

Research report

Two types of memory-based (pantomime) reaches distinguished by gaze anchoring in reach-to-grasp tasks

Jessica R. Kuntz^a, Jenni M. Karl^b, Jon B. Doan^c, Melody Grohs^d, Ian Q. Whishaw^{a,*}^a Department of Neuroscience, Canadian Centre for Behavioral Neuroscience, University of Lethbridge, Lethbridge, Canada^b Department of Psychology, Thompson Rivers University, Kamloops, Canada^c Department of Kinesiology & Physical Education, Engineering & Human Performance Lab, University of Lethbridge, Lethbridge, Canada^d Alberta Children's Hospital Research Institute, Department of Neuroscience, University of Calgary, Calgary, Canada

ARTICLE INFO

Keywords:

Action perception theory and pantomime

Dual visuomotor channel theory

Gaze anchoring

Memory-based reach

Pantomime reaching

Reach-to-eat and pantomime

Reach-to-grasp and pantomime

Target-based reach

Visually guided reaching

Visual attention and reach-to-grasp

ABSTRACT

Comparisons of target-based reaching vs memory-based (pantomime) reaching have been used to obtain insight into the visuomotor control of reaching. The present study examined the contribution of gaze anchoring, reaching to a target that is under continuous gaze, to both target-based and memory-based reaching. Participants made target-based reaches for discs located on a table or food items located on a pedestal or they replaced the objects. They then made memory-based reaches in which they pantomimed their target-based reaches. Participants were fitted with hand sensors for kinematic tracking and an eye tracker to monitor gaze. When making target-based reaches, participants directed gaze to the target location from reach onset to offset without interrupting saccades. Similar gaze anchoring was present for memory-based reaches when the surface upon which the target had been placed remained. When the target and its surface were both removed there was no systematic relationship between gaze and the reach. Gaze anchoring was also present when participants replaced a target on a surface, a movement featuring a reach but little grasp. That memory-based reaches can be either gaze anchor-associated or gaze anchor-independent is discussed in relation to contemporary views of the neural control of reaching.

1. Introduction

Reaching to grasp an object (reach-to-grasp) is an everyday act that includes picking up a pencil, a book, or a morsel of food [1]. The control of the movement is proposed to come from visual guidance [2–5] and a candidate visual behavior is gaze anchoring. In a seminal study, Prablanc [6] observed that when participants point to a target, they fixed their gaze on the target from the initiation of the movement to its completion. Gaze anchoring is also found to be associated with a reach-to-grasp movements, in which participants make a saccade to anchor their gaze on an item from the point of reach initiation to the grasp, at which time they visually disengage, often with a blink and/or head shift [7–15]. The importance of gaze for a reach for a food item but not the withdraw movement to place the food item in the mouth is demonstrated by a disruption produced by visual occlusion during the reach [9,16]. The relation between reaching and gaze anchoring is not obligatory, however. Gaze anchoring is reported to be absent when participants make memory-based reaches in a variety of test situations

in which most cues related to the task are altered. For example, gaze anchoring is absent when participants make a memory-based reach with the target object and the surface on which it had been located removed or when they perform memory-based reaches in the dark [17,18].

The presence of gaze anchoring during target-based reaches vs its absence during memory-based reaches raises the question of whether gaze anchoring would also be absent in conventional memory-based (pantomime) tasks in which only the target is removed but the context; i.e., the surface on which the target had been placed remains [19–26]. This question was examined in the present study by asking participants to make target-based reaches for three different sized discs placed at different distances on a table in a task similar to that used by Goodale et al. [20] or reach for food items located on a pedestal in a task similar to that used by Kuntz et al. [18]. Target-based reaches were followed by memory-based reaches with only the target removed. In addition, to confirm that gaze anchoring is absent when additional contextual cues are changed, participants in the pedestal task were also asked to make

* Corresponding author at: Department of Neuroscience, Canadian Centre for Behavioral Neuroscience, 4401 University Drive West, University of Lethbridge, Lethbridge, AB, T1K 3M4, Canada.

E-mail address: whishaw@uleth.ca (I.Q. Whishaw).

<https://doi.org/10.1016/j.bbr.2019.112438>

Received 9 July 2019; Received in revised form 13 December 2019; Accepted 14 December 2019

Available online 16 December 2019

0166-4328/ © 2019 Elsevier B.V. All rights reserved.

memory-based reaches with the pedestal moved or removed. An additional experiment examined whether a reach alone, without the concurrent hand shaping for grasping, is associated with gaze anchoring. Reaching and hand shaping were examined as participants reached for a food item that they placed in the mouth whereas only reaching was examined as participants replaced the food item at the location that it had previously occupied.

Second year university students made target-based reaches for different sized discs located on a table or made memory-based reaches with the disc removed. They also made target-based reaches for food items located on a pedestal and made memory-based reaches with only the pedestal present, the pedestal moved or removed. Finally, they either made a target-based reach for food from a pedestal to be placed in the mouth or took food items from the mouth and placed them on the pedestal. Hand movements were recorded with electromagnetic sensors attached to the thumb, index, and wrist and eye movements were recorded with a head-mounted, video-based eye tracker.

2. Materials and methods

2.1. Participants

Participants were 32 right-handed young adults (26 male, 26 female, mean age 19.95 ± 0.9 months) recruited from Thompson Rivers University introductory psychology classes. Participants were confirmed to be right-handed by completing the Brainmapping questionnaire adapted from the Edinburgh inventory [27]. Each participant gave informed consent, authorized use of photos or videos, were self-reported as having no history of neurological, sensory, or motor disorders as well as normal, or corrected-to-normal, visual acuity. The Thompson Rivers University, Human Subject Research Ethics Committees approved the study. Participants received class credit for their participation.

2.2. Target objects

2.2.1. Discs

The participants reached for three black discs that had a diameter of 30 mm, 50 mm, and 60 mm, and were 10mm thick. Discs were chosen as target objects in order to minimize the demands of changing hand orientation associated with reaching for quadrilateral objects, as used by [20,28].

2.2.2. Food items

Two target food objects were used. One group of participants reached for skittles, an oval candy with approximate diameter of 8.3 mm (average of 10 measurements) and the other group reached for a round donut ball (Timbit) with a diameter of approximately 28.8 mm (average of 10 measurements). The donut ball was firm and did not indent when normally grasped [18,24].

2.3. Video recording

Two video cameras recorded behavior throughout the experiment. Filming was performed at a sampling rate of 30 Hz and 1/1000 shutter speed. For the reach-for-disc task, one camera was placed to capture a lateral view and one camera was placed to capture a dorsal view, which was also used to facilitated correct placement of the target. For the reach-to-eat task, cameras were placed to capture both frontal and lateral views.

2.4. Hand kinematics

Thumb, index, and wrist movements were acquired at a sampling rate of 60 Hz using a trakSTAR® (Ascension Technology Corporation) system. At the distances recorded, sensitivity is 1.4 mm RMS Position

and 0.5° RMS orientation. The position of the digits and wrist were 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. The relation between the digit location and the pedestal was measured in relation to a sensor on the pedestal. Measurement of grasp aperture was made from the sensors on the thumb and index finger, with adjustment made for the approximate distance of the sensor from the center of the digit pad. 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. The record obtained from the wrist was synchronized to the video record so that movements of interest could be concurrently identified from both records.

2.5. 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 90 Hz. A sixteen-point eye calibration was performed with a calibration grid prior to data collection and was adjusted, as necessary, during the experiment when there was a discrepancy between gaze-point and the target to be fixated. Prior to beginning an experiment, calibration was checked by having the participants look at a number of target objects in the room while their gaze location was monitored by the experimenter who observed the world view on the video screen. By default, the calculated *GazePoint* [this is the point of visual fixation in the subsequently generated video] is given in normalized window coordinates, that is: 0.0,0.0 at the top left, 0.5,0.5 in the center, and 1.0,1.0 at the bottom right and these values are always correct. Because the eye tracker provided a world view of the participant's gaze and hand as they reached, this view obtained on Point Picker (ImageJ, Natick, MA, USA) was used to obtain measures of the relationship of gaze and the hand in x/y coordinates and to count any saccades associated with each reach movements.

3. Reaching tasks

3.1. Reach-for-disc task

Ten participants performed the reach-for-disc task. Each of the participants reached for each of the three discs at each of the three distances. Trials were given in pairs and consisted of three trial pairs; a target-based trial followed by a target-based trial, a target-based trial followed by a memory-based trial with vision, or a target-based trial followed by a memory-based trial without vision.

Participants were seated at a table and immediately before them, aligned with the table's edge, was a 55.8 cm \times 35.5 cm sheet of white cardboard that formed the work area and on which the target discs could be placed (Fig. 1). An "x" marked on the lower center of the cardboard served as the reach starting location upon which a participant placed their opposed thumb and index finger. The work area was video monitored and the experimenter used the monitor to place the target disc at predefine locations at the midline of the workspace at distances of 10, 20 and 30 cm from the "x". The task was modeled on that used by Goodale et al. [28]. Three types of reaching trials were given:

Target-based reach

The disc was present, and the participant picked it up and placed it beside the work area. A participant was given the instruction, "we would like you to reach for the disc, pick it up, and place it to one side".

Memory-based reach

The disc was absent, and the participant pretended to pick up the disc at the location at which it had been located on the previous trial. A

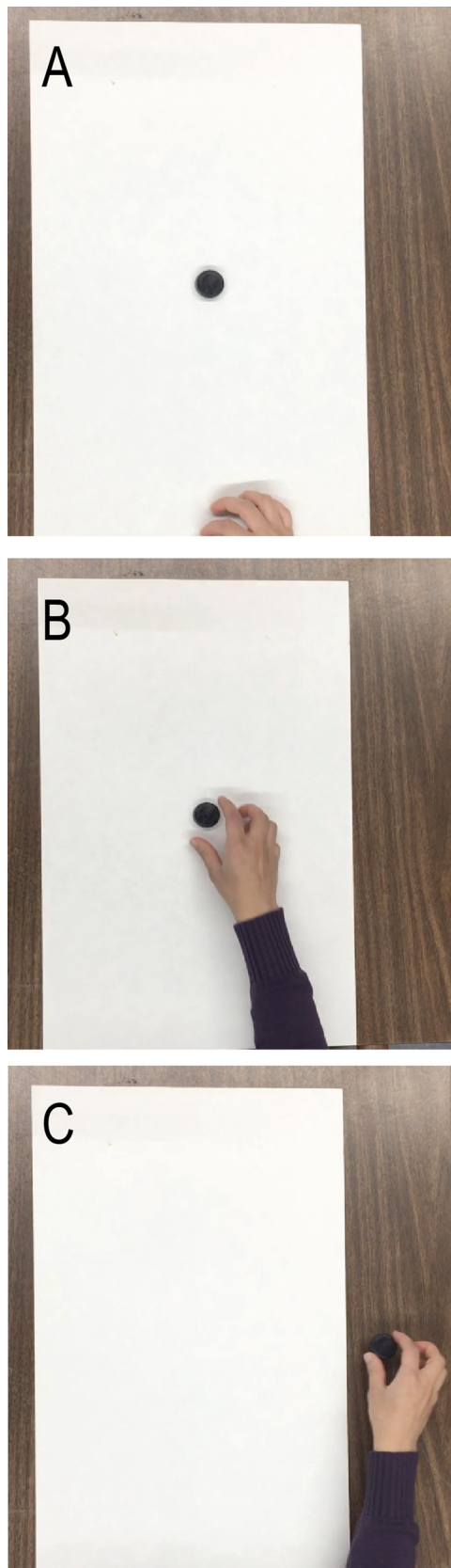


Fig. 1. The reach for disc task. (A) The hand at the starting position of the workspace. (B) The hand about to grasp a small disc at a 20 cm distance. (C) Placing the disc to the side of the workspace.

participant was given the instruction, “if the disc is not there, we would like you to pretend to pick up the disc that you reached for on the previous trial at its previous location and place it to one side”.

Memory-based reach without vision

The disc was absent, and the participant pretended to pick up the disc at the location at which it had been on the previous trial without using vision. A participant was given the instruction, “we would like you to keep your eyes closed and to pretend to reach for and pick up the disc that you reached for on the previous trial at its previous location and place it to one side”.

The participants were asked to close their eyes to begin each trial. On the command “open reach” they were to open their eyes and make a target-based reach if the target was there, and if it was not there to make a memory-based reach for the previous target at its previous location. On the command “close reach” they were to keep their eyes closed and make a memory-based reach for the preceding target at its preceding location. Participants were given a number of practice trials so that they understood the instructions. Because some participants performed a pantomime grasp by completely closing their thumb and index finger [24], this was pointed out to them in the practice trials, and they were asked to pretend to actually grasp the object for which they were pretending to reach.

The participants completed three trial pairs at each of the three locations with each of the different sized discs and the result were taken from the second trial of each pair (27 target-based, 27 memory-based vision, and 27 memory-based no vision). The trial pairs were presented in a mixed order in such a way that a participant would not be certain about the disc size or its distance on any target-based reach and they would not be certain whether they were to make a another target-based reach, a memory-based reach with vision, or a memory-based reach without vision. Trials were given at about 30 s intervals with a participant instructed to close their eyes followed by a prompt to begin a designated trial.

3.2. Reach-to-eat task

Participants were seated in an upright position with feet flat on the floor, with a self-standing height-adjustable pedestal placed in front of them (Fig. 2). The surface of the pedestal was a triangular metal plate with each side of the triangle measuring 9 cm. The pedestal was placed at a horizontal reach distance normalized to the participant’s arm length (100 % of the length from the shoulder to the tip of the index finger with the elbow at about 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 [29,30]. A flat edge of the pedestal faced the participant. This experimental setup allowed participants to reach with their right hand towards the pedestal to pick up the target.

The start position for the right reaching hand was marked by a piece of tape on the thigh, and participants started with their thumb and index finger in opposition. The left hand was resting in an open and relaxed position on the left upper thigh. Because participants display a wide variety of natural grasping preferences [31], the participants were given no instructions on how they should reach or grasp the target. Pretraining was done to ensure the participants were practiced on the task and 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 from the investigator. The reach-to-eat task was given in the four different contexts as is illustrated in Fig. 2. The idea was that following performance of a number of real reaches, participants were to pantomime that movement in the three additional contexts as described by Kuntz and Whishaw [24].

One group of 12 participants reached for the skittle and one group of 10 participants reached for the donut ball. Kinematic measures of

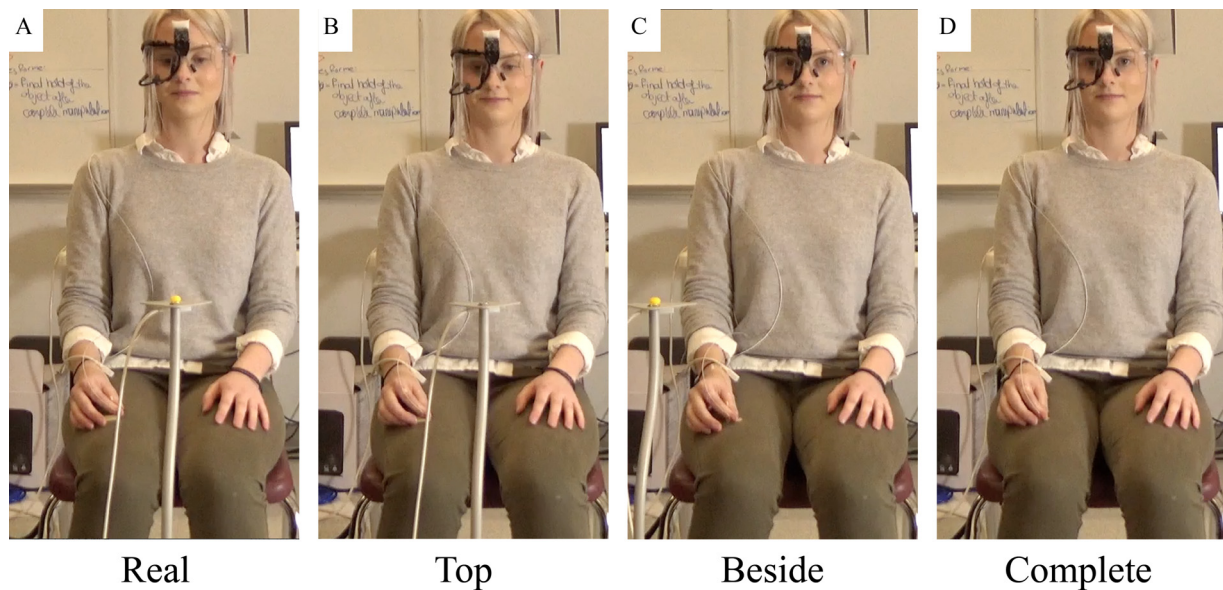


Fig. 2. Target-based and memory-based reaching contexts. (A) Target-based, a skittle target is on the pedestal. (B) Memory-based top, pedestal present but target absent, (C) Memory-based beside, the pedestal and target are displaced to the right side of their previous location but they do not obstruct the reach to the pedestal's former location. (D) Memory-based complete, neither the pedestal nor the target is present. In all conditions, participant reached from the lap to pick up (context A) or pantomime (contexts B–D) picking up the target object to bring it back to their mouth as if to eat it.

reach movements and hand shaping were made from all participants. Adequate eye movement results were only successfully obtained from 10 participants who reached for the skittle and 7 participants who reached for the donut ball. The participants received 8 practice trials in which they reached out and grasped an object and brought it back toward their mouth. Accordingly, the participants viewed the experimenter place the food on the pedestal, or displace or remove the food and pedestal, and they had a number of seconds to view the target before they were required to reach for it.

Reaches in the real condition were completed prior to the pantomime conditions to ensure that the participants were familiar with the real condition and then they performed pantomime movements in different contexts. Thus, after performing 8 real reaches, the participants then performed 3 sequential reaches in each pantomime condition, but the order of the pantomime tasks was different for each participant [32].

Target-based reach

Pedestal and target present. For the real condition, participants were instructed to “reach out and grasp the target and bring it to your mouth as if to eat it”.

Top, memory-based reach

With the pedestal present and the target absent, the participants were instructed to, “pretend to reach out and grasp the target object and bring it to your mouth as if to eat it as you did when the target was present.”

Beside memory-based reach

Pedestal and target present but shifted to the right about 10 cm. The participants were instructed to, “pretend to reach out and grasp the target object and bring it to your mouth and pretend to eat it as you did when the target was present at its previous location.”

Complete memory-based reach

Pedestal and target absent. The participants were given the instruction, “pretend to reach out and grasp the target object and bring it to your mouth as if to eat it, as you did when the target was present”.

3.3. Reach-to-replace task

Of twenty-two participants (the same participants that performed the reach-to-eat task), 12 reached for the skittle and 10 reached for the donut ball, and the eye tracker was used to monitor eye movements. Both groups of participants performed the reach-to-eat task and the reach-to-replace task. Participants adopted the start position between trials and waited for a start prompt which was a verbal 1-2-3- GO command from the investigator. Accordingly, the participants viewed the experimenter place the food on the pedestal or the participant placed the food object in their mouth, and they had a number of seconds to view the pedestal before they were required to reach. Participants were seated in an upright posture with the height-adjusting pedestal placed directly in front of them, as described for the reach-to-eat task. Participants performed two tasks, the reach-to-eat task and the reach-to-replace task:

Reach-to-eat

Participants began in the starting position, hands on the lap, reached towards the food item placed on the pedestal, grasped it, and placed it into their mouth as if to eat it. They were given the instruction, “we would like you to reach for the food item and place it in your mouth as if to eat it”. Participants performed 4 reach-to-eat trials.

Reach-to-replace

A participant took a food item and placed it between their lips after which they placed their hands on their lap. A trial began with hands in the starting position on the lap. The instruction was, “we would like you to reach for the food item in your mouth and place it on the pedestal”. Participants performed 4 reach-to-replace trials.

4. Behavioral measures

4.1. Gaze

Visual fixation, relative to the visual scene, was analyzed using Point Picker (ImageJ, Natick, MA, USA) or PixelStick Graphics (Plum Amazing Software LLC), programs for measuring x/y pixel distances on a screen for the following measurements:

Spatial relationship between gaze location and the pedestal in the reach-to-eat task

Measures of gaze point, the point indicated by the eye tracker of where a participant was looking, were made on each frame for each reaching trial relative to the center of the pedestal. On memory-based trials, the location at which the pedestal had been on the target-based trials was used to define the location of the “center of the pedestal”. Measurements began 10 frames prior to reach initiation and ended 10 frames after grasp completion. Because reach durations could vary slightly between trials and subjects, for statistical analyses, data were interpolated to plot average visual trajectory in relation to reach time.

Temporal Relationship between gaze location and the grasp location in the reach-to-eat task

On the memory-based trials on which the pedestal was absent, it was thought possible that participants might choose a point in space to which to first direct their gaze and then direct their hand to that location. If they did this, then at the instance of the pretend grasp, their gaze location and their grasp location would coincide. Therefore, a measure of gaze location, the location indicated by the eye tracker of where a participant was looking, was made relative to the tip of the index finger. Measurements began 10 frames prior to reach initiation and ended 10 frames after grasp completion. For statistical analyses, data were interpolated to plot average visual trajectory in relation to reach time.

Gaze ratings

On target-based trials, the gaze location was usually very close to the target’s location and so the hand moved to this point. On memory-based trials with the platform absent, the gaze location relative to the hand’s location was observed to be much different, with a participant sometimes tracking the hand or looking away from the location to which they were reaching. A scoring system was used to assess these gaze behaviors. The reaches were examined frame-by-frame and subject to a three-point rating (Fig. 3). A score of “0” was given if the gaze point was proximate to the target (on or right beside the target) at the time that the digits were closing to grasp; a score of “1” was given if the gaze point was on the upper hand or arm, a score of “2” was given if the gaze point was at a location other than the target, hand, or body.

Number of saccades and blinks

Counts of saccades were made from the eye tracker worldview by stepping through the video record frame-by-frame and noting the position of the gaze relative to the scene. Any saccade, a rapid shift of gaze from one location to another during a reach (between hand movement

initiation and withdraw), was counted as one saccade. Smooth pursuit movements, which sometimes shifted gaze slightly as the hand approached the target or which sometimes followed the hand on trials on which a target was not present, were not included in the saccade count. Saccades that were directed toward the region of the platform’s location just as hand motion began or saccades that occurred at about the time of the grasp; i.e., engage and disengage saccades, were also not included in the saccade count. Thus, the count of saccades was limited to the period from the initiation of the reach to the occurrence of grasp of the target (see below). Blinking was defined as any closure of the eyelid as viewed by the disappearance and reappearance of the gaze point marker on the worldview video record. Blinks were included in the saccade count if they occurred between reach initiation and the occurrence of the grasp.

4.2. Hand movement kinematics

Kinematic events were processed using custom-written algorithms created in Matlab® (Version R2016b; The Mathworks, Natick, MA, USA). To mark the beginning of a trial, a participant made a lateral movement with the reaching hand before they placed the hand on the start position with the first two digits in opposition. Movement initiation was defined as a minimum forward wrist velocity of 5 mm/sec after the start command with continued forward motion to the grasp. The time of movement initiation on the tracker record of wrist movement was used to link the tracker record to the video record so that each hand measure from the tracking record measurement could be confirmed by inspecting the video record. Movement withdrawal was defined as a negative wrist velocity movement of 5 mm/sec that was associated with continued hand movement to task completion. The following measures were made of the reach and the grasp as defined by Karl et al. (2012):

Maximum pre-grasp aperture (MPA)

The maximum pre-grasp aperture or MPA, was defined as the maximum index-thumb aperture obtained between movement initiation and withdraw.

Terminal grasp aperture (TGA)

Terminal grasp aperture or TGA (the grasp or pretend grasp) was defined as the minimal closing aperture between the index finger and thumb between the beginning of the reach and the beginning of the withdraw.

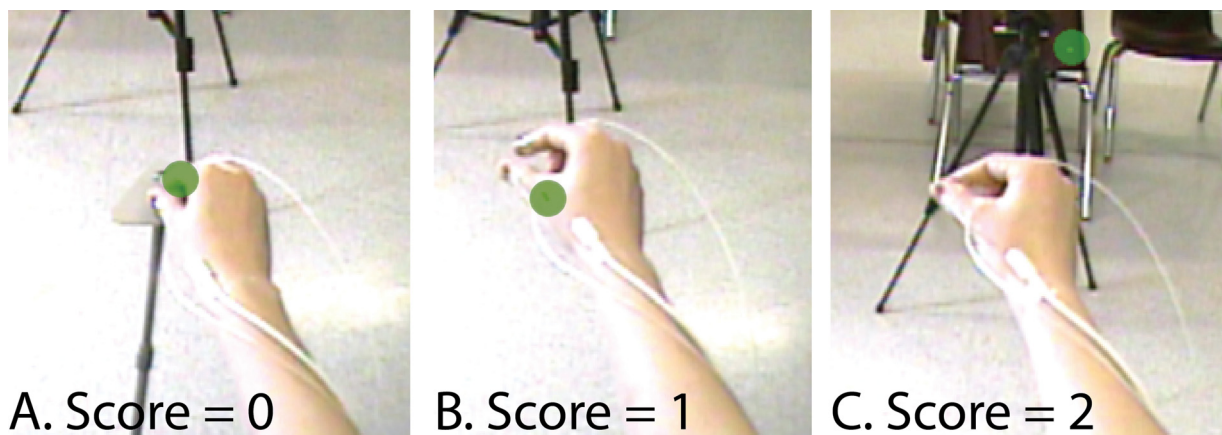


Fig. 3. Rating scale for scoring the relationship between the hand at the grasp and concurrent gaze point. (A) A score of “0” was given if the gaze point was remained throughout the reach on a point to which the index finger and thumb arrived for the grasp. (B) A score of “1” was given if the gaze point was on the hand or followed the hand during the reach. (C) A score of “2” was given if the gaze point was at a location to which the hand did not reach. Note: only for a score of “0” was the gaze anchored at a point to which the thumb and index finger were directed.

Reach distance relative to the target

Reach distance relative to a real target was the distance from the center of the platform to the tip of the index finger at TGA. Reach distance relative to a virtual target was the distance from the virtual center of the platform to the tip of the index finger at TGA.

Reach duration

The duration of the reach was measured from the point of first movement of the hand to the point of the first withdraw movement after TGA.

4.3. Statistical analysis

The numerical data were analyzed using repeated-measures analyses of variance (ANOVA) with the statistical program SPSS (v.24.0.0). Results are reported as mean \pm standard error. A p value of < 0.05 was considered significant.

5. Results

5.1. Reach-for-disc task

5.1.1. Gaze measures for reaching for a disc

On target-based trials, the target disc present, participants directed their gaze to the disc just as they initiated the reaching movement. Their gaze remained close to, or on, the target until it was grasped. As the target was grasped, their gaze shifted to a point beside the work area at which location they placed the disc. Gaze was similar on memory-based trials. Gaze was directed to a point close to the previous location of the disc as the reach was initiated and remained there until the participants made a memory-based grasp. When participants pantomimed the movement of placing the disc beside the work area, gaze was directed to the point at which they pantomimed the release of the disc.

Fig. 4 shows that the gaze point relative to the target location for target-based reaches and the gaze point of the pretend grasp for memory-based reaches was similar. Fig. 4A gives examples of the relation between gaze location and the disc at the midpoint of the reach (when gaze point variance is typically low, Kuntz et al. [18]) on one trial for each participant. Fig. 4A-left gives examples of the location of the gaze point and the location of the disc for a target-based reach. Fig. 4A-right gives examples of gaze point and the estimated disc location (as defined as the location at which a participant made a memory-based grasp) for a memory-based reach.

Fig. 4B shows a summary (for all disc sizes and locations) of the distance between the gaze point and the target at reach initiation, midpoint, and grasp. Overall, gaze was anchored in close proximity to the edge of the disc on target-based trials and close to the grasping point of the pretend target on memory-based trials at all three time points of the reach. Note that the average distance of the edge of the disc to its center was 23.3 mm and so gaze point averages shown in Fig. 4B close to the disc's real or estimated edge throughout both target-based and memory-based reaches.

The statistical analysis of distance (x/y measure from the center of the gaze marker to the center of the target) indicated the target-based and memory-based reaches were not different in contexts in which the disc was present or absent, Context $F(1,9) = 4.27$, $p = 0.069$. Gaze did get slightly closer to the target between reach initiation and the grasp, Distance $F(2,18) = 11.78$, $p < 0.001$, and this relationship was similar for target-based reaches and memory-based reaches as indicated by the absence of a significant interaction of Context by Distance $F(2,18) = 0.17$, $p = 0.849$.

5.1.2. Kinematic measures of reaching for a disc

Fig. 5 summarizes the results of kinematic measures in the reach-for-disc task. For the analyses, disc size and reach distances were

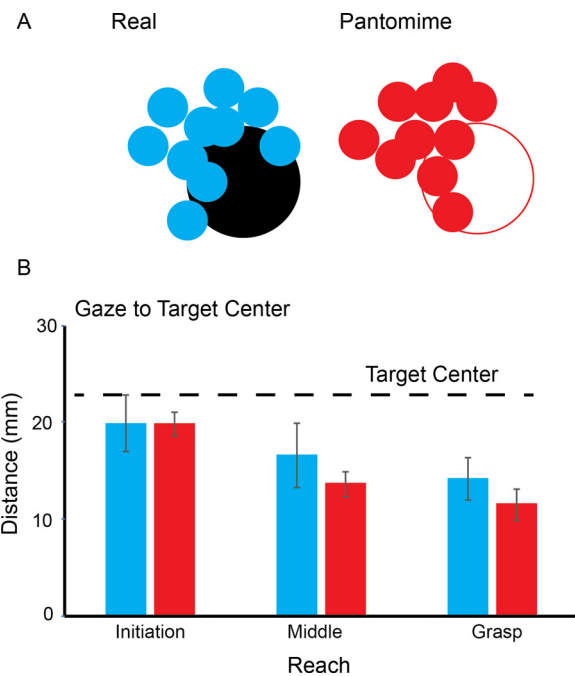


Fig. 4. Gaze point and target disc location for target-based and memory-based reach-to-grasp. (A) Solid circles illustrate gaze point locations relative to the small disc target at the midpoint of a target-based (right) and memory-based (left) reach. The disc location for the memory-based reach is normalized relative to the grasp location at terminal grasp aperture. (B) Distance from gaze point to the midpoint of the disc target for real and pantomime reaches. Note: there is no significant difference in gaze point/target distance for target-based and memory-based reaches.

averaged. There were differences in most kinematic measures between target-based and memory-based reach to grasp movements, and the changes depended upon whether the memory-based reaches were made with or without vision. In short, as detailed below, memory-based reaches were largely different from target-based reaches and memory-based reaches were still more different without vision, confirming previous studies [24,28]:

Maximum pregrasp aperture (MPA)

Fig. 5A shows MPA was smaller for the memory-based reach made with vision than for the target-based reach and the MPA was larger for the memory-based reach without vision than the target-based reach, Context $F(2,18) = 10.44$, $p = 0.001$. The smaller MPA for a memory-based reach with vision is similar to that obtained by Goodale et al. [28] whereas the larger MPA without vision is consistent with the report of Kuntz and Whishaw [24].

Terminal grasp aperture (TGA)

Fig. 5B shows that TGA was similar for the target-based reaches and the memory-based reaches, Context $F(2,18) = 1.03$, $p = 0.377$.

Distance hand-target

Fig. 5C shows that the distance between the grasp location for the memory-based condition with vision was larger than for the target-based reach and was larger still for the memory-based reach made without vision, Context $F(2,18) = 7.96$, $p < 0.001$. The better accuracy with vision than without vision confirms that participants are using vision to assist memory-based reaches.

Reach duration

Fig. 5D shows that reach duration for the memory-based reach with vision was smaller than for the target-based reaches and smaller still for the memory-based reaches without vision, Context $F(1,18) = 10.33$,

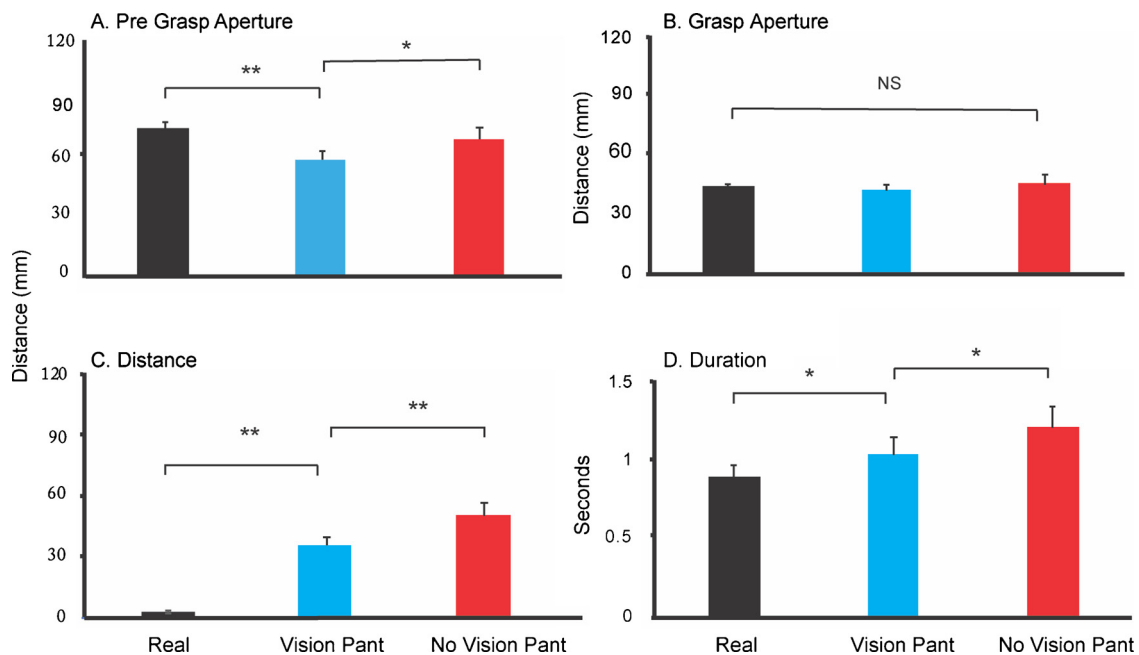


Fig. 5. Reach-for-disc kinematic measures (mean \pm se) for real and pantomime movements. Results averaged for different sized discs located at different distances. (A) Maximum pre-grasp aperture. (B) Terminal grasp aperture. (C) Minimum distance between the platform's location at terminal grasp aperture, (D) Reach duration from grasp initiation to terminal grasp. Differences, * $p < 0.05$, ** $p < .01$.

$p < 0.001$.

5.2. Reach-to-eat task

5.2.1. Gaze measures for reaching for a food item

Overall, gaze was anchored close to the food target on target-based trials throughout a reach for a food item (Video 1). Gaze was similarly anchored in proximity to the center of the platform throughout the reach when participants made memory-based reaches with the platform present and the food item absent (Video 2). For the memory-based reaches made with the platform moved (beside) or absent (complete), there was no systematic relationship between gaze and the former location of the target or to the location at which a participant made a pantomime grasp (Video 3).

Fig. 6 summarized the relation between the gaze point and the spatial location at which the grasp occurred. Fig. 6-top gives a summary of the closeness to the target rating and Fig. 6 bottom gives a summary of saccade counts. Scores on both measures were similar for the donut and for the skittle. Scores were also similar for the target-based and memory-based trials with the pedestal present. With the food item and pedestal moved or removed, there was no systematic relation between gaze and the platform's previous location and participants made saccades during the reach.

These conclusions were supported by the statistical analyzes that gave similar ratings for the two targets, the skittle and for the donut ball, Target $F(1,15) = 0.15$, $p > 0.05$ and similar saccade counts for the two targets, Target $F(1,15) = 0.26$, $p > 0.05$. There was an effect of context, the gaze point and the grasp points were significantly different when the pedestal was moved or absent, Context, $F(3,45) = 23.20$, $p < 0.001$. In addition, more saccades occurred during reaches when the pedestal was moved or absent, Context, $F(3,45) = 35.60$, $p < 0.001$. Because the point of gaze was variable for the beside and complete pantomime contexts between subjects, it was not possible to determine whether there was any systematic relationship of gaze to the grasp (see also Kuntz et al. [18]). For example, some participants looked at their hand and following it during the reach, some participants looked elsewhere, and gaze changed during the reach for many participants.

5.2.2. Temporal relations of the gaze point

It was expected that gaze would be directed to the target on target-based reaches. With the target absent, gaze anchoring could still occur and be directed either to the target's previous location or gaze could also be directed to the location at which a participant was directing their reach at a location other than the target's previous location. Therefore, one measurement made was of gaze in relation to the pedestal's previous location and a second measurement was made of gaze in relation to the point at which the grasp was made:

Temporal relationship between gaze point and the pedestal

The reach durations were longer for the skittle than the donut and so separate group analyses were used to confirm an overall effect of time for the Skittle, $F(52,468) = 7.91$, $p < 0.001$, and for the Donut ball, $F(44,264) = 3.83$, $p < 0.001$.

Fig. 7 presents gaze x/y location curves illustrating the location of gaze relative to the center (or virtual center), of the platform as the reaching movement was performed. (The curves begin 10 frames before the initiation of hand movement and end 10 frames after the completion of the grasp.) Because the participants were given no instructions with respect to where and when they should look, pre reach gaze was haphazardly directed around the room for each subject [9]. The curves show that in the real and top conditions, participants visually engaged the pedestal as the reach began, looked at the pedestal throughout the reach, and visually disengaged the pedestal at about the point that the grasp took place. The change in the curves at about reach initiation and grasp termination appear to have a smooth onset, but this is related to the averaging of gaze locations across all of the participants.

The curves for the skittle (Fig. 7, top) and for the donut ball (Fig. 7, bottom) show that gaze point shifted in the direction of the grasping work area as a reach was initiated and shifted away from the direction of the grasping work area at about the time that the grasp was made. The gaze curves in Fig. 7 indicate that the gaze location for the real and top conditions came close to the target, remained proximate to target for much of the reach, and featured the smallest variance at about the midpoint of the reach, features that reflect gaze anchoring (confirming Kuntz et al. [18]). The gaze curves for the beside and complete contexts were not closely related to the pedestal's previous center and had high

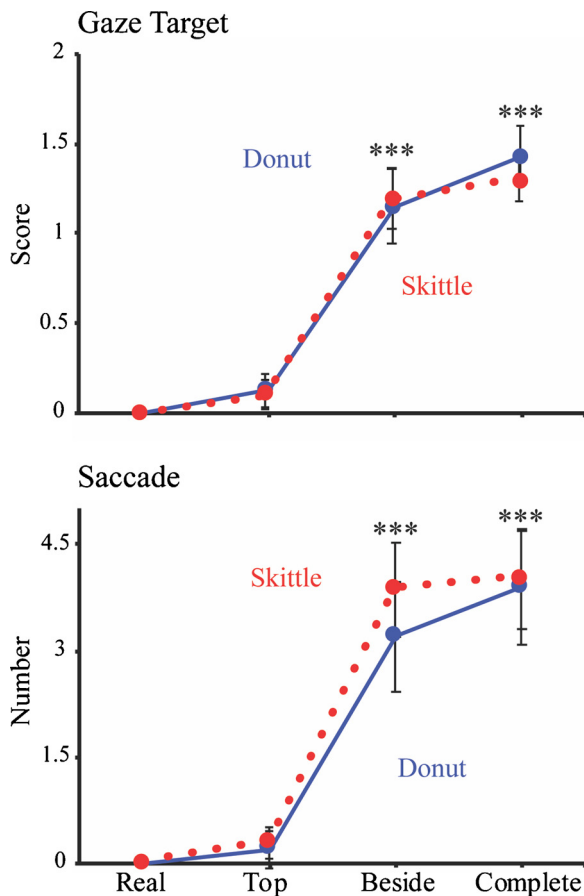


Fig. 6. Score of gaze anchoring and number of saccades (mean \pm se) for the skittle and donut targets as a function of context. Top: Gaze anchoring score. Bottom: Number of saccades made between grasp initiation and grasp completion. (Real, food item present on the pedestal; Top, only pedestal present; Beside; pedestal and food moved to right. Complete; neither food nor pedestal present. Difference between real and pantomime, $**p < 0.01$). Note: gaze anchoring occurred for the real and top contexts but not for the beside and complete contexts.

variance, indicating an absence of gaze directed at the previous platform location. These results were confirmed by significant group and context main effects for both targets: Skittle, $F(3,27) = 9.30$, $p < 0.001$; Donut ball, $F(3,18) = 29.07$, $p < 0.001$; Context by Time Skittle $F(156,1404) = 1.78$, $p = 0.001$, Context by Time Donut, $F(132,792) = 1.28$, $p = 0.024$.

Temporal Relationship between gaze point and the grasp point

Fig. 8 illustrates the gaze trajectory throughout the reach-to-grasp movement relative to the participant's thumb/index finger (skittle, top; donut ball, bottom) targets. The expectation of this analysis was, that if participants were attempting to gaze anchor on the remembered location of the pedestal, even if their remembered location were to be inaccurate, their gaze should go to a location at which their hand should ultimately make a movement of grasping (as occurs for a real reach). It was found, however, that whereas the gaze location and hand location did converge for real reaches and for memory-based reaches with the pedestal present, they did not do so for the memory-based reaches for which the pedestal was moved or absent. Thus, these results indicate that the hand enters the field of view in all contexts but only in the real and top pantomime contexts is the hand directed to the location at which the gaze is anchored. The high variance in the curves for the beside and complete contexts suggest that there is no systematic relation between gaze location and the location at which the grasp is made for the beside and complete memory-based grasps.

This summary was confirmed by the statistical analyses that show that there was a significant difference between fixation point and the position of the reaching hand for both targets as a function of Context: Skittle, $F(3,27) = 3.698$, $p = 0.024$; Donut ball $F(3,18) = 11.338$, $p < 0.001$. Post-hoc analysis revealed that for both the skittle and donut ball targets, the Real and Top pantomime contexts were significantly different from the Beside and Complete pantomime contexts ($p < 0.05$). In addition, for both targets there was a significant effect of Time: Skittle, $F(52,468) = 67.947$, $p < 0.001$; Donut, $F(44,264) = 166.528$, $p < 0.001$ and a significant interaction of Context by Time: Skittle, $F(156,1404) = 1.672$, $p < 0.005$; Donut, $F(132,792) = 1.945$, $p < 0.001$.

5.2.3. Kinematic measures of reach-for-food

As has been reported in many previous studies, the kinematic features of the reach-to-eat and reach-for-disc tasks were different from the pantomime grasps of the same tasks. The pantomime grasps were influenced by the context in which they were performed [24]. Fig. 9 summarizes the results of kinematic measures in the reach to-eat-task and these results confirm a previous study using this task [24]. There were changes in all kinematic measures between real and pantomime reach-to-grasp movements as summarized in the following sections:

Maximum pregrasp aperture (MPA)

Fig. 9A shows that the MPA was larger overall for the donut ball than for the skittle, Group, $F(1,20) = 63.71$, $p < 0.001$. Although there was no significant effect of Context, $F(3,60) = 2.594$, $p = .061$, there was a significant Target Size by Context interaction, $F(3,60) = 8.416$, $p < 0.001$. For both targets, MPA was smaller for pantomime reaches than for real reaches, although for the skittle, MPA was larger for pantomime reaches performed when the pedestal was absent.

Terminal grasp aperture (TGA)

The TGA was smaller for the skittle than for the donut ball as indicated in Fig. 9B, Group $F(1,20) = 15.52$, $p < 0.001$. Overall, the TGA was smaller for pantomime reaches than for real reaches, Context, $F(3,60) = 22.95$, $p < 0.001$. The TGA for the donut pantomime conditions were much smaller than the actual size of the donut, and this was due to the fact that many of the participants completely closed (pressed together) their thumb and index finger to pantomime the grasp (as previously described by Kuntz and Whishaw [24]).

Hand proximity to target

Fig. 9C summarizes the measure of distance between the platform center, or virtual platform center, and the index finger at TGA. For the Real and Top contexts, the hand came closer to the food location on the pedestal than it did for the for Beside and Complete contexts. That the relation between food type and distance was similar for both the skittle and donut ball was confirmed by a nonsignificant effect of Target Size, $F(1,20) = 1.750$, $p > 0.05$, and a significant effect of Context $F(3,60) = 20.132$, $p < 0.001$.

Reach duration

Fig. 9D shows that reach duration was longer for the Skillet than the Donut, Group $F(1,20) = 6.216$, $p = < 0.05$. In addition, reach durations were longer for the real skittle context than the pantomime contexts, Context by Target, $F(3,60) = 28.08$, $p < 0.05$. The long duration of reaches for the skittle in the Real context is likely related to the care required to pick up the small and unstable skittle vs the larger more easily purchased donut ball.

5.3. Reach-to-replace task

Fig. 10 shows when the participants reached to the pedestal for the food or to replace the food, they visually engaged the target and gaze anchored on it during the reach (Video 4). They often made saccades as

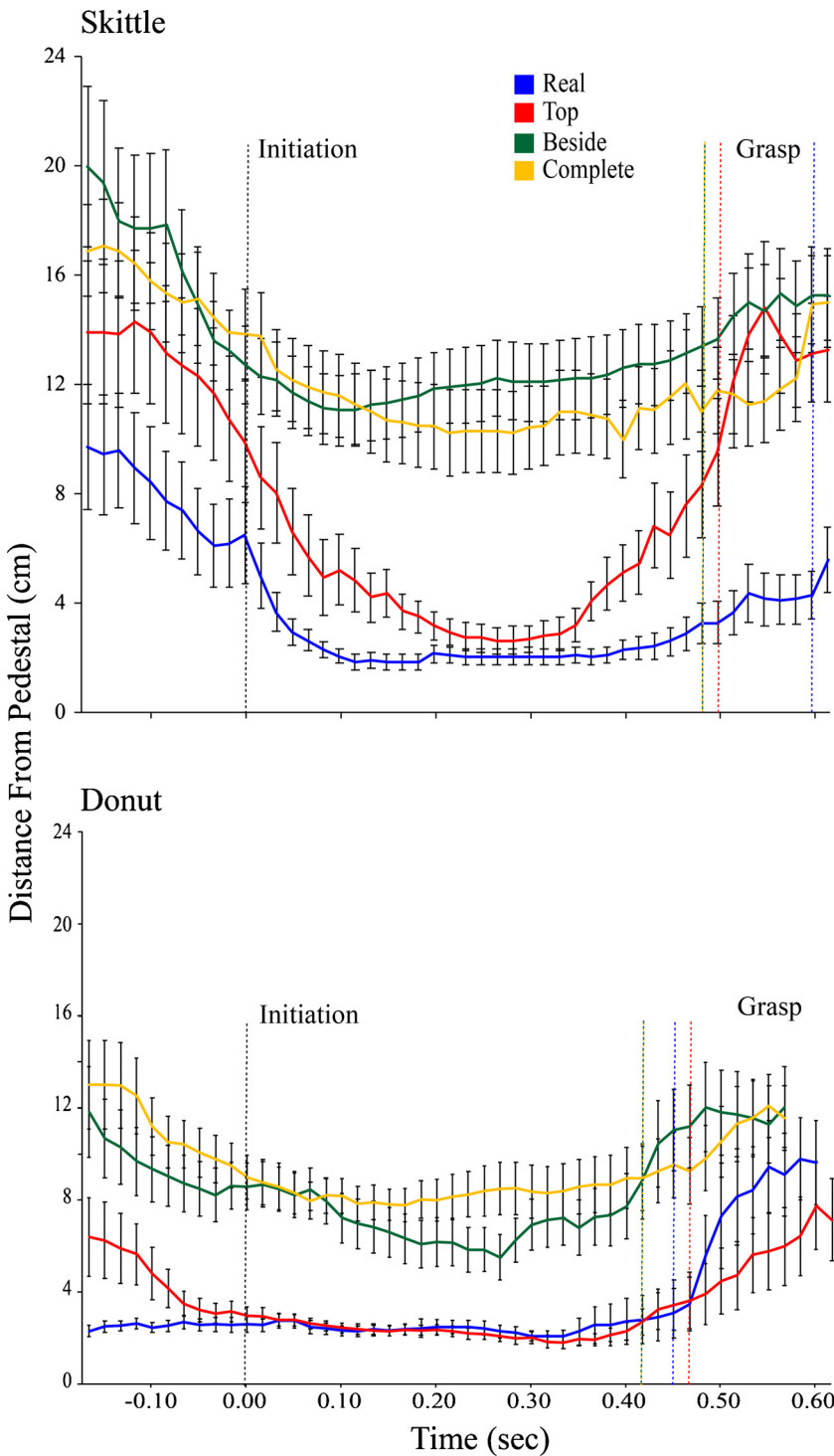


Fig. 7. Temporal relationship between gaze point and the pedestal. Gaze anchoring curves as measured by the distance (mean ± se) from gaze point to the center of the pedestal during the course of the reach for the skittle (top) and donut ball (bottom). Note: (1) The shortest gaze-pedestal distance with the smallest variance occurred for the real reach and the top pantomime contexts at about the midpoint of the reach and reflect gaze anchoring in these contexts. (2). The slow engage and disengage times for gaze reflect individual difference in engage and disengage. (Real, food item located on the pedestal; Top, food item removed from the pedestal; Beside, pedestal and food item moved to the side; Complete food item and pedestal removed from view.

they withdrew the food to the mouth. There was no significant difference in saccade number related to targets, the skittle vs the donut ball, and so the results are collapsed for targets $F(1,17) = 2.13, p > 0.05$. There was a significant difference in the direction of movement with fewer saccades associated with directing the hand to the platform than for withdrawing the hand to the mouth, Movement Direction $F(1,17) = 17.289, p = 0.001$. Thus, the participants gaze anchored on to the platform both when they reached to pick up the food item, during which they shaped their hand to grasp it, and when they replaced the food item on the pedestal, a movement that was not associated with hand shaping because the hand was holding the food item.

6. Discussion

Participants reached for discs or food items in a number of target-based tasks and then pantomimed the same movements in memory-base versions of the tasks. On target-based reaches, gaze was directed throughout the reach to the target for which a participant reached. On memory-based reaches, similar gaze anchoring was directed to the approximate place on the work surface that had held the target. Gaze anchoring was also associated with reaches on which a participant put down a target object or pretended to put down a target object. If both the target and the surface were removed for memory-based trials, however, gaze was not systematically related to the reach. Thus, the

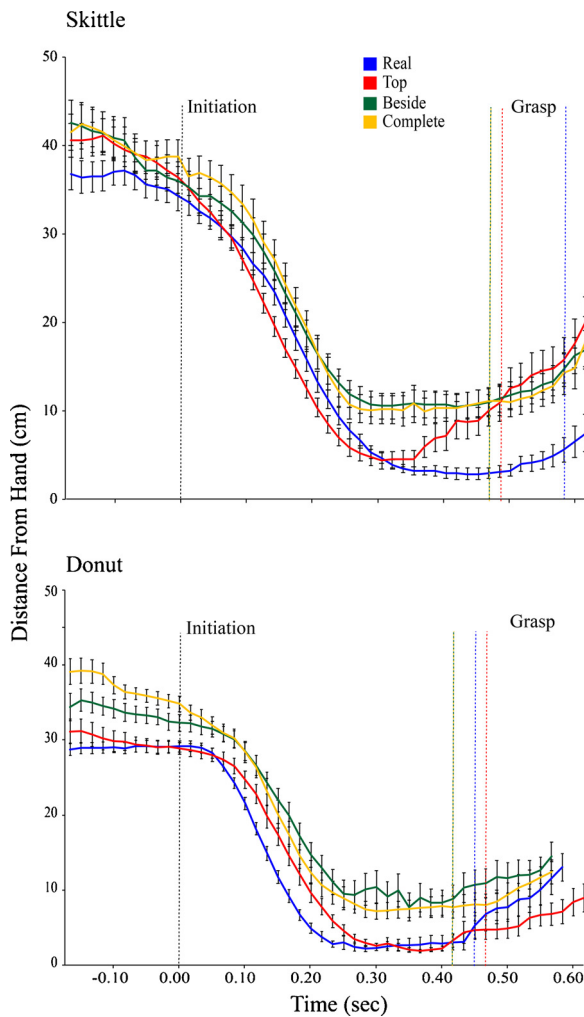


Fig. 8. Temporal Relationship between gaze point and the grasp point. Gaze anchoring curves as measured by the distance (mean \pm se) between the gaze point and the index finger tip during the course of the reach for the skittle (top) and donut ball (bottom). Note: (1) If a participant's gaze was anchored at the target of the reach, the gaze and hand location should coincide (be separated by the shortest distance) toward the middle of the reach, which is reflected in the real and top context curves. (Real, food item located on the pedestal; Top food item removed from the pedestal; Beside, pedestal and food item moved to the side; Complete, food item and pedestal removed from view).

occurrence or absence of gaze anchoring distinguishes two forms of memory-based reaching.

In the present study, two measures of gaze anchoring were used. First, gaze had to be fixated on or in close proximity to the target from about reach initiation to about the completion of the grasp. Therefore, if a participant made a saccade or blink during the period that demarcated the reach, as identified from the eye tracking record, that trial was defined as one on which gaze anchoring did not occur. Second, measures were made between gaze location and target location throughout the reach. A previous study using the pedestal reach-to-eat task found that the variance in the distance between gaze point and the target decreases to a minimum at about the midpoint of the reach. Therefore, measures of gaze anchoring were made throughout the reach [18]. Using this methodology, it was found that target-based hand movements were associated with gaze anchoring whether or not a grasp is to take place; i.e., for either reaching or replacing an object. This finding is consistent with studies that show that gaze anchoring is associated with a variety of target-based reaching movements, including reach-to-grasp and pointing [6–16]. When the platform was moved or removed, gaze

and the reach target were unrelated [18].

In retrospect, it may not seem surprising that gaze anchoring was associated with memory-based reaches of picking up the disc. The instruction given to the participants was to pretend to pick up the disc at its previous location. This same instruction has been used in previous studies of memory-based (pantomime) reaching (e.g., [20,21]). Clearly, the participants were likely using contextual cues to define the remembered location. The sheet of white cardboard on which the target object was placed and formed the work area likely provides a cue for location and the surface itself provides a cue for distance. That participants were using visual cues, and not just somatosensory memory, to guide their reaches is supported by the more accurate memory-based reaches that were made with vision vs without vision on the disc task. For memory-based trials given with the pedestal at its previous location, participants were given no instructions about where to pantomime the reaching movement, but all participants chose to pantomime their reach to the location on the pedestal where the target had been placed. It is likely that participants are strongly motivated to make gaze anchoring related reaches even when given no instruction to do so as well as pantomime their movement to locations to which they had reached on real reach trials. It is interesting that on a task similar to the disc task, the participant DF also made accurate memory-based reaches although her memory-based hand shaping was very poor [28]. In support of the idea that participants have a propensity to use gaze anchoring to guide reaches even when no instructions are given, it was observed that when participants placed the disc to one side of the workspace, they also gaze anchored for both target-based and memory-based trials.

In previous studies of memory-based reaching, kinematic features of the reach and the grasp have been found to be altered on memory-based reaches [19–21,23–26,33]. Although not a primary focus of the present study, similar findings were made, suggesting that the participants were displaying reaching behavior that is similar to that displayed by participants in other studies of memory-based reaching. One explanation given for the kinematic differences between target-based and memory-based reaching is that the former are online and dependent upon dorsal stream action pathways, whereas the latter are off-line and dependent upon ventral stream perceptual pathways [20,21,25,26]. The finding that some memory-based reaching can be associated with gaze anchoring suggest that although perceptual process may be used to identify a target for a memory-based reach, once so defined, the reach nevertheless may sometimes have gaze-related characteristics of a target-based reach suggesting that the movement has visual online control.

In the memory-based tasks in which the platform that held the target food item was moved to one side or removed, gaze locations were found to be variable in relation to the reach and so it appears that these reaches are not being directed to any particular predefined visual spatial location. Flannigan et al. [17] report that when participants were required to mark a location on a screen at which a target object had been projected in peripheral vision, their gaze was erratic in that they did not lock their gaze at target's former location. The same study also reports that when participants pointed in the dark, gaze was similarly erratic. In the contexts in which the pedestal was moved in the present study, the absence of associated gaze anchoring and the altered kinematic measures associated with both the reach and the grasp suggest that these movements have largely perceptual origins and may be dependent upon somatosensory and not visual guidance [21,25,26].

Although a strong case can be made with respect to the relationship between gaze anchoring and the reach, the relationship of gaze to the grasp is less clear. Clearly gaze must ordinarily contribute to hand shaping for grasping when participants are sighted. A number of studies demonstrate that if target properties are altered during the course of the reach, the grasp adapts [34–38]. In addition, in the present study and in previous work, memory-based hand shaping to grasp is also found to be influenced by contextual cues. For example, pregrasp aperture can become larger as visual cues are removed for memory-based trials

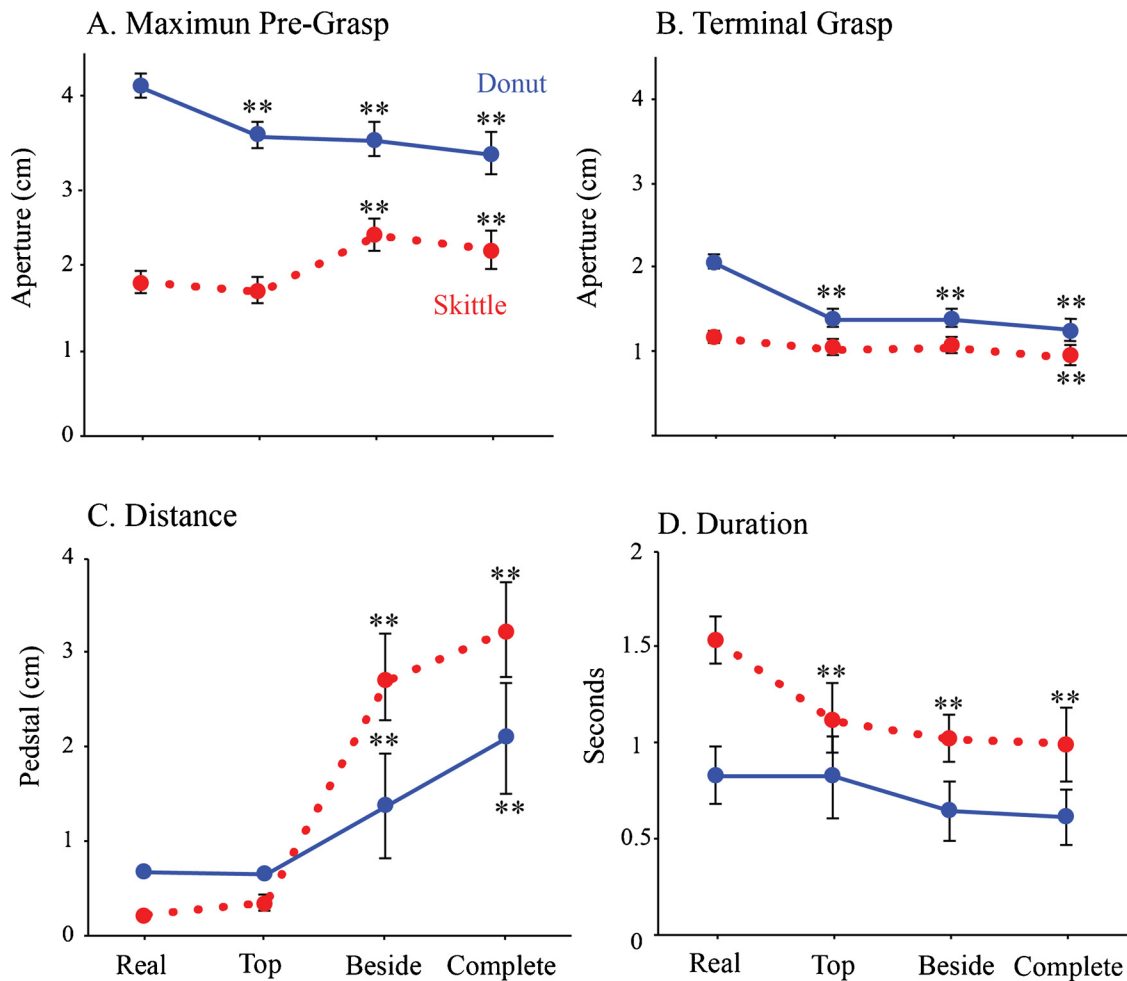


Fig. 9. Reach-to-eat kinematic measures (mean ± se) for real and pantomime movements in the reach-to-eat task. (A) Maximum pre-grasp aperture. (B) Terminal grasp aperture. (C) Minimum distance between the platform’s location at terminal grasp aperture, (D) Reach duration from grasp initiation to terminal grasp. (Real, food item present on the pedestal; Top, only pedestal present; Beside; pedestal and food moved to right. Complete; neither food nor pedestal present. Differences, **p < 0.01.

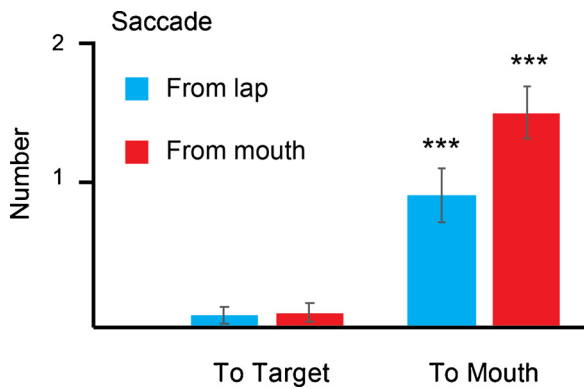


Fig. 10. Reach-to-eat and reach-to-replace saccade number during the reach (mean ± se). Note, measure indicate similar gaze anchoring on both tasks. Differences ***p < 0.001.

[19,24]. Possibly, vision may provide information for hand shaping only in the latter portion of the reach or else only a brief visual “snapshot” of the target is sufficient to mediate hand shaping for the grasp. In support of the snapshot view, shaping movements for the grasp can be made using tactile cues obtained from a brief touch of a target object [29] and accurate hand shaping can also quickly occur in anticipation of grasping when participant are given repeated reaching trials without

vision [32]. Thus, it is possible that continuous visual guidance may not be necessary for the grasp, a conclusion that favors the view that the reach and the grasp are mediated by separate visuomotor channels [3,4,29].

In conclusion, the present results confirm that memory-based reaching movements are influenced by testing context [19,24]. Memory-based reaches can take two forms, one associated with gaze anchoring and the other independent of gaze anchoring. It is interesting that in fMRI studies of participants performing target-based vs memory-based reaches, clear-cut relationships between the reaches and dorsal vs ventral stream activation have not been obtained as has been predicted from some behavioral studies [39–45]. Perhaps a relevant factor is that a memory-based task is sometimes associated with gaze anchoring and is sometimes gaze independent [24,46–48], thus requiring that visual control of a memory-based reach be concurrently assessed in such studies.

Authors statement

Jessica R. Kuntz (investigation, analysis, writing), Jenni M. Karl (curation), Jon B. Doan (curation), Melody Grohs (investigation, analysis, writing), Ian Q. Wishaw (analysis, writing, reviewing, editing)

Declaration of Competing Interest

The authors declare no competing financial interests.

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, Kalob Barr for his help with data analysis, and Ali Mashhoori for his expertise and assistance with MATLAB.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.bbr.2019.112438>.

References

- [1] D. Corbetta, M. Santello, *Reach-to-grasp Behaviour: Brain, Behavior, and Modelling Across the Life Span*, Routledge, New York, 2019.
- [2] M.A. Arbib, *Perceptual Structures and Distributed Motor Control*, (1981).
- [3] M. Jeannerod, Intersegmental coordination during reaching at natural visual objects, in: J. Long, A. Baddeley (Eds.), *Attention and Performance IX*, Erlbaum, Hillsdale, 1981, pp. 153–168.
- [4] M. Jeannerod, Visuomotor channels: their integration in goal-directed prehension, *Hum. Mov. Sci.* 18 (2–3) (1999) 201–218, [https://doi.org/10.1016/S0167-9457\(99\)00008-1](https://doi.org/10.1016/S0167-9457(99)00008-1).
- [5] M. Jeannerod, J. Decety, F. Michel, Impairment of grasping movements following a bilateral posterior parietal lesion, *Neuropsychologia* 32 (4) (1994) 369–380, [https://doi.org/10.1016/0028-3932\(94\)90084-1](https://doi.org/10.1016/0028-3932(94)90084-1).
- [6] C. Prablanc, J.E. Echallier, M. Jeannerod, E. Komilis, 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) (1979) 183–187, <https://doi.org/10.1007/Bf00337063>.
- [7] A.M. Brouwer, V.H. Franz, K.R. Gegenfurtner, Differences in fixations between grasping and viewing objects, *J. Vision* 9 (1) (2009) doi: Artn 1810.1167/9.1.18.
- [8] C. Cavina-Pratesi, C. Hesse, Why do the eyes prefer the index finger? Simultaneous recording of eye and hand movements during precision grasping, *J. Vision* 13 (5) (2013) doi: Artn 1510.1167/13.5.15.
- [9] N. de Bruin, L.A.R. Sacrey, L.A. Brown, J. Doan, I.Q. Whishaw, 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) (2008) 337–346, <https://doi.org/10.3200/Jmbr.40.4.337-346>.
- [10] D.D.J. de Grave, C. Hesse, A.M. Brouwer, V.H. Franz, Fixation locations when grasping partly occluded objects, *J. Vision* 8 (7) (2008) doi: Artn 510.1167/8.7.5.
- [11] L. Desanghere, J.J. Marotta, “Graspability” of objects affects gaze patterns during perception and action tasks, *Exp. Brain Res.* 212 (2) (2011) 177–187, <https://doi.org/10.1007/s00221-011-2716-x>.
- [12] R.S. Johansson, G.R. Westling, A. Backstrom, J.R. Flanagan, Eye-hand coordination in object manipulation, *J. Neurosci.* 21 (17) (2001) 6917–6932.
- [13] S.F.W. Neggers, H. Bekkering, Ocular gaze is anchored to the target of an ongoing pointing movement, *J. Neurophysiol.* 83 (2) (2000) 639–651.
- [14] S.F.W. Neggers, H. Bekkering, Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal, *J. Neurophysiol.* 86 (2) (2001) 961–970.
- [15] D. Voudouris, J.B. Smeets, E. Brenner, Fixation biases towards the index finger in almost-natural grasping, *PLoS One* 11 (1) (2016) e0146864, <https://doi.org/10.1371/journal.pone.0146864>.
- [16] L.A.R. Sacrey, I.Q. Whishaw, 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) (2012) 356–365, <https://doi.org/10.1016/j.bbr.2011.07.031>.
- [17] J.R. Flanagan, Y. Terao, R.S. Johansson, Gaze behavior when reaching to remembered targets, *J. Neurophysiol.* 100 (3) (2008) 1533–1543, <https://doi.org/10.1152/jn.90518.2008>.
- [18] J.R. Kuntz, J.M. Karl, J.B. Doan, I.Q. Whishaw, Gaze anchoring guides real but not pantomime reach-to-grasp: support for the action-perception theory, *Exp. Brain Res.* 236 (4) (2018) 1091–1103, <https://doi.org/10.1007/s00221-018-5196-4>.
- [19] T. Fukui, T. Inui, How vision affects kinematic properties of pantomimed prehension movements, *Front. Psychol.* 4 (2013) doi: ARTN 4410.3389/psyq.2013.00044.
- [20] M.A. Goodale, A.D. Milner, L.S. Jakobson, D.P. Carey, A neurological dissociation between perceiving objects and grasping them, *Nature* 349 (6305) (1991) 154–156, <https://doi.org/10.1038/349154a0>.
- [21] M.A. Goodale, D.A. Westwood, An evolving view of duplex vision: separate but interacting cortical pathways for perception and action 2, *Curr. Opin. Neurobiol.* 14 (2) (2004) 203–211, <https://doi.org/10.1016/j.conb.2004.03.002>.
- [22] M. Heath, J.L. Chan, S.D. Jazi, Tactile-based pantomime grasping: knowledge of results is not enough to support an absolute calibration, *J. Motor. Behav.* 51 (1) (2019) 10–18, <https://doi.org/10.1080/00222895.2017.1408559>.
- [23] S.A. Holmes, J. Lohmus, S. McKinnon, A. Mulla, M. Heath, Distinct visual cues mediate aperture shaping for grasping and pantomime-grasping tasks, *J. Motor. Behav.* 45 (5) (2013) 431–439, <https://doi.org/10.1080/00222895.2013.818930>.
- [24] J.R. Kuntz, I.Q. Whishaw, Synchrony of the Reach and the Grasp in pantomime reach-to-grasp, *Exp. Brain Res.* 234 (11) (2016) 3291–3303, <https://doi.org/10.1007/s00221-016-4727-0>.
- [25] A.D. Milner, M.A. Goodale, *The Visual Brain in Action*, Oxford University Press, 2006.
- [26] A.D. Milner, M.A. Goodale, Two visual systems re-viewed, *Neuropsychologia* 46 (3) (2008) 774–785, <https://doi.org/10.1016/j.neuropsychologia.2007.10.005>.
- [27] R.C. Oldfield, The assessment and analysis of handedness: the edinburgh inventory, *Neuropsychologia* 9 (1) (1971) 97–113, [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4).
- [28] M.A. Goodale, L.S. Jakobson, J.M. Keillor, Differences in the visual control of pantomimed and natural grasping movements, *Neuropsychologia* 32 (10) (1994) 1159–1178, [https://doi.org/10.1016/0028-3932\(94\)90100-7](https://doi.org/10.1016/0028-3932(94)90100-7).
- [29] J.M. Karl, L.A.R. Sacrey, J.B. Doan, I.Q. Whishaw, Hand shaping using hapsis assemblies visually guided hand shaping, *Exp. Brain Res.* 219 (1) (2012) 59–74, <https://doi.org/10.1007/s00221-012-3067-y>.
- [30] I.Q. Whishaw, O. Suchowersky, L. Davis, J. Sarna, G.A. Metz, S.M. Pellis, 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) (2002) 165–176, [https://doi.org/10.1016/S0166-4328\(01\)00479-x](https://doi.org/10.1016/S0166-4328(01)00479-x).
- [31] Y.J. Wong, I.Q. Whishaw, Precision grasps of children and young and old adults: individual differences in digit contact strategy, purchase pattern, and digit posture, *Behav. Brain Res.* 154 (1) (2004) 113–123, <https://doi.org/10.1016/j.bbr.2004.01.028>.
- [32] J.M. Karl, L.R. Schneider, I.Q. Whishaw, Nonvisual learning of intrinsic object properties in a reaching task dissociates grasp from reach, *Exp. Brain Res.* 225 (4) (2013) 465–477, <https://doi.org/10.1007/s00221-012-3386-z>.
- [33] D.A. Westwood, C.D. Chapman, E.A. Roy, Pantomimed actions may be controlled by the ventral visual stream, *Exp. Brain Res.* 130 (4) (2000) 545–548, <https://doi.org/10.1007/s002219900287>.
- [34] M. Desmurget, C. Prablanc, M. Arzi, Y. Rossetti, Y. Paulignan, C. Urquizar, Integrated control of hand transport and orientation during prehension movements, *Exp. Brain Res.* 110 (2) (1996) 265–278, <https://doi.org/10.1007/bf00228557>.
- [35] R. Goodman, L. Tremblay, Using proprioception to control ongoing actions: dominance of vision or altered proprioceptive weighting? *Exp. Brain Res.* 236 (7) (2018) 1897–1910, <https://doi.org/10.1007/s00221-018-5258-7>.
- [36] H. Grea, M. Desmurget, C. Prablanc, Postural invariance in three-dimensional reaching and grasping movements, *Exp. Brain Res.* 134 (2) (2000) 155–162, <https://doi.org/10.1007/s002210000427>.
- [37] C. van de Kamp, R.M. Bongers, F.T.J.M. Zaal, Effects of changing object size during prehension, *J. Motor. Behav.* 41 (5) (2009) 427–435.
- [38] D. Voudouris, S. Radhakrishnan, V. Hatzitaki, E. Brenner, Does postural stability affect grasping? *Gait Posture* 38 (3) (2013) 477–482, <https://doi.org/10.1016/j.gaitpost.2013.01.016>.
- [39] F. Binkofski, G. Buccino, S. Posse, R.J. Seitz, G. Rizzolatti, H. Freund, A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study, *Eur. J. Neurosci.* 11 (9) (1999) 3276–3286, <https://doi.org/10.1046/j.1460-9568.1999.00753.x>.
- [40] F. Binkofski, C. Dohle, S. Posse, K.M. Stephan, H. Hefter, R.J. Seitz, H.J. Freund, Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study, *Neurology* 50 (5) (1998) 1253–1259, <https://doi.org/10.1212/wnl.50.5.1253>.
- [41] C. Cavina-Pratesi, J.D. Connolly, S. Monaco, T.D. Figley, A.D. Milner, T. Schenk, J.C. Culham, Human neuroimaging reveals the subcomponents of grasping, reaching and pointing actions, *Cortex* 98 (2018) 128–148, <https://doi.org/10.1016/j.cortex.2017.05.018>.
- [42] C. Cavina-Pratesi, S. Monaco, P. Fattori, C. Galletti, T.D. McAdam, D.J. Quinlan, M.A. Goodale, J.C. Culham, 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) (2010) 10306–10323, <https://doi.org/10.1523/JNEUROSCI.2023-10.2010>.
- [43] G. Krolczak, C. Cavina-Pratesi, D.A. Goodman, J.C. Culham, What does the brain do when you fake it? An fMRI study of pantomimed and real grasping, *J. Neurophysiol.* 97 (3) (2007) 2410–2422, <https://doi.org/10.1152/jn.00778.2006>.
- [44] M. Vesia, D.A. Bolton, G. Mochizuki, W.R. Staines, Human parietal and primary motor cortical interactions are selectively modulated during the transport and grip formation of goal-directed hand actions, *Neuropsychologia* 51 (3) (2013) 410–417, <https://doi.org/10.1016/j.neuropsychologia.2012.11.022>.
- [45] M. Vesia, J.D. Crawford, Specialization of reach function in human posterior parietal cortex, *Exp. Brain Res.* 221 (1) (2012) 1–18, <https://doi.org/10.1007/s00221-012-3158-9>.
- [46] K. Fieher, I. Schutz, D.Y.-P. Henriques, Gaze-centered spatial updating of reach targets across different memory delays, *Vision Res.* 51 (2011) 890–897.
- [47] S.P. Price, J.J. Marotta, Gaze strategies during visually-guided versus memory-guided grasping, *Exp. Brain Res.* 225 (2013) 291–305, <https://doi.org/10.1007/s00221-012-3358-3>.
- [48] I. Schutz, D.Y.P. Henriques, K. Fieher, Gaze-centered spatial updating in delayed reaching even in the presence of landmarks, *Vision Res.* 87 (2013) 46–52.