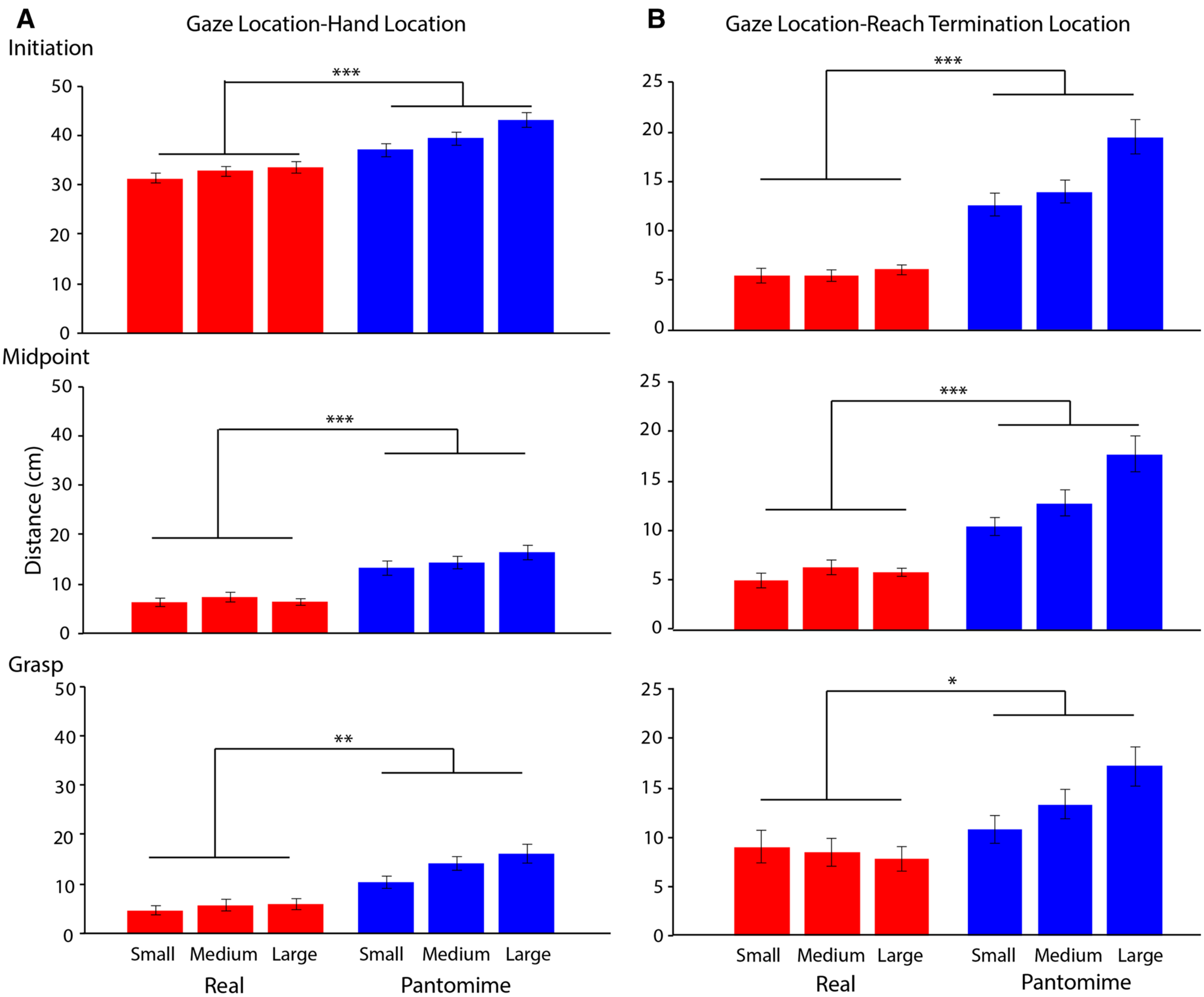

Fig. 8 Gaze location distance. **a** Gaze location—hand location distance. Average absolute distance from point-of-gaze coordinates to digit midpoint coordinate (mean ± standard error). **b** Gaze location-reach termination location distance. Average absolute distance from point-of-gaze to reach termination point. For the real (red) and pantomime (blue) condition at three timepoints: **a** initiation, **b** midpoint, and **c** grasp. (*$p<0.05$, **$p<0.01$, ***$p<0.001$)

Gaze anchoring associated with real reaches for balls in the present study was similar to that reported in previous work for participants reaching to grasp a food item (de Bruin et al. 2008; Sacrey and Whishaw 2012b). For a real reach, a saccade moved visual fixation to the target as the reach was initiated and then, about the time of the grasp, visual fixation on the target was disengaged, often with a blink and head movement. Gaze anchoring was not observed during pantomime reaches, as there was little systematic change in gaze direction from before the initiation of the reach until after the grasp was completed. Whereas for real reaches, the variance in eye fixation relative to the pedestal surface decreased to its lowest values in the second third of the reach, there was no such systematic change in variance during pantomime reaches. To further investigate whether gaze in pantomime reaches was systematically directed to any target, including a participant's reaching hand or the virtual location of the target they were reaching for, measures were made of gaze direction relative to these targets. Although some participants clearly looked at their hand at some point during the reach and other subjects looked towards the virtual target that they were grasping, it was clear that there was no systematic relation of gaze to these targets. Indeed, inspection of gaze in individual subjects suggested that the gaze direction for each participant could change during the reach and was dissimilar across participants and even dissimilar from trial to trial. Taken together, gaze anchoring is absent in any form during pantomime reaching.

Substantial evidence proposes that a reach-to-grasp is the composite of two separate movements, a reach and a grasp, each mediated by a different anatomical pathway from visual cortex through the parietal cortex to the motor cortex (Arbib 1981; Jeannerod 1981; Jeannerod et al. 1994; Culham and Valyear 2006; Cavina-Pratesi et al. 2010; Karl et al. 2013). It is likely that gaze anchoring contributes to some feature of online integration of the reach and the grasp; because if vision is altered by blindfolding or asking a participant to reach for a target in peripheral vision, the reaching movement decomposes, with the reach occurring first to locate the target and the grasp following in response to tactile information obtained from touching the target (Karl et al. 2012; Hall et al. 2014). Although the participants in the present pantomime task were sighted, the results suggested that they made little functional use of vision in relation with their pantomime reaches. Nevertheless, their pantomime movements did reflect experimental contingencies. They did direct their reaches in the general direction of the pedestal's previous location and they did make larger hand shapes for larger targets. Their ability to pantomime a semblance of both the reach and the grasp is likely due to their previous experience with reaching for the different sized balls and to the instructions that requested that they reach for a ball of a particular size, memory features that depend upon perceptual mechanisms.

A number of experiments have attempted to normalize pantomime reaching, mainly by providing the participant with tactile information about the size of the target (Bingham et al. 2007; Chan and Heath 2017; Jazi and Heath 2017; Rinsma et al. 2017). It is also clear from other work that even when participants reach without vision they begin to make more accurate maximum pre-grasp hand shapes for a target if they are able to learn about target features by touching the target a number of times (Karl et al. 2013). Furthermore, magicians, who are professionals at using sleight-of-hand, perform similar real and pantomime reach-to-grasps as long as the target has only been displaced and not removed entirely, which also suggests that practice may improve pantomime kinematics (Cavina-Pratesi et al. 2011). Given that gaze anchoring is a feature of real reaching, it seems possible that were participants given instructions with respect to the use of vision during pantomime, e.g., by asking them to look, or giving them training in looking, their performance may come to more closely resemble real reaching. This possibility could be investigated in future studies. Nevertheless, perhaps, the more relevant question is whether improving pantomime measures through experiential or instructional shifts its performance to neural substrates that mediate real reaching. This question could only be answered by experimental investigation using brain-imaging techniques concurrently with uninstructed and instructed pantomime reaches.

The present study is relevant to other aspects of the relationship between gaze anchoring and reaching movements. Neggers and Bekkering (2000) have discussed the possible relationships between the neural control of both attentional saccades and reaching movements. They suggest that there is an obligatory relation between arm movements and visual saccades. The present study, by demonstrating that pantomime-reaching movements are not associated with gaze anchoring, suggests that any obligatory relationship depends upon the presence of a visual target. Although the neural basis of the coupling of gaze anchoring and reaching is uncertain, Neggers and Bekkering (2000) also review evidence that suggests a role for superior colliculus projections into the cortical dorsal stream in gaze anchoring. Indeed, the monkey Helen who had received a bilateral primary visual cortex removal is reported to display gaze anchoring when reaching for food items (Whishaw et al. 2016). With respect to this idea, a simple distinction between real and pantomime reaching is that the former involves collicular mediation and the latter does not. In this respect, the present findings are also consistent with the idea that the neural basis of exogeneous (bottom up) vs. endogeneous (top–down) attentional processes (Posner 1980; Casarotti et al. 2012) may be dissociated with respect to subcortical vs. cortical sensory guidance. The present results show that whatever neural processes may be involved in generating a pantomime reach movement that resembles a real-reaching movement, in that a fascimily of both the reach and grasp are present, those processes need not concurrently evoke a fascimily of gaze anchoring eye movements.

In conclusion, substantial evidence supports the idea that pantomime reaching, as an intransitive action, is a largely visually independent action. This idea is supported by combined fMRI/DTI imaging of imitative, imagined, and pantomime movements (Vry et al. 2015; Goldenberg 2017). These studies suggest that a ventral parietal/frontal pathway represents the imagined target, whereas a temporal/frontal pathway independent of visual cortex represents the pantomime movement. Collectively, the current study highlights the differences in visual attention in real- and pantomime-grasping movements. Furthermore, this study shows that online visual guidance is essential and tightly coupled to real reach-to-grasp movement, whereas when a reach-to-grasp movement is completed in the absence of a real target, hand and eye movements are uncoupled. Based on these results, we concur that the differential task demands of real vs. pantomime reaching evoke different neural systems, a central tenant of the action–perception theory (Milner and Goodale 2006).

Acknowledgements This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) [JRK], NSERC Discovery Grant [JBD], and NSERC Discovery Grant [JMK]. The authors would like to thank Tsz Yin (Ian) Fung for his help with data collection.

Compliance with ethical standards

Conflict of interest The authors declare no competing financial interests.

References

Arbib MA (1981). Perceptual structures and distributed motor control. Comprehensive physiology

Bingham G, Coats R, Mon-Williams M (2007) Natural prehension in trials without haptic feedback but only when calibration is allowed. Neuropsychologia 45(2):288–294. https://doi.org/10.1016/j.neuropsychologia.2006.07.011

Bridge H, Thomas OM, Minini L, Cavina-Pratesi C, Milner AD, Parker AJ (2013) Structural and Functional changes across the visual cortex of a patient with visual form agnosia. J Neurosci 33(31):12779–12791. https://doi.org/10.1523/Jneurosci.4853-12.2013

Casarotti M, Lisi M, Umilta C, Zorzi M (2012) Paying attention through eye movements: a computational investigation of the premotor theory of spatial attention. J Cogn Neurosci 24(7):1519–1531. https://doi.org/10.1162/jocn_a_00231

Cavina-Pratesi C, Monaco S, Fattori P, Galletti C, McAdam TD, Quinlan DJ, Goodale MA, Culham JC (2010) Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. J Neurosci 30(31):10306–10323. https://doi.org/10.1523/Jneurosci.2023-10.2010

Cavina-Pratesi C, Kuhn G, Ietswaart M, Milner AD (2011). The magic grasp: motor expertise in deception. Plos One, 6(2), e16568

Chan J, Heath M (2017) Haptic feedback attenuates illusory bias in pantomime-grasping: evidence for a visuo-haptic calibration. Exp Brain Res 235(4):1041–1051. https://doi.org/10.1007/s00221-016-4860-9

Coats R, Bingham GP, Mon-Williams M (2008) Calibrating grasp size and reach distance: interactions reveal integral organization of reaching-to-grasp movements. Exp Brain Res 189(2):211–220. https://doi.org/10.1007/s00221-008-1418-5

Cohen NR, Cross ES, Tunik E, Grafton ST, Culham JC (2009) Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: a TMS approach. Neuropsychologia 47(6):1553–1562. https://doi.org/10.1016/j.neuropsychologia.2008.12.034

Culham JC, Valyear KF (2006) Human parietal cortex in action. Curr Opin Neurobiol 16(2):205–212. https://doi.org/10.1016/j.conb.2006.03.005

de Bruin N, Sacrey L-AR, Brown LA, Doan J, Whishaw IQ (2008) Visual guidance for hand advance but not hand withdrawal in a reach-to-eat task in adult humans: reaching is a composite movement. J Motor Behav 40(4):337–346

De Stefani E, Innocenti A, De Marco D, Busiello M, Ferri F, Costantini M, Gentilucci M (2014) The spatial alignment effect in near and far space: a kinematic study. Exp Brain Res 232(7):2431–2438. https://doi.org/10.1007/s00221-014-3943-8

Fukui T, Inui T (2013) Utilization of visual feedback of the hand according to target view availability in the online control of prehension movements. Hum Mov Sci 32(4):580–595. https://doi.org/10.1016/j.humov.2013.03.004

Gentilucci M, Chieffi S, Daprati E, Saetti MC, Toni I (1996) Visual illusion and action. Neuropsychologia 34(5):369–376

Goldenberg G (2017) Facets of pantomime. J Int Neuropsychol Soc 23(2):121–127. https://doi.org/10.1017/S1355617716000989

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349(6305):154–156. doi:https://doi.org/10.1038/349154a0

Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. Neuropsychologia 32(10):1159–1178. https://doi.org/10.1016/0028-3932(94)90100-7

Hall LA, Karl JM, Thomas BL, Whishaw IQ (2014) Reach and Grasp reconfigurations reveal that proprioception assists reaching and hapsis assists grasping in peripheral vision. Exp Brain Res 232(9):2807–2819. https://doi.org/10.1007/s00221-014-3945-6

Hoeren M, Kummerer D, Bormann T, Beume L, Ludwig VM, Vry MS, Mader I, Rijntjes M, Kaller CP, Weiller C (2014) Neural bases of imitation and pantomime in acute stroke patients: distinct streams for praxis. Brain 137:2796–2810. https://doi.org/10.1093/brain/awu203

Holmes SA, Lohmus J, McKinnon S, Mulla A, Heath M (2013) Distinct visual cues mediate aperture shaping for grasping and pantomime-grasping tasks. J Motor Behav 45(5):431–439. https://doi.org/10.1080/00222895.2013.818930

James TW, Culham J, Humphrey GK, Milner AD, Goodale MA (2003) Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain 126:2463–2475. https://doi.org/10.1093/brain/awg248

Jazi SD, Heath M (2017) The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. Brain Cogn 114:29–39. https://doi.org/10.1016/j.bandc.2017.03.002

Jeannerod M (1981). Intersegmental coordination during reaching at natural visual objects. Attention and Performance IX

Jeannerod M, Decety J, Michel F (1994) Impairment of grasping movements following a bilateral posterior parietal lesion. Neuropsychologia 32(4):369–380. https://doi.org/10.1016/0028-3932(94)90084-1

Karl JM, Sacrey L-AR, Doan JB, Whishaw IQ (2012) Hand shaping using hapsis resembles visually guided hand shaping. Exp Brain Res 219(1):59–74

Karl JM, Schneider LR, Whishaw IQ (2013) Nonvisual learning of intrinsic object properties in a reaching task dissociates grasp from reach. Exp Brain Res 225(4):465–477

Króliczak G, Cavina-Pratesi C, Goodman DA, Culham JC (2007) What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. J Neurophysiol 97(3):2410–2422. https://doi.org/10.1152/jn.00778.2006

Kuntz JR, Whishaw IQ (2016) Synchrony of the reach and the grasp in pantomime reach-to-grasp. Exp Brain Res 234(11):3291–3303. https://doi.org/10.1007/s00221-016-4727-0

Milner AD, Goodale MA (2006). The visual brain in action. Oxford University Press

Milner AD, Goodale MA (2008) Two visual systems re-viewed. Neuropsychologia 46(3):774–785. https://doi.org/10.1016/j.neuropsychologia.2007.10.005

Milner A, Dijkerman H, Pisella L, McIntosh R, Tilikete C, Vighetto A, Rossetti Y (2001) Grasping the past: delay can improve visuomotor performance. Curr Biol 11(23):1896–1901

Neggers SFW, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. J Neurophysiol 83(2):639–651

Posner MI (1980) Orienting of attention. Q J Exp Psychol 32(1):3–25

Prablanc C, Echallier JE, Jeannerod M, Komilis E (1979) Optimal response of eye and hand motor systems in pointing at a visual target. 2. Static and dynamic visual cues in the control of hand movement. Biol Cybern 35(3):183–187. https://doi.org/10.1007/Bf00337063

Rinsma T, van der Kamp J, Dicks M, Canal-Bruland R (2017) Nothing magical: pantomimed grasping is controlled by the ventral system.

Exp Brain Res 235(6):1823–1833. https://doi.org/10.1007/s00221-016-4868-1
Sacrey L-AR, Whishaw IQ (2012a) Subsystems of sensory attention for skilled reaching: Vision for transport and pre-shaping and somatosensation for grasping, withdrawal and release. Behav Brain Res 231(2):356–365. https://doi.org/10.1016/j.bbr.2011.07.031
Sacrey LAR, Whishaw IQ (2012b) Subsystems of sensory attention for skilled reaching: Vision for transport and pre-shaping and somatosensation for grasping, withdrawal and release. Behav Brain Res 231(2):356–365. https://doi.org/10.1016/j.bbr.2011.07.031
Vry MS, Tritschler LC, Hamzei F, Rijntjes M, Kaller CP, Hoeren M, Umarova R, Glauche V, Hermsdoerfer J, Goldenberg G, Hennig J, Weiller C (2015) The ventral fiber pathway for pantomime of object use. Neuroimage 106:252–263. https://doi.org/10.1016/j.neuroimage.2014.11.002
Westwood DA, Chapman CD, Roy EA (2000). Pantomimed actions may be controlled by the ventral visual stream. Exp Brain Res, 130(4)
Whishaw IQ, Suchowersky O, Davis L, Sarna J, Metz GA, Pellis SM (2002) Impairment of pronation, supination, and body co-ordination in reach-to-grasp tasks in human Parkinson's disease (PD) reveals homology to deficits in animal models. Behav Brain Res 133(2):165–176
Whishaw IQ, Karl JM, Humphrey NK (2016) Dissociation of the reach and the grasp in the destriate (V1) monkey Helen: a new anatomy for the dual visuomotor channel theory of reaching. Exp Brain Res 234(8):2351–2362. https://doi.org/10.1007/s00221-016-4640-6