RESEARCH ARTICLE



Manipulation of physical 3-D and virtual 2-D stimuli: comparing digit placement and fixation position

Ryan W. Langridge¹ · Jonathan J. Marotta¹

Received: 3 November 2020 / Accepted: 30 March 2021 © The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

The visuomotor processes involved in grasping a 2-D target are known to be fundamentally different than those involved in grasping a 3-D object, and this has led to concerns regarding the generalizability of 2-D grasping research. This study directly compared participants' fixation positions and digit placement during interaction with either physical square objects or 2-D virtual versions of these objects. Participants were instructed to either simply grasp the stimulus or grasp and slide it to another location. Participants' digit placement and fixation positions did not significantly differ as a function of stimulus type when grasping in the center of the display. However, gaze and grasp positions shifted toward the near side of non-central virtual stimuli, while consistently remaining close to the horizontal midline of the physical stimulus. Participants placed their digits at less stable locations when grasping the virtual stimulus in comparison to the physical stimulus on the right side of the display, but this difference disappeared when grasping in the center and on the left. Similar outward shifts in digit placement and lowered fixations were observed when sliding both stimulus types, suggesting participants incorporated similar adjustments in grasp selection in anticipation of manipulation in both Physical and Virtual stimulus conditions. These results suggest that while fixation position and grasp point selection differed between stimulus type as a function of stimulus position, certain eye-hand coordinated behaviours were maintained when grasping both physical and virtual stimulu.

Keywords Eye-hand coordination · Grasp point selection · Virtual 2-D stimuli · Grasp axis

Humans are skilled at grasping objects of varying shape and size without devoting a significant amount of cognitive effort or attention toward the task. When grasping an object, we unconsciously interpret the visual information available, such as its shape and position, and use this information to direct an accurate reaching movement toward the object and place the digits appropriately. The shape of the object being grasped has been known to influence various aspects of the reach-to-grasp movement, beginning as early as the planning of the grasping action (Janssen and Scherberger 2015; Vargas-Irwin et al. 2015), and will predict where people direct

Communicated by Melvyn A. Goodale.

 Ryan W. Langridge langrirw@myumanitoba.ca
Jonathan J. Marotta

Jonathan.Marotta@umanitoba.ca

 Perception and Action Lab, Department of Psychology, University of Manitoba, 190 Dysart Rd, Winnipeg, MB R3T-2N2, Canada their gaze (Brouwer et al. 2009; Desanghere and Marotta 2015), the trajectory and shaping of the approaching hand during the reaching movement (Rouse and Schieber 2015; Schettino et al. 2003), and the placement of the digits when grasping (Cuijpers et al. 2004; Santello and Soechting 1998; Schettino et al. 2013).

Another critical component influencing how a person will grasp an object is the intended manipulation of the object (Rosenbaum et al. 2012; Sartori et al. 2011). For example, when grasping an object such as a coffee cup or a pencil, we typically do so with the intention to manipulate or use the object in a pre-determined, purposeful manner; one usually grasps a coffee cup so that it can be subsequently raised and drank from, while a pencil may be picked up in a way that allows you to write. Fixations are directed toward task-relevant landmarks, such as the grasp points on the object (Belardinelli et al. 2016; Johansson et al. 2001) and the particular end-goal, such as pouring from a water bottle versus simply moving it to another location, will produce unique visuomotor behaviours relevant to the particular action (Ansuini et al. 2008; Sartori et al. 2011). Even prior

to the grasp, the intended action on an object influences the posture of the hand during the reaching phase (Ansuini et al. 2008), and in cases when the action end-goal of the grasping movement is unexpectedly changed during the reach, these postures are modified accordingly during the reaching movement to ensure the placement of the digits serves the updated goal (Hughes et al. 2012). It is therefore believed that the final posture of the hand is determined prior to the movement using feedforward modelling of the upcoming action (Elsinger and Rosenbaum 2003; Herbort and Butz 2010), and is then updated accordingly by feedback mechanisms during the movement to ensure digit placement at the time of the grasp serves effective and comfortable manipulation.

Ultimately, a successful grasp is one that places the digits at comfortable locations on the object, while simultaneously generating the necessary amount of force on the object to successfully perform the intended action. When using a precision grip to grasp symmetrical objects, the index finger and thumb are typically positioned on opposite sides of the object, such that an imaginary grasp axis connecting the digits would bisect or fall close to the object's center of mass (COM), thus applying sufficient force to the COM and minimizing the amount of torque around the grasp axis (Goodale et al. 1994; Lederman and Wing 2003). Visibility of the object being grasped will also influence how the digits are placed, as digit placement that causes the hand to obscure one's view of the object will make it difficult to grasp effectively and may interfere with future manipulation. Paulun et al. (2014) demonstrated a rightward shift in digit placement when participants grasped objects using their right hand, and a leftward shift when using the left hand regardless of the start position of the hand, suggesting grasp selection may have served to promote the visibility of the object being grasped rather than minimize energy expenditure (Maiello et al. 2019; Paulun et al. 2014). These results suggest that in order to efficiently grasp and manipulate an object, digit placement must not only ensure a stable grasp, but also minimize the extent to which the position of the hand obstructs the view of the object.

Recent work involving visually guided reaching and grasping movements toward 2-D virtual targets has indicated certain similarities in the way participants fixate their gaze and place their digits when grasping both 3-D and 2-D stimuli. For example, when using a precision grip to grasp 2-D on-screen symmetrical square targets, participants place their index finger and thumb on the top and bottom of the target respectively, at locations near the horizontal midline, suggesting participants use the shape of the stimuli to infer the location of the target's geometric center, and place their digits at locations that generate a grasp axis bisecting or falling near to this location (Bulloch et al. 2015; Thulasiram et al. 2020; Langridge and Marotta 2020). Humans are naturally adept at judging the location of a flat object's COM (Bingham and Muchisky 1993) and appear to use this information when grasping 2-D on-screen symmetrical shapes. Participants' fixations are directed toward the position of the index finger when grasping 2-D targets, as is the case when grasping 3-D objects (Belardinelli et al. 2016; Brouwer et al. 2009; Cavina-Pratesi and Hesse 2013; Desanghere and Marotta 2011; Voudouris et al. 2016), suggesting a similar emphasis on index finger placement when grasping both 3-D objects and virtual 2-D targets. There is even some evidence to suggest that participants appropriately scale their grip apertures to some degree when grasping 2-D targets as they do when grasping 3-D objects (Westwood et al. 2002).

Despite these apparent similarities, a number of studies have clearly demonstrated the differences between grasping 3-D objects compared to 'pantomimed grasps' toward 2-D stimuli, including functional (discrimination during the planning phase within key grasping regions of the brain; Freud et al. 2018) and perceptually mediated (adherence to Weber's law; Holmes and Heath 2013; Ozana and Ganel 2017, 2019; Ozana et al. 2020) aspects of the grasping action. These differences are to be expected, as the action of grasping a 2-D target is inherently different from that of grasping a 3-D object, which necessarily involves more extensive processing of certain object properties such as mass, 3-D shape, surface texture, and the material from which it is made. The material properties of an object (e.g., rough versus smooth, light versus heavy) have been shown to influence primarily temporal aspects of a reachto-grasp-movement (e.g., overall movement time, velocity, and deceleration; Weir et al. 1991), and digit placement is typically directed toward positions that are lower on the object (Glowania et al. 2017) and closer to the COM (Paulun et al. 2016) when grasping heavier objects with slippery surfaces, for which grasping is more difficult and requires more careful placement of the digits.

The fact that one's intent to manipulate an object will influence how the object is grasped highlights another critical limitation associated with the use of 2-D virtual stimuli in grasping research, namely that interaction with a 2-D stimulus does not allow for the type of physical manipulation afforded by a 3-D object. The typically available sources of information which are necessary for successful manipulation of a 3-D object (e.g., haptic feedback), are unavailable when interacting with 2-D virtual stimuli, and at best can be inferred by the visual presentation of the stimulus. Further, one does not need to consider the amount of force required to manipulate a virtual target (as there is none), nor risk mishandling or dropping such stimuli, factors which are characteristic of physical interaction with a physical 3-D object. Considering these disparities, it is difficult to compare and generalize the results of 2-D grasping studies to those involving manipulation of physical 3-D objects.

In recent years, however, efforts have been made to increase the realism of 2-D virtual target interaction by introducing tasks involving active manipulation of a 2-D target, thus allowing researchers to study how this type of manipulation influences grasping behaviours. For example, in line with previous work investigating the perceptual influence on 2-D grasping (Ozana and Ganel 2017, 2019), Ozana et al. (2020) demonstrated grip aperture trajectories adhere to Weber's law during active manipulation of a virtual 2-D target (i.e., swiping or resizing a virtual rectangle) indicating perceptual mediation of the task, in contrast to the absolute, analytic processing involved when grasping physical objects. These results suggest the intended manipulation of a virtual target may not be sufficient to fully activate the same visuomotor processes dedicated for the visual control of action toward physical objects.

In the present study, we also introduce a task involving the manual manipulation of a virtual 2-D computergenerated target. The manipulation in this study involved grasping and sliding a target from its original position to another on-screen location. The action end-goal varied to compare how the intention to move the target influenced grasping behaviours compared to when simply grasping it. An identical version of the task using a physical 3-D object was used to compare the visually guided grasping behaviours observed during interaction with each type of stimulus. While acknowledging the previously reported differences regarding actions toward 2-D and 3-D stimuli, our goal was to explore those visuomotor behaviours that have demonstrated potential similarities when grasping 3-D objects and virtual 2-D targets, namely participants' digit placement and fixation positions in relation to the stimulus' center.

Based on previous research demonstrating a spatial relationship between participants' gaze and index finger placement in relation to the center of a 2-D virtual target, it was hypothesized that the location of the stimulus, as well as the nature of the task being performed would influence participants' fixation positions and digit placement to the same degree and direction when interacting with both virtual and physical stimuli. Participants were expected to fixate toward task-related locations, corresponding to the placement of the index finger when interacting with both the virtual and physical stimulus as well. Observing similar taskrelated adjustments when grasping both types of stimulus would provide evidence for humans' similar use of certain visuomotor strategies when grasping both virtual 2-D and physical 3-D stimuli. The distance between the grasp axis and the stimulus' center, as well as the amount of torque generated by the horizontal placement of the digits was used to measure the stability of the grasp. These measures were included to examine if participants were grasping the virtual 2-D stimulus in a stable manner similar to the 3-D objects,

despite stability not being critical in the absence of a true COM.

Methods

Participants

Forty-two undergraduate psychology students (36 female, 5 male, 1 undeclared) between the ages of 17 and 45 years (M = 19.36, SD = 4.46) were recruited through the Psychology Department Undergraduate Participant Pool at the University of Manitoba and participated for course credit toward their Introductory Psychology course. Participants were randomly sorted into two groups, and each group interacted exclusively with either a physical (n=21), or virtual (n=21)stimulus. All participants had normal or corrected to normal vision (e.g., wearing contact lenses, corrective eye surgery, etc.) and were right-hand dominant, as determined by a modified version of the Edinburgh Handedness Inventory (Oldfield 1971). All participants provided informed consent prior to participation. All procedures were approved by the psychology/sociology research ethics board (PSREB) at the University of Manitoba.

Apparatus

Participants were seated in a height-adjustable chair with their head stabilized in a chin rest, positioned 54 cm in front of a Dell U2414H 24 in. computer monitor (resolution: 1920×1080, refresh rate: 60 Hz). Reaching and grasping movements were recorded using an Optotrak Certus 3-D motion tracking system (Northern Digital Inc., Waterloo, ON, Canada) sampled at 175 Hz. Six infrared light-emitting diodes (IREDS) were attached to the participants' right hand and wrist; 2 IREDS each were placed on the proximal edge of the index finger cuticle, the proximal edge of the thumb cuticle, and on the distal radius of the wrist. At each location, the IRED with the least amount of disrupted data (e.g., missing or extreme values due to rotation of the hand) was used to analyze the participant's movement. An Eyelink II (SR Research Ltd., Ottawa, ON, Canada) sampled at 250 Hz was used to record binocular eye movements. Three additional IREDs were placed on the Eyelink II's headset to account for any incidental movement of the head during data collection. MotionMonitor software (Innovative Sports Training Inc., Chicago, IL, USA) was used to integrate the motion tracking data into a common spatial and temporal frame of reference using a 7 Hz Butterworth filter. The MotionMonitor was also used to generate the on-screen stimulus in the Virtual condition. Both eyes were calibrated using a nine-point calibration/validation procedure, followed by an accuracy check requiring participants to fixate on a dot presented in the middle of the computer screen for 8 s. An average gaze displacement error exceeding 0.5 cm in the horizontal axis, or 1.0 cm in the vertical axis required recalibration/validation of the Eyelink II.

Stimuli and materials

Figure 1 illustrates the experimental setup for a participant in the Physical Stimulus condition (Fig. 1a) and in the Virtual Stimulus condition (Fig. 1b). The stimulus in the Physical condition consisted of a 3-D square block made of white foam-core board (height: 4 cm, width: 4 cm, depth: 0.5 cm). A black foam-core presentation board (height: 51 cm, width: 54 cm) was attached to the front of the computer monitor. Four low-strength organizational magnets were attached to the backside of the square block (the combined weight of the block and the magnets was 11.0 g), and additional sets of magnets were attached to the rear-facing surface of the presentation board at positions corresponding to the 3 stimulus presentation positions. During the experiment, the physical stimulus was presented at one of 3 locations: positioned either in the center of the board (aligned with the mid-sagittal axis of the participant and starting position of the hand), or 20 cm to the right or left of center, always at a vertical position of 38.5 cm above the tabletop. The stimulus in the Virtual condition consisted of a 2-D, computergenerated square, matched to the dimensions and colour of the physical stimulus and presented on the computer screen against a black background. The virtual on-screen stimulus was presented at the same horizontal and vertical positions as the 3-D stimulus in the Physical condition, so participants in both conditions were required to reach the same distance and toward the same locations.

Procedure

At the beginning of the experiment, participants in both conditions were given the opportunity to hold the physical stimulus. Calibration and validation of the Eyelink were then performed, followed by the first accuracy check. The

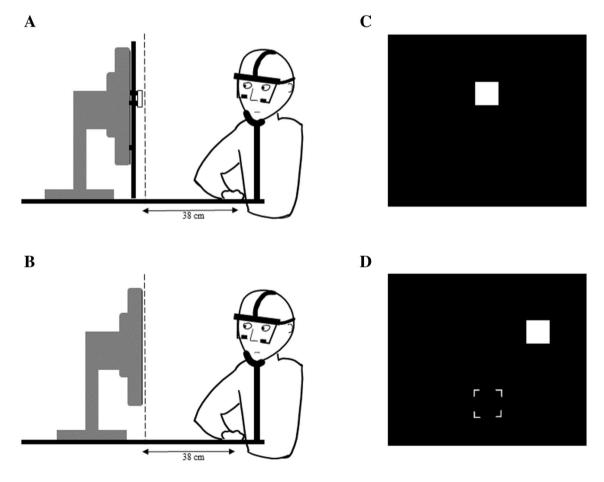


Fig. 1 Illustration of the experimental setup in the physical stimulus condition (**a**) and in the virtual stimulus condition (**b**). The dotted line refers to the threshold 1 cm away from the object's surface (**a**) and 1 cm in front of the screen (**b**). The grasp was defined as the point

at which the IRED on the proximal edge of the index finger cuticle reached this threshold. An example of the participant's view during an only grasp trial with a centrally positioned stimulus (c), and during a slide trial with a rightward positioned stimulus (d)

experimental task ('only grasp' or 'slide') order was counterbalanced, so that half the participants in each condition performed a block of only grasp task trials before the block of slide task trials, while the other half performed the tasks in the reverse order. All participants were instructed to grasp the stimulus with their index finger and thumb on the top and bottom of the stimulus, respectively, and to not make contact with the stimulus using their other digits. All participants completed the task using their right hand. The time of the grasp was defined as the point at which the IRED on the participant's index finger reached within 1 cm of the object's surface (physical condition) or the computer screen (virtual condition). The proximal placement of the IRED on the index finger cuticle was set so this timing corresponded to the tip of the digit making contact with the stimulus.

Prior to performing each block of experimental trials, participants performed three practice trials (grasping the stimulus and performing the appropriate task once at each of the three stimulus positions) to familiarize themselves with the upcoming task, and to ensure data from the IREDs and Eyelink was being collected properly. Each task involved 15 experimental trials. This meant (excluding the practice trials) participants grasped the stimulus 5 times at each position. The trial-by-trial stimulus position ordering was determined randomly at the beginning of the study, and this set order was used for all participants. Participants were given a short break after completing the first task, and a second accuracy check was conducted prior to the second task practice trials.

Physical stimulus condition

Before each block of trials began, a stylus with 4 IREDs attached to its distal tip was used to demarcate the real-world coordinates corresponding to the three stimulus positions on the board. The dimensions of the stylus were virtually configured during the experimental set-up, prior to each experimental session. A square block (dimensions matched those of the experimental stimulus) with a mark on its surface visually displaying the stimulus' geometrical center was placed at each of the three stimulus positions, and the tip of the stylus was aligned with this marking at each location in sequence. These coordinates were recorded and used during analysis to represent the center of the physical stimulus at each of the three positions. This step was carried out each time the board was re-attached to the computer screen following removal, to ensure the virtual center of the physical stimulus used for analysis reflected the stimulus' true position on the board during the experimental trials.

Participants began each trial with the index finger and thumb of their right hand pinched together on the tabletop in the 'start position', centered 38 cm in front of the display, and aligned with the mid-sagittal plane of the body. Participants were instructed to begin each trial with their eyes closed, while the experimenter placed the physical stimulus at one of the 3 positions on the board. An auditory cue at the beginning of each trial signalled the participant to open their eyes, followed 1 s later by an auditory 'reach tone' cueing participants to grasp the stimulus on the presentation board. When performing the only grasp task, participants were instructed to grasp the physical stimulus using their index finger and thumb, but to not pick it up or move it. Afterward, participants returned their hand to the start position and closed their eyes. The experimenter then repositioned the stimulus as necessary before the beginning of the next trial.

The slide task involved using a different presentation board, identical to the board used for the only grasp task, with the addition of a single red 4×4 cm square outline presented in the horizonal middle of the presentation board, 13 cm below the center stimulus' position, and 25.5 cm above the tabletop. Upon presentation of the reach tone, participants were instructed to grasp the physical stimulus with their index finger and thumb and slide it downward until it was positioned within the red square. Due to the low strength of the magnets and the stimulus' light weight, a very minimal force was required to slide it. To maintain consistency with the version of the task in the Virtual condition, participants were instructed to slide the physical stimulus to the red square, rather than pick it up off the board. Magnets attached to the back of the board were used to re-secure the stimulus once aligned with the red square. Following successful relocation of the stimulus, participants returned their hand to the start position and closed their eyes.

Virtual stimulus condition

Participants began each trial with their right hand in the start position on the tabletop. No viewing instructions were given, and participants were allowed to freely view the monitor throughout the trial. The virtual stimulus appeared at one of the 3 on-screen positions at the beginning of each trial, followed 1 s later by the reach tone. Participants were instructed to grasp the virtual stimulus using their index finger and thumb "as if they were grasping an actual 3-D object". In the only grasp task, participants were only required to grasp the virtual stimulus. After making contact with the screen, participants returned their hand to the start position, and the next trial was initiated manually by the experimenter.

When performing the slide task, a virtual red square outline appeared in the horizontal middle of the screen 13 cm below the virtual stimulus, 25.5 cm above the tabletop. As in the 3-D condition, the goal was to grasp and slide the virtual stimulus so that it was aligned with the red outline. To make this possible, user-defined formulas within the MotionMonitor were used to lock the on-screen position of the virtual stimulus to the relative position of the IRED attached to the index finger at the time the stimulus was grasped (i.e., once the IRED positioned at the proximal edge of the index finger cuticle reached a 1 cm distance from the screen). This allowed participants to grasp the stimulus by placing their index finger and thumb on the screen and then control its movement by moving their fingers along the screen's surface as if they were in fact sliding it. For these trials, participants were instructed to first grasp the stimulus, and then slide it toward the red outline presented at the bottom of the screen. Once the center of the stimulus was positioned within the red outline's center, the trial concluded, and participants returned their hand to the start position.

Data analysis

Trial data for each dependent variable were averaged to create a mean value per unique condition for each participant. The horizontal placement of the index finger, as well as the horizontal and vertical fixations at the time of the grasp, distance between the grasp axis and stimulus center, and amount of torque inferred by the horizontal distance between the index finger and thumb were analyzed using five 2 (stimulus type: physical versus virtual) × 3 (position: left versus center versus right) × 2 (task: slide versus only grasp) mixedfactorial ANOVAs, with stimulus type as the between-subjects factor, and position and task as within-subject factors. The ANOVA summary tables are provided as supplementary material (Online Resource 1). SPSS (version 23.0) was used to analyze the data. Violations to sphericity were corrected using a Greenhouse-Geiser correction. Bonferroni adjusted p values were applied to all post hoc comparisons used to analyze any significant interactions, and all analyses were conducted using alpha = 0.05.

Bayesian analysis of posterior probabilities

Using methods described by Masson (2011), Bayesian Information Criterion approximations were calculated and used to generate posterior probabilities for the main effects, interactions, and simple effects tests of each ANOVA when appropriate. This method allowed us to calculate the probability of either a non-zero effect favouring the alternative hypothesis $[p(H_1/D)]$, or a zero-effect favouring the null hypothesis $[p(H_0/D)]$, being true given the data. As these probabilities sum to 1.0, only the larger of the two values are reported, thus providing evidence in favour of either the alternative or null hypothesis. The posterior probabilities are reported along with the results for each associated test and are interpreted using Raftery's (1995) grading of evidence, where 0.50-0.75 = `weak'; 0.75-0.95 = `positive'; 0.95-0.99 = `strong', and > 0.99 = `very strong'.

The dependent variables are defined as follows:

Horizontal index finger placement

The horizontal distance between participants' average index finger placement and the stimulus' horizontal midline at the time of the grasp was measured and used to indicate accuracy of the grasp.

Horizontal and vertical fixation positions

Participants' raw horizontal and vertical gaze positions were recorded for the duration of each trial and characterized into fixations using custom algorithms developed using MATLAB (R2016a, The MathWorks Inc., Natick, MA, USA), based on a dispersion-threshold identification (I-DT) algorithm (Salvucci and Goldberg 2000). The horizontal and vertical distances between the participants' fixations and the stimulus' center at the time of the grasp were analyzed separately.

Absolute distance between grasp axis and stimulus center

Previous research has used the distance between the grasp axis and an object's COM as an indication of grasp stability when grasping 3-D objects (Goodale et al. 1994; Lederman and Wing 2003; Marotta et al. 2003). Using custom programming developed with MATLAB, the shortest distance between the participant's grasp axis and the stimulus' center was calculated, and the average absolute distance in each condition was compared.

Horizontal distance between the index finger and thumb

As an additional measure of grasp stability, the average horizontal distance between the index finger and thumb was used to indicate the amount of torque that would be generated by the opposing force of each digit at the time of the grasp. In this case, larger horizontal distances between the digits indicated an increased amount of torque and decreased stability.

Results

Excluded data

Experimental data were excluded from analysis if the participant failed to execute the task properly during an experimental trial, if visibility of the IRED on the participant's hand was compromised during the execution of the task, or due to equipment failure. In total 9.5% of all experimental trials were excluded from the final analysis.

Horizontal index finger placement

A significant stimulus type \times position interaction [*F*(1.722, $(68.865) = 15.460, p < 0.001, \eta_p^2 = 0.279, p(H_1/D) = 0.999;$ Fig. 2a] was observed, and post-hoc tests of the simple effects indicated that collapsing across task, there were no significant differences in horizontal index finger placement when grasping the physical stimulus at any of the three positions (all ps > 0.05), and the posterior probabilities calculated suggested only weak evidence in favour of differences between the left and center $[p(H_1/D) = 0.512]$, and between the right and center $[p(H_1/D=0.531)]$, while suggesting positive evidence for the lack of difference between left and right $[p(H_0/D) = 0.800]$. In the Virtual condition, however, the average placement of the index finger was shifted toward the near side of the stimulus (i.e., biased toward the center of the screen, and the starting position of the hand) when grasping non-central stimuli [left versus center: $p(H_1/D) = 0.999$; left versus right: $p(H_1/D) = 0.999$; center versus right: $p(H_1/D) = 0.987$]. Index finger placement did not significantly differ when grasping the physical stimulus compared to the virtual stimulus when presented

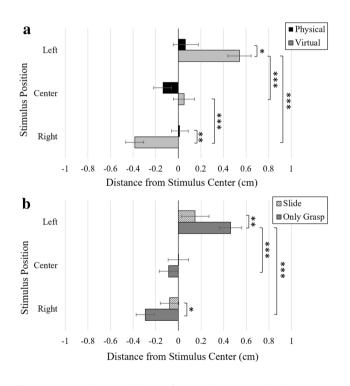


Fig.2 Average horizontal index finger placement collapsing across task (**a**) and collapsing across stimulus type (**b**). Negative values in the horizontal axis refer to the distance to the left of the stimulus' horizontal midline. Error bars represent the standard error of the means. *p < 0.05, **p < 0.01, ***p < 0.001

in the center $[p > 0.05, p(H_0/D) = 0.742]$. However, the bias toward the near side of non-central virtual stimuli resulted in significant differences in index finger placement when grasping the virtual stimulus compared to the physical stimulus presented at the left $[p(H_1/D) = 0.813]$ and at the right $[p(H_1/D) = 0.966]$.

A significant position × task interaction was also revealed $[F(2, 80) = 10.024, p < 0.001, \eta_p^2 = 0.200, p(H_1/D) = 0.993;$ Fig. 2b], and the pairwise comparisons indicated that collapsing across stimulus type, participants' horizontal index finger placement was positioned closer to the near side of non-centrally located stimuli when only grasping, compared to a more exaggerated outward horizontal index finger placement near the horizontal midline when sliding [left: $p(H_1/D) = 0.886$; right: $p(H_1/D) = 0.657$]. When the stimuli were presented in the center, index finger placement did not significantly differ when sliding compared to when only grasping $[p > 0.05, p(H_0/D) = 0.801]$.

In fact, there were no significant differences in index finger placement between stimulus position when the task involved sliding [left versus center: p > 0.05, $p(H_0/D) = 0.653$; left versus right: p > 0.05, $p(H_0/D) = 0.655$; center versus right: p > 0.05, $p(H_0/D) = 0.816$]. When only grasping the stimulus however, index finger placement was significantly different when the stimulus was presented on the left versus presented in the center $[p(H_1/D) = 0.999]$, and when presented on the left versus on the right $[p(H_1/D) = 0.999]$. There was no significant difference when only grasping the stimulus presented in the center compared to the stimulus presented on the right [p > 0.05, $p(H_1/D) = 0.541$]. The stimulus type × task [$F(1, 40) = 0.043, p > 0.05, \eta_p^2 = 0.001,$ $p(H_0/D) = 0.864$] and position × task × stimulus type [F(2, $80 = 0.551, p > 0.05, \eta_p^2 = 0.014, p(H_0/D) = 0.980$] interactions were non-significant.

Fixation positions

Accuracy check results

The mean absolute gaze displacement error, defined as the average absolute distance between participants' gaze and the center fixation dot during the accuracy checks, combined across all participants in the Virtual stimulus conditions was 0.33 cm in the horizontal axis (SE=0.02 cm); 0.51 cm in the vertical axis (SE=0.05 cm), and combined across all participants in the Physical stimulus condition was 0.28 cm in the horizontal axis (SE=0.02 cm); 0.55 cm in the vertical axis (SE=0.05 cm).

Horizontal fixations

A significant stimulus type × position interaction [F(2, 80) = 12.696, p < 0.001, $\eta_p^2 = 0.241$, $p(H_1/D) = 0.999$]

indicated that participants' average horizontal fixations followed a similar pattern as their index finger placement. Horizontal fixations did not significantly differ when the physical stimulus was presented on the left (M = 0.02 cm to the left of stimulus center, SE = 0.09) compared to the physical stimulus presented in the center [M=0.04 cm to the left of]stimulus center, SE = 0.10 cm; p > 0.05, $p(H_0/D) = 0.820$], or the physical stimulus presented on the right [M=0.13 cm]to the left of stimulus center, SE = 0.11 cm; p > 0.05, $p(H_0/D) = 0.780$]. There was also no difference between the physical stimulus presented in the center and the physical stimulus presented on the right $[p > 0.05, p(H_0/D) = 0.792]$. However, as seen with horizontal index finger placement, horizontal fixations were shifted toward the near side of non-central virtual stimuli. Fixations were positioned significantly farther rightward when the virtual stimulus was on the left (M=0.29 cm to the right of stimulus center,)SE = 0.10 cm) compared to the virtual stimulus in the center [M=0.14 cm to the left of stimulus center, SE=0.10 cm;p = 0.009, $p(H_1/D) = 0.956$], and compared to the virtual stimulus on the right [M=0.93 cm to the left of target]center, SE = 0.11 cm; p < 0.001, $p(H_1/D) = 0.999$]. Average fixations also significantly differed between the virtual stimulus presented in the center and on the right [p < 0.001, $p(H_1/D) = 0.998$].

Horizontal fixations did not significantly differ between stimulus type when the stimuli were presented in the center $[p > 0.05, p(H_0/D) = 0.849]$, or presented on the left $[p > 0.05, p(H_0/D) = 0.526]$. However, fixations were positioned significantly closer to the near side of the virtual stimulus compared to the physical stimulus when presented on the right $[p < 0.001, p(H_1/D) = 0.997]$. The main effect of task $[F(1, 40) = 2.537, p > 0.05, \eta_p^2 = 0.060, p(H_0/D) = 0.640]$, as well as the stimulus type × task $[F(1, 40) = 2.576, p > 0.05, \eta_p^2 = 0.061, p(H_0/D) = 0.636]$, position × task $[F(1.652, 66.097) = 2.272, p > 0.05, \eta_p^2 = 0.054, p(H_0/D) = 0.892]$, and stimulus type × position x task $[F(1.652, 66.097) = 1.531, p > 0.05, \eta_p^2 = 0.037, p(H_0/D) = 0.946]$ interactions were not significant.

Vertical fixations

A main effect of task $[F(1, 40) = 10.072, p = 0.003, \eta_p^2 = 0.201, p(H_1/D) = 0.945]$ indicated that participants' average fixations were positioned significantly lower when sliding the stimulus (M = 0.70 cm above stimulus center, SE = 0.16 cm) compared to when only grasping (M = 0.96 cm above stimulus center, SE = 0.16 cm). The main effects of stimulus type $[F(1,40) = 0.364, p > 0.05, \eta_p^2 = 0.009, p(H_0/D) = 0.843]$, position $[F(2, 80) = 1.152, p > 0.05, \eta_p^2 = 0.028, p(H_0/D) = 0.962]$, and the stimulus type x position $[F(2, 80) = 0.760, p > 0.05, \eta_p^2 = 0.019, p(H_0/D) = 0.974]$, stimulus type x task $[F(1, 40) = 0.180, p(H_0/D) = 0.180, p(H_0/D) = 0.180, p(H_0/D) = 0.180]$

p > 0.05, $\eta_p^2 = 0.004$, $p(H_0/D) = 0.855$], position x task [F(2, 80) = 0.086, p > 0.05, $\eta_p^2 = 0.002$, $p(H_0/D) = 0.987$], and stimulus type x position x task [F(2, 80) = 0.799, p > 0.05, $\eta_p^2 = 0.020$, $p(H_0/D) = 0.973$] interactions were not significant.

Absolute distance between grasp axis and stimulus center

A three-way stimulus type \times position \times task interaction reached significance, however the posterior probabilities suggested near positive evidence in favour of the null hypothesis [F(2, 80) = 3.327, p = 0.041, $\eta_p^2 = 0.077$, $p(H_0/D) = 0.746$] and therefore this interaction was not analyzed further. Instead, the significant lower-order position \times stimulus type interaction was analyzed [F(1.720, $(68.781) = 5.285, p = 0.010, \eta_p^2 = 0.117, p(H_1/D) = 0.686;$ Fig. 3]. Collapsing across task, the distance between the grasp axis and the stimulus' center did not significantly differ when interacting with the physical stimulus presented on the left compared to the physical stimulus in the center $[p > 0.05, p(H_1/D) = 0.665]$, or compared to the physical stimulus on the right $[p > 0.05, (p(H_1/D) = 0.681],$ however, the posterior probabilities did suggest weak evidence in favour of these differences. There was no evidence of a significant difference between grasp axis distances when comparing the physical stimulus when presented in the center and on the right $[p > 0.05, p(H_0/D) = 0.775]$. When interacting with the virtual stimulus, the grasp axis distance was significantly larger when the stimulus was presented on the left compared to in the center $[p(H_1/D) = 0.965]$ and was also significantly larger when the stimulus was presented on the right compared to in the center $[p(H_1/D) = 0.990]$. There was no significant difference between grasp axis distances

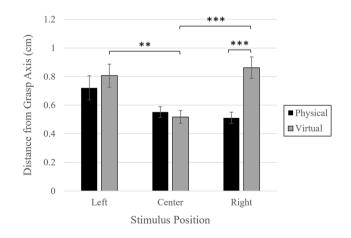


Fig.3 Absolute shortest distance between the grasp axis and the stimulus' center. Error bars represent standard error of the means. **p < 0.01, ***p < 0.001

when the virtual stimulus was presented on the left versus the right $[p > 0.05, p(H_0/D) = 0.799]$.

There were no significant differences between physical and virtual stimuli when the stimulus was presented on the left [p > 0.05, $p(H_0/D) = 0.830$], or in the center [p > 0.05, $p(H_0/D) = 0.844$]. However, the grasp axis distance was significantly larger when interacting with the virtual stimulus compared to the physical stimulus when presented on the right side [$p(H_1/D) = 0.997$].

The main effect of task [F(1, 40) = 1.321, p > 0.05, $\eta_p^2 = 0.032$, $p(H_0/D) = 0.766$], as well as the position × task [F(2, 80) = 2.314, p > 0.05, $\eta_p^2 = 0.055$, $p(H_0/D) = 0.888$] and stimulus type × task [F(1, 40) = 0.784, p > 0.05, $\eta_p^2 = 0.019$, $p(H_0/D) = 0.812$] interactions were not significant.

Horizontal distance between the index finger and thumb

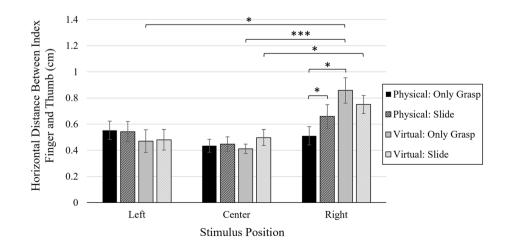
A significant three-way stimulus type \times position \times task interaction [F(1.732, 69.294) = 5.310, p = 0.010, $\eta_{\rm p}^2 = 0.117$, $p(H_1/D) = 0.691$; Fig. 4] was shown, and post-hoc tests indicated that the horizontal distance between the index finger and thumb at the time of the grasp did not significantly differ when only grasping the physical stimulus presented on the left compared to in the center $[p > 0.05, p(H_0/D) = 0.555]$, when only grasping the physical stimulus presented on the left compared to on the right $[p > 0.05, p(H_0/D) = 0.809]$, or when only grasping the physical stimulus in the center compared to on the right $[p > 0.05, p(H_0/D) = 0.712]$. There were also no significant differences when sliding the physical stimulus presented on the left compared to in the center $[p > 0.05, p(H_0/D) = 0.735]$ or on the right $[p > 0.05, p(H_0/D) = 0.735]$ $p(H_0/D) = 0.761$]. The post hoc comparison between sliding the physical stimulus presented in the center and on the right was deemed non-significant, however, the posterior probabilities suggested positive evidence in favour of the difference $[p = 0.052, p(H_1/D) = 0.802]$. When only

grasping the virtual stimulus, the horizontal distance between the index finger and the thumb was significantly larger when the stimulus was presented on the right compared to on the left $[p(H_1/D) = 0.852]$ and compared to in the center $[p(H_1/D) = 0.997]$. There was no significant difference when only grasping the virtual stimulus presented on the left versus in the center $[p > 0.05 (p(H_0/D) = 0.790]]$. When sliding the virtual stimulus, there was also a significantly larger horizontal distance between the digits when the stimulus was presented on the right in comparison to in the center $[p(H_1/D) = 0.898]$, but not in comparison to sliding the virtual stimulus on the left, despite the posterior probabilities suggesting weak evidence for the difference $[p > 0.05, p(H_1/D) = 0.705]$. There was no significant difference when sliding the virtual stimulus presented on the left compared to in the center $[p > 0.05, p(H_0/D) = 0.817]$.

The only significant difference between task type occurred when interacting with the physical stimulus presented on the right, where the horizontal distance between the index finger and thumb was significantly larger when sliding compared to only grasping, however the posterior probabilities showed little evidence of this difference $[p(H_1/D)=0.514]$. Otherwise, there were no significant differences between task types when interacting with the physical stimulus presented on the left $[p > 0.05, p(H_0/D)=0.818]$ and in the center $[p > 0.05, p(H_0/D)=0.817]$, or when interacting with the virtual stimulus on the left $[p > 0.05, p(H_0/D)=0.652]$, or on the right $[p > 0.05, p(H_0/D)=0.510]$.

Again, the only significant difference between stimulus type occurred on the right, where the horizontal distance between the index finger and thumb was significantly larger when only grasping the virtual stimulus in comparison to the physical stimulus $[p(H_1/D) = 0.896]$. There were no significant differences between stimulus type when only grasping stimuli presented on the left $[p > 0.05, p(H_0/D) = 0.828]$, and in the center $[p > 0.05, p(H_0/D) = 0.857]$, or when manipulating stimuli presented on the left $[p > 0.05, p(H_0/D) = 0.845]$,

Fig. 4 Average horizontal distance between placement of the index finger and thumb. Error bars represent standard error of the means. *p < 0.05, ***p < 0.001



in the center $[p > 0.05, p(H_0/D) = 0.843]$, or on the right $[p > 0.05, p(H_0/D) = 0.823]$.

Discussion

The use of virtual 2-D computer-generated targets to study visually guided reaching and grasping behaviours is an attractive option for behavioural visuomotor research, as it allows the incorporation of increasingly complex experimental paradigms, in which target presentation and visual feedback can be manipulated with a higher degree of experimental control. However, a grasping action directed toward a 2-D stimulus is inherently different than a grasping action toward a 3-D object, and therefore the results of research utilizing 2-D grasping may not be immediately generalizable to the grasping of 3-D objects. This study directly compared eye-hand coordination when grasping physical and virtual stimuli, while varying the task's action end-goal to explore how the intended manipulation influenced these behaviours.

Influence of stimulus position

The horizontal positions participants placed their index finger and fixated their gaze, as well as the stability of the grasp and the amount of torque inferred by the placement of the digits did not significantly differ between the virtual and physical stimulus types when presented in the center of the display. However, this study demonstrated clear differences between the grasping behaviours when the stimulus was presented to the left and right of center; participants generally grasped the near side of the non-central virtual stimulus, and closer to the horizontal midline of the physical stimulus at all three positions. As hypothesized, participants' average horizontal fixations also followed these patterns, suggesting participants were fixating toward their grasp points. Similar biases in gaze and grasp position toward the near side of non-central 2-D targets have been observed when grasping the same virtual stimuli used in this study (Langridge and Marotta 2020), and likely occur because participants are less motivated to place their digits at 'stable' positions aligned with the horizontal midline, as stability is not critical when interacting with virtual 2-D stimuli, and participants are therefore free to grasp the near side of the target, minimizing the amount of energy required to perform the task.

Paulun et al. (2014) reported digit placement shifted away from an object's COM, in the direction of the particular hand used to grasp it, suggesting participants were prioritizing visibility of the object when grasping (see also Maiello et al. 2019). Our results suggest that when grasping the virtual stimulus, participants minimized the need for increased visibility of the target in exchange for a more convenient (i.e., energy efficient) digit placement. This was apparent when the stimulus was presented on the right, which meant a grasp biased toward the near side of the stimulus would obstruct a larger portion of the stimulus from view. Even in the Physical condition, digit placement generally remained close to the stimulus' horizontal midline, rather than deviate rightward to increase visibility.

These observed differences may be related to several important methodological differences between our study and the work by Paulun et al. (2014). First, participants in Paulun et al.'s (2014) study consistently grasped a centrally located stimulus while the start point of the reach varied, whereas our study manipulated the position of the stimuli, and held the start point of the reaching movement constant. This suggests one's motivation to prioritize visibility versus energy efficiency when grasping may vary as a function of stimulus position. Second, while the manipulation of the stimulus in this study involved sliding the stimulus, Paulun et al. (2014) required participants to actually lift and move the object to another location, a movement more characteristic of the type of actions we perform every day. The different action end-goals may have placed a different emphasis on the importance of object visibility when grasping. The sliding task utilized in this study was chosen because it more closely replicates the type of action people typically perform when interacting with virtual 2-D stimuli and allowed us to make comparisons between the manipulation of the stimulus in both a physical and virtual environment. However, it is important to recognize that the eye-hand coordination behaviours observed when sliding the stimulus may not generalize to other tasks involving grasping and lifting, for which stability of the grasp and visibility of the stimulus may be more critical for success.

Digit placement was more stable and generated less torque in the Physical condition compared to the Virtual condition when the stimulus was presented on the right side of the display. When using a precision grip to grasp a rightward stimulus, participants would need to rotate their forearm inward to place their index finger and thumb at similar horizontal positions on the top and bottom of the stimulus. Although the distance participants were required to reach was not extreme, participants may have foregone the required pronation of the forearm to some degree when grasping the rightward virtual stimulus and settled on a more leftward placement of the thumb, producing a more angled grasp axis reducing stability and increasing torque. The stability of the grasp did not appear to differ as a function of stimulus type when grasping stimuli on the left or in the center of the display. Altogether, these findings suggest an overall reduction in precision when participants grasped the virtual stimulus at non-central locations, and in particular when the stimulus was presented on the right side of the display.

Influence of task: sliding versus only grasping

Participants lowered their fixations toward more central positions when sliding both types of stimuli, which could be interpreted as an adjustment of gaze enabling participants to monitor both the index finger and thumb at the time of the grasp (Desanghere and Marotta 2011; Belardinelli et al. 2015; Thulasiram et al. 2020). In anticipation of the intended manipulation of the stimulus, selection of each digit's contact point would need to serve both the effective execution of the grasp, and comfortable relocation of the stimulus, increasing the importance of participants' grasp point selection. The fact that similar adjustments in fixation position were made ahead of manipulation in both stimulus conditions suggests participants were also emphasizing careful digit placement when sliding the virtual stimulus.

This emphasis on precise digit placement was also reflected in the horizontal position participants placed their index finger when sliding both types of stimuli. The action of sliding the stimulus was associated with a shift in index finger placement and fixation position farther leftward when sliding the left stimulus, and farther rightward when sliding the right stimulus (i.e., away from the stimulus' near side) compared to when only grasping the stimulus these positions. This exaggerated digit placement could serve several purposes. First, digit placement closer to the horizontal midline would generate more control when manipulating the stimulus-increased control that would not be necessary when simply grasping the stimulus. Second, when the stimulus was presented on the right, a more rightward digit placement increases the amount of visual feedback of the stimulus during the subsequent manipulation (Maiello et al. 2019; Paulun et al. 2014). While an exaggerated digit placement toward the horizontal midline of a leftward stimulus in fact obstructs a larger portion of the stimulus than when only grasping, average digit placement in both the sliding and only grasp conditions remained on the right side of the leftward stimulus, leaving a large region of the stimulus visible, even if slightly less so when sliding.

A third possibility is that participants may have directed their grasps farther outward in anticipation of the subsequent inward movement of the stimulus toward the center of the display. According to the 'elastic-energy hypothesis' a person may bring a limb to an exaggerated or extreme position in preparation for a subsequent movement in the opposite direction. As the manipulation in this study always involved sliding the stimulus downward to the same central location, a more extreme outward digit placement when grasping the non-central stimuli may have allowed participants to exploit the stored potential energy in the arm and facilitate the subsequent inward movement toward the center of the display. Future studies manipulating the direction participants move the stimuli once grasped may help clarify the role of elastic energy in this type of task.

These findings suggest that certain task-related adjustments were observed in both the physical and virtual stimulus conditions, despite these adjustments not technically being necessary when interacting with the virtual stimulus. Considering the inherent differences between physical and virtual stimuli, these adjustments might only be expected in the physical condition, for which these aspects of the grasp are more critical to the success of the action. How then can we explain these similarities?

As the on-screen target lacked the true physical properties that would typically be used by the visuomotor system when planning and executing the grasping action, participants likely relied to some extent on their perceptual representation of the stimulus to guide their movement. When given the opportunity to manipulate the virtual stimulus (an option not typically possible with 2-D virtual stimuli), participants' perceptual representation of the target may have been updated to include features typically associated with physical object manipulation. The familiarization with the 3-D version of the virtual stimulus at the beginning of the experiment and the experimenter's instructions to 'grasp the target as if it were an actual 3-D object' may also have inspired an attribution of physical features traditionally associated with graspable objects.

Viewing 2-D images of manipulable objects is known to activate motor regions within the brain associated with physical interaction with the imaged object (Chao and Martin 2000; Proverbio et al. 2011), and manual responses are faster when participants are primed with images of those objects prior to the reach (Masson et al. 2011; Squires et al. 2016; Tucker and Ellis 1998). When instructed to touch images of objects as if they were lifting them, participants fixate and place their digits near the center of the imaged object, whereas these positions shift toward the object's lid when instructed to touch the object as if they were opening it (Belardinelli et al. 2015). Thus, participants can effectively incorporate their knowledge of an imaged object's physical properties and execute appropriate digit placement in response to the particular demands of the task. In the current study, presentation of the manipulable virtual stimulus may have primed the motoric response typically associated with and afforded by manipulation of a physical square 3-D object, priming participants to make responses similar to those that would be expected when grasping a physical 3-D stimulus, including adjustments accounting for a non-existent COM.

Implications, limitations, and future directions

The shape of the stimulus, as well as the dependent variables measured in the current study were chosen to match those used in our previous investigations of virtual 2-D grasping, thus allowing us to interpret the results within the context of past research using similar stimuli. In this study, participants' fixations and digit placement did not significantly differ as a function of stimulus type when the grasp occurred in the center of the display. Our previous investigations have also primarily involved centrally presented stimuli (Bulloch et al. 2015; Desanghere and Marotta 2011; Langridge and Marotta 2017; Thulasiram et al. 2020), and the current results suggest the gaze and grasp behaviours measured in these previous studies may also generalize to the natural grasping of 3-D objects similar to the type used in this study. However, these results also question the generalizability of research measuring grasp behaviour directed toward non-central virtual 2-D stimuli (e.g., Langridge and Marotta 2020). We also cannot assume these similarities will hold true when comparing stimuli of drastically different shape and size than those used here. It is also still unclear how stimulus motion influences the comparisons between virtual and physical stimulus interaction. Future comparisons involving increasingly complex and diverse stimuli are needed to explore the extent to which similar eye-hand coordination is maintained during interaction with virtual 2-D stimuli. Considering the advances in 3-D virtual reality and its relevant applications for visuomotor research, an interesting direction is to investigate this type of reaching and grasping behaviour in an immersive virtual reality environment, in which participants could interact with visually and haptically enriched stimuli of varying shapes and sizes, further bridging the gap between virtual and physical grasping research.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00221-021-06101-z.

Author contributions All authors contributed to methodology. Conceptualization, formal analysis, investigation and writing—original draft by RWL. Funding acquisition, project administration, resources, supervision and writing—review and editing by JJM. All authors read and approved the final manuscript.

Funding This research was supported by a University of Manitoba Graduate Fellowship (UMGF) held by R.W.L. and a grant from the Natural Science and Engineering Research Council of Canada (NSERC; Grant Number RGPIN 04964-18) held by J.J.M.

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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

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

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

References

- Ansuini C, Giosa L, Turella L, Altoè G, Castiello U (2008) An object for an action, the same object for other actions: effects on hand shaping. Exp Brain Res 185(1):111–119. https://doi.org/10.1007/ s00221-007-1136-4
- Belardinelli A, Herbort O, Butz MV (2015) Goal-oriented gaze strategies afforded by object interaction. Vis Res 106:47–57. https:// doi.org/10.1016/j.visres.2014.11.003
- Belardinelli A, Stepper MY, Butz MV (2016) It's in the eyes: planning precise manual actions before execution. J Vis 16(1):1–18. https:// doi.org/10.1167/16.1.18
- Bingham GP, Muchisky MM (1993) Center of mass perception and inertial frames of reference. Percept Psychophys 54(5):617–632. https://doi.org/10.3758/BF03211785
- Brouwer A-M, Franz VH, Gegenfurtner KR (2009) Differences in fixations between grasping and viewing objects. J Vis 9(1):18–24. https://doi.org/10.1167/9.1.18
- Bulloch MC, Prime SL, Marotta JJ (2015) Anticipatory gaze strategies when grasping moving objects. Exp Brain Res 12:3413–3423. https://doi.org/10.1007/s00221-015-4413-7
- Cavina-Pratesi C, Hesse C (2013) Why do the eyes prefer the index finger? Simultaneous recording of eye and hand movements during precision grasping. J Vis 13(5):15. https://doi.org/10.1167/13.5.15
- Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. Neuroimage 12(4):478–484. https:// doi.org/10.1006/nimg.2000.0635
- Cuijpers RH, Smeets JBJ, Brenner E (2004) On the relation between object shape and grasping kinematics. J Neurophysiol 91(6):2598– 2606. https://doi.org/10.1152/jn.00644.2003
- Desanghere L, Marotta JJ (2011) "Graspability" of objects affects gaze patterns during perception and action tasks. Exp Brain Res 212(2):177–187. https://doi.org/10.1007/s00221-011-2716-x
- Desanghere L, Marotta JJ (2015) The influence of object shape and center of mass on grasp and gaze. Front Psychol 6:1–13. https:// doi.org/10.3389/fpsyg.2015.01537
- Elsinger CL, Rosenbaum DA (2003) End posture selection in manual positioning: evidence for feedforward modeling based on a movement choice method. Exp Brain Res 152(4):499–509. https://doi. org/10.1007/s00221-003-1573-7
- Freud E, Macdonald SN, Chen J, Quinlan DJ, Goodale MA, Culham JC (2018) Getting a grip on reality: grasping movements directed to real objects and images rely on dissociable neural representations. Cortex 98:34–48. https://doi.org/10.1016/j.cortex.2017.02.020
- Glowania C, van Dam LCJ, Brenner E, Plaiser MA (2017) Smooth at one end and rough at the other: Influence of onject texture on grasping behaviour. Exp Brain Res 235:2821–2827. https://doi. org/10.1007/s00221-017-5016-2
- Goodale MA, Meenan JP, Bulthofft HH, Nicolle DA, Murphy K, Racicot C (1994) Separate neural pathways for the visual analysis of object shape in perception and prehension. Curr Biol 4(7):604– 610. https://doi.org/10.1016/S0960-9822(00)00132-9
- Herbort O, Butz MV (2010) Planning and control of hand orientation in grasping movements. Exp Brain Res 202(4):867–878. https:// doi.org/10.1007/s00221-010-2191-9

- Holmes SA, Heath M (2013) Goal-directed grasping: the dimensional properties of an object influence the nature of the visual information mediating aperture shaping. Brain Cogn 82(1):18–24. https:// doi.org/10.1016/j.bandc.2013.02.005
- Hughes CML, Seegelke C, Spiegel MA, Oehmichen C, Hammes J, Schack T (2012) Corrections in grasp posture in response to modifications of action goals. PLoS ONE. https://doi.org/10.1371/journ al.pone.0043015
- Janssen P, Scherberger H (2015) Visual guidance in control of grasping. Annu Rev Neurosci 38(1):69–86. https://doi.org/10.1146/ annurev-neuro-071714-034028
- Johansson RS, Westling G, Bäckström A, Flanagan R (2001) Eye–hand coordination in object manipulation. J Neurosci 21(17):6917– 6932. https://doi.org/10.1523/JNEUROSCI.21-17-06917.2001
- Langridge RW, Marotta JJ (2017) Grasping occluded targets: investigating the influence of target visibility, allocentric cue presence, and direction of motion on gaze and grasp accuracy. Exp Brain Res 235(9):2705–2716. https://doi.org/10.1007/s00221-017-5004-6
- Langridge RW, Marotta JJ (2020) Grasping a 2D virtual target: the influence of target position and movement on gaze and digit placement. Hum Mov Sci. https://doi.org/10.1016/j.humov.2020. 102625
- Lederman SJ, Wing AM (2003) Perceptual judgement, grasp point selection and object symmetry. Exp Brain Res 152(2):156–165. https://doi.org/10.1007/s00221-003-1522-5
- Maiello G, Paulun VC, Klein LK, Fleming RW (2019) Object visibility, not energy expenditure, accounts for spatial biases in human grasp selection. i-Percept. https://doi.org/10.1177/2041669519827608
- Marotta JJ, Mckeeff TJ, Behrmann M (2003) Hemispatial neglect: Its effects on visual perception and visually guided grasping. Neuropsychologia 41:1262–1271. https://doi.org/10.1016/S0028-3932(03)00038-1
- Masson MEJ (2011) A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. Behav Res 43:679–690. https://doi.org/10.3758/s13428-010-0049-5
- Masson MEJ, Bub DN, Breuer AT (2011) Priming of reach and grasp actions by handled objects. J Exp Psychol Hum Percept Perform 37(5):1470–1484. https://doi.org/10.1037/a0023509
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9(1):97–113. https://doi.org/10.1016/0028-3932(71)90067-4
- Ozana A, Ganel T (2017) Weber's law in 2D and 3D grasping. Psychol Res 83:977–988. https://doi.org/10.1007/s00426-017-0913-3
- Ozana A, Ganel T (2019) Obeying the law: speed–precision tradeoffs and the adherence to Weber's law in 2D grasping. Exp Brain Res 237(8):2011–2021. https://doi.org/10.1007/s00221-019-05572-5
- Ozana A, Namdar G, Ganel T (2020) Active visuomotor interactions with virtual objects on touchscreens adhere to Weber's law. Psychol Res 84(8):2144–2156. https://doi.org/10.1007/ s00426-019-01210-5
- Paulun VC, Kleinholdermann U, Gegenfurtner KR, Smeets JBJ, Brenner E (2014) Center or side: biases in selecting grasp points on small bars. Exp Brain Res 232:2016–2072. https://doi.org/10. 1007/s00221-014-3895-z
- Paulun VC, Gegenfurtner KR, Goodale MA, Fleming RW (2016) Effects of material properties and object orientation on precision grip kinematics. Exp Brain Res 234:2253–2265. https://doi.org/ 10.1007/s00221-016-4631-7
- Proverbio AM, Adorni R, D'Aniello GE (2011) 250 Ms to code for action affordance during observation of manipulable objects.

Neuropsychologia 49(9):2711–2717. https://doi.org/10.1016/j. neuropsychologia.2011.05.019

- Raftery AE (1995) Bayesian model selection in social research. Sociol Methodol 25:111–163. https://doi.org/10.2307/271063
- Rosenbaum DA, Chapman KM, Weigelt M, Weiss DJ, van der Wel R (2012) Cognition, action, and object manipulation. Psychol Bull 138(5):924–946. https://doi.org/10.1037/a0027839.COGNITION
- Rouse AG, Schieber MH (2015) Spatiotemporal distribution of location and object effects in reach-to-grasp kinematics. J Neurophysiol 114(6):3268–3282. https://doi.org/10.1152/jn.00686.2015
- Salvucci DD, Goldberg JH (2000) Identifying fixations and saccades in eye-tracking protocols. Proc Eye Track Res Appl Symp. https:// doi.org/10.1145/355017.355028
- Santello M, Soechting JF (1998) Gradual molding of the hand to object contours. J Neurophysiol 79(3):1307–1320. https://doi.org/10. 1152/jn.1998.79.3.1307
- Sartori L, Straulino E, Castiello U (2011) How objects are grasped: the interplay between affordances and end-goals. PLoS ONE. https:// doi.org/10.1371/journal.pone.0025203
- Schettino LF, Adamovich SV, Poizner H (2003) Effects of object shape and visual feedback on hand configuration during grasping. Exp Brain Res 151(2):158–166. https://doi.org/10.1007/ s00221-003-1435-3
- Schettino LF, Pallottie A, Borland C, Nessa S, Nawroj A, Yu Y-C (2013) The organization of digit contact timing during grasping. Exp Brain Res 227(4):477–486. https://doi.org/10.1007/ s00221-013-3524-2
- Squires SD, Macdonald SN, Culham JC, Snow JC (2016) Priming tool actions: are real objects more effective primes than pictures? Exp Brain Res 234(4):963–976. https://doi.org/10.1007/ s00221-015-4518-z
- Thulasiram MR, Langridge RW, Abbas HH, Marotta JJ (2020) Eyehand coordination in reaching and grasping vertically moving targets. Exp Brain Res 238(6):1433–1440. https://doi.org/10.1007/ s00221-020-05826-7
- Tucker M, Ellis R (1998) On the relations between seen objects and components of potential actions. J Exp Psychol Hum Percept Perform 24(3):830–846. https://doi.org/10.1037/0096-1523.24.3.830
- Vargas-Irwin CE, Franquemont L, Black MJ, Donoghue JP (2015) Linking objects to actions: encoding of target object and grasping strategy in primate ventral premotor cortex. J Neurosci 35(30):10888–10897. https://doi.org/10.1523/JNEUROSCI. 1574-15.2015
- Voudouris D, Smeets JBJ, Brenner E (2016) Fixation biases towards the index finger in almost-natural grasping. PLoS ONE 11(1):1– 29. https://doi.org/10.1371/journal.pone.0146864
- Weir PL, Mackenzie CL, Marteniuk RG, Cargoe SL (1991) Is object texture a constraint on human prehension?: kinematic evidence. J Motor Behav 23(3):205–210. https://doi.org/10.1080/00222895. 1991.10118363
- Westwood DA, Danckert J, Servos P, Goodale MA (2002) Grasping two-dimensional images and three-dimensional objects in visualform agnosia. Exp Brain Res 144(2):262–267. https://doi.org/10. 1007/s00221-002-1068-y

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.