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RESEARCH ARTICLE

# Human string-pulling with and without a string: movement, sensory control, and memory

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**Abstract**
String-pulling is a behavior that is allied to many daily acts and is an easily performed action featuring hand-over-hand movements to reel in a string (or rope). String-pulling has been used as a test of perceptual and cognitive functions in many animal species, including human children, but its movements and sensory control have not been characterized. Male and female university students ($n = 68$) performed target-based or memory-based string-pulling in which they pulled down a string suspended on an overhead pulley and immediately afterwards attempted to make the same movement in a memory-based test. Frame-by-frame video scoring was used to describe movements, eye-tracking and visual occluding glasses were used to assess sensory control, and a Matlab video-analysis procedure was used to describe kinematics. The string was advanced using five arm/hand movements: with lift and advance comprising fast up movements, and grasp, pull and push comprising slow down movements. Fingers closed 5 (pinky) through 1 (thumb) to make a whole-hand grasp and release in target-based string pulling but moved in a reverse sequence for the memory-based task. Target-based string pulling was not visually guided unless participants were instructed to grasp at a cue, and then vision featured eye-tracking of the target and pupil dilation with the grasp, but there was no relation between eye events for memory-based string-pulling. For target-based string-pulling the left and right hands advanced the string with both independent and concurrent movement but only independent movements were featured in a more symmetrical memory-based movement. The results are discussed in relation to the sensory control of hand movements, contemporary theories of the neural control of hand movements, and species differences in string-pulling.

**Keywords** String-pulling · Sensory control · Reach and grasp · Pantomime · Bimanual coordination · Kinematics

## Introduction

The investigation of skilled hand movements used to reach out and grasp an object is an area of central interest in the study of motor control, brain organization, robotics and evolution (Karl and Whishaw 2013; Whishaw and Karl 2014; Kilteni and Ehrsson 2017; Salvietti 2018; Isa 2019; Lemon 2019; Wu et al. 2019). The present study was conducted to describe a bilateral form of reaching, string-pulling, in which participants pull down a string (rope) with hand-over-hand movements of a type used in many daily tasks (Swinnen and Wenderoth 2004). For example, a string-pulling task, "endless rope" is used for exercise and rehabilitation and is subject to a number of patents for rope-pulling equipment. Jacobs and Osvath (2015) report that over 160 bee, bird, and mammalian species display versions of string-pulling behavior. String-pulling has been viewed as a prototool task and has been mainly exploited to study cognitive processes.

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For example, does a subject know there is a food item at the end of the string and which of two crossed strings is attached to a food item. The hand movements and the kinematic cycle of string-pulling have only been recently described for rats and mice with the idea that the task could provide insights into the evolution of skilled hand movements and also serve as a neurological test in animal analogues of human neurological disease (Blackwell et al. 2018a, b, c). Although human infants and children have been studied in string-pulling tasks (Richardson 1932; Piaget 1952; Redshaw 1978; Brown 1990; Silva et al. 2005, 2008; Albiach-Serrano et al. 2012; Taylor et al. 2012; Rat-Fischer et al. 2014) there is no description of its movement or sensory control. A description of string-pulling could contribute to its use as a simple task for investigating bilateral hand function, could provide an assessment of motor function in neurological conditions, and could be applied to questions related to comparative movement control.

In the string-pulling task, a participant stands upright, with a string that is suspended in front of them from a pully, and pulls the string down using hand-over-hand movements. At its simplest, string-pulling can be conceived of as two single-handed reach-to-grasp movements in which the hands alternate. As such, the movements could be expected to have many of the same sensory, movement, and kinematic features that have been described for single-handed reach-to-grasp movements (Jeannerod 1981; Jeannerod et al. 1994) allowing a number of predictions with respect to the form that string-pulling reaching movements should take. First, string-pulling should be a visually guided task in which participants visually engage the points on the string for which they will reach, as occurs for single-handed pointing or reaching (Prablanc et al. 1979; Neggers and Bekkering 2000, 2001; de Bruin et al. 2008; Sacrey and Whishaw 2012). Accordingly, participants were tested when sighted and when blindfolded and gaze and pupil responses were recorded with eye-tracking glasses. Second, it was expected that the kinematic measures of reaching and hand shaping for string-pulling would be similar to those of a single-hand reach. Thus, participants would display a bell-shaped curve featuring rapid hand advancement toward the string followed by slower hand preshaping and precision grasping (Jeannerod 1981; Jeannerod et al. 1994). Therefore, kinematic measures of reaching and hand use were recorded. Third, it was expected that were the participants given a memory-based version of string-pulling, in which they pantomimed target-based string-pulling movements that they had just made, the memory-based string-pulling movements would display alterations in the kinematic features of the movements similar to those described for single-handed reaching (Goodale et al. 1991, 1994; Westwood et al. 2000; Milner et al. 2001; Fukui and Inui 2013; Holmes et al. 2013; Kuntz and Whishaw 2016; Kuntz et al. 2018). Therefore, after performing the target-based string-pulling task, the participants were immediately asked to pantomime those same movements.

For the study, male and female undergraduates were filmed from a frontal view and were asked to pull a string (a soft rope) using hand-over-hand pull movements. Participants wore color-coded gloves on the left and right hand and their movements were tracked using Matlab-based software (Singh et al. 2016, 2019). To assess the role of vision in string-pulling, different groups of participants were tested with eye-tracking glasses to measure gaze and pupil dilation or glasses that occluded vision. Target-based string pulling had the string present for pulling and memory-based string pulling had participants reproduce the movements generated during the previous target-based task.

## Methods

*Participants* Participants were 68 undergraduate students aged 18–23 enrolled in a neuroscience class at the University of Lethbridge. All participants were selected from a larger group of students on the basis of a short questionnaire that ascertained that they were right-handed. Participants were confirmed to be right-handed by completing the Brainmapping questionnaire adapted from the Edinburg inventory (Oldfield 1971). In one experiment, 48 participants were divided into four groups of 12, with each group comprised of six females and six males. In a second experiment, 20 (ten male, ten female) participants performed string-pulling while wearing eye-tracking glasses. Before beginning the experiment, the participants read a short summary of the experiment, gave their written consent to participate, and gave consent to their images being used for experimental analysis and dissemination. The experiments were approved by the University of Lethbridge human subject ethics committee.

*String* Two 14 mm diameter strings (ropes) were used, each 1341 cm long. One was a plain white string and the other had 2 cm wide bands of black electrician's tape wrapped around it to demark the string into 30 cm segments. The strings were suspended through a pully in the ceiling. A knot tied at the end of each string prevented the string from passing through the pulley. A smaller string tied to the knot allowed the main string to be pulled back to its starting position.

*Attire* Participants were asked to dress in a dark top and bottom. Before initiating string-pulling, the participants put on VWR nitrile gloves (VRW International, LLC Ranor, PA). Participants put a blue glove on the right hand and a green glove on the left hand. Preliminary experiments indicated that string-pulling movements were similar in ungloved and gloved participants.

## Eye and pupil tracking and visual attention

*Eye tracking and pupil measurement* To gaze target and pupil change, participants performed target-based string-pulling followed by memory-based string-pulling while wearing eye-tracking glasses. Gaze and the pupil diameter were monitored using a Pupil-Lab eye tracker (Kassner et al. 2014). Pupil-Lab is a wearable mobile eye-tracking headset with one scene camera and two infrared (IR) spectrum eye cameras for dark pupil detection. The cameras connect to a laptop computer platform via high-speed USB 2.0. The camera video streams were read using Pupil Capture software for real-time pupil detection and gaze mapping. Pupil captures a view of the gaze scene at 30 Hz and gaze focus and pupil diameter at 120 Hz. The Worldview window of the software was used to display the video stream from the scene camera with gaze location superimposed on the scene as a small round dot. The gaze camera was calibrated using a 9-point calibration method and the accuracy of calibration was checked by having participants fixate their gaze on selected objects in the test room before and after string pulling. Frame-by-frame inspection of the Worldview video was used to determine whether participants were looking at the string when pulling and for determining what portion of the string was the focus of gaze. On line changes in gaze and pupil diameter were similarly monitored in relation to string-pulling hand movements.

*Visual attention* In an experiment in which participants did not wear eye-tracking glasses, the relationship between looking and reaching was determined from their head orientation and grasp location in the y-plane. Orientation was assessed using a three-point scale: 1 = looking up, 0 = looking straight ahead, − 1 = looking down) and the grasp location of the hand was also assessed on a three-point scale: 1 = reaching above the head, 0 = reaching to the level of the face, − 1 = reaching below the level of the face. Correlations between head orientation and grasp location determined whether participants were looking toward the location on which their hand grasped the string. Head orientation and hand placement were rated for five up-down sequences by each hand from one real and one pantomime string-pulling act to obtain a mean score.

## Release and grasp movements

A rating scale was used to quantify how the hands released and grasped the string. The order of finger extension when the hand was opening and finger flexion when the hand was closing was rated on a three-point scale. If the fingers extended or flexed in the order 5 through 1 (pinky first, thumb last) the movement was rated as "0"; if the fingers opened or closed concurrently, the movement was rated as "0.5"; if the fingers opened or closed in the order 1 through 5, the movement was rated as "1". Five hand release and hand grasp movements were rated for each hand for each participant from one target-based and one memory-based string-pulling act to obtain a mean score.

## Tracking hand movements

In computer vision, image segmentation clusters pixels into salient groups to identify regions of interest. Multiple methods exist to perform image segmentation, e.g., thresholding methods (Otsu 1979), color-based segmentation such as K-means clustering (Arthur and Vassilvitskii 2007), transform methods such as watershed segmentation (Meyer 1994) and texture filter methods (Gonzalez et al.2003). Here participants wore green (left hand) and blue (right hand) nitrile gloves to provide high-target contrast relative to the black background (body and wall sheet), thus, making the image segmentation process amenable to a thresholding-based segmentation method. The Color Thresholder app in MATLAB® was used to perform color-based segmentation of the left/right hand for each participant.

A random frame from the recorded behavior was opened in the Color Thresholder app, which in turn displayed the image along with point clouds representing the same image in several popular color spaces: RGB, HSV, YCbCr, and L*a*b*. The color space that provided best color separation for left/right hands from the background was selected. The colorspace and range for each channel of the colorspace were set within the app and a thresholding function was autogenerated to recreate the segmentation in all frames of the video. Using a similar approach presented in Singh et al. (2016, 2019), the centroid of hands was detected in each segmented frame and presented as the track plot once the video was processed.

To describe the movements of one hand with respect to another, the instantaneous phase of the real-valued $y$ axis motion $y(t)$ was extracted using an analytic signal representation as follows:

$$y_{\mathrm{A}}(t) = y(t) + j\hat{y}(t)$$

where, $y_{A}(t)$ is the analytic signal, $\hat{y}(t)$ is the Hilbert transform of $y(t)$. The analytic signal obtained is expressed in exponential notation:

$$y_{\mathrm{A}}(t) = A(t)e^{j\phi(t)}$$

where, $A(t)$ is the instantaneous amplitude and $\phi(t)$ is the instantaneous phase and $\phi(t)$ values gave timepoints when the participants were grasping or releasing the string.

The best fit to an ellipse for the given set of $x$–$y$ coordinates of each hand's trajectory (Bookstein 1979; Gander et al. 1994) was used to describe the spatial occupancy patterns of left/right hand. A Least-Squares criterion for estimation was performed for the following conic representation:

$$Q(x, y) = Ax^2 + Bxy + Cy^2 + Dx + Ey + F = 0$$

After finding the $x$–$y$ coordinates of the center, long and short lengths were used to find the area of the ellipse from which to extract amplitude, and the spatial occupancy patterns in real and pantomime tasks.

The MATLAB® tracking procedure was used to assess one target-based and one memory-based string-pulling act by each of the participants, i.e., a series of 5–7 pulls by each hand. In addition, a second string-pulling act was manually digitized using PhysicsTracker [Open Source Physics (OSP) Java framework] to confirm the accuracy to the Matlab procedure. Because the two methods gave the same statistical results only the Matlab-obtained results are reported here.

## Procedure

A participant was asked to stand in front of the string in front of a black sheet and at a distance of 152.4 cm from the camera. Participants were asked to take the string in one hand to stabilize it. They were then instructed that on a "go" command they should pull the string with alternating left-and-right hand overhand pulls until the string was stopped by its knot. Participants were given no instructions with respect to which hand they should start with, but most participants used their right hand to stabilize the string. Each participant was given four trials.

1. *Practice* The first trial was used as practice, and the participants pulled a real string to ensure that they understood the instructions. The participant was instructed, "I would like you to pull down the string using hand-over-hand movements."
2. *Target-based string-pulling* Participants were given three trials in which they pulled the real string to its end.
3. *Memory-based string-pulling*. The participants were given three trials in which they reproduced string-pulling in the same way that they had pulled in the target-based string-pulling condition. For the pantomime trial, the string was moved to one side and the participant was instructed: "Now I would like you to pretend to pull the sting in the same way that you actually pulled it." Each string-pulling trial generated about 4–7 pulling cycles by each hand.

### Experiment 1: condition comparisons

Twelve participants (six female and six male) were assigned to each of the following groups.

1. *Unmarked string* The group pulled the plain string that had no markings.
2. *Marked string* The marked string group pulled a string that had black markings at 30 cm intervals but they were given no instructions with respect to the markings.
3. *Visual occluded* The visual occluded group wore opaque glasses and pulled the plain string that had no markings.
4. *Visual cue* The visual-cue group were asked to grasp the string at every second black cue on each pull with the left hand and on each pull with the right hand.

### Experiment 2: eye and pupil tracking

Twenty participants who wore eye-tracking glasses were assigned to each of the following groups of ten participants each (five male and five female).

1. *Marked string* The marked string group pulled a string that had black markings, but they were given no instructions with respect to the markings. After performing two target-based string-pulling trials they performed two memory-based string-pulling trials.
2. *Visual cue* The visual-cue group were asked to grasp the string at every second black cue for each pull with the left hand and each pull with the right hand. After performing two target-based string-pulling trials they performed two memory-based string-pulling trials.

### Statistical analyses

The results were analyzed using repeated Analysis of Variance (ANOVA) for repeated measures and Bonferroni follow-up tests using SPSS®. The independent variables were Groups (participant groups), Hands (left and right hands) Sex (male and female), and Conditions (target-based and memory-based string-pulling). Independent measures included Direction (up and down hand movements), Velocity (distance/s) including Maximum and Minimum velocity of up and down movements, Frequency (number of pulls by a hand per/s), Amplitude (distance/cm of up and down movements), Spatial Occupancy (the area enclosed by an up or down string-pulling movement relative to a direct path), the Cartesian volume enclosed by a complete up/down hand excursion, and Asymmetry (difference in measure by one hand compared to the other). Pearson-product correlations were used to relate gaze orientation to hand location. A value of $p < 0.05$ was accepted as significant.

## Results

There were some similarities and many differences between target-based and memory-based string-pulling behavior and these results are summarized in the following descriptions of: (1) movements of string-pulling (2) sensory control of string-pulling, and (3) kinematic measures of string-pulling.

## Movements of string-pulling

### Arm and hand movements

String-pulling is a cyclic movement in which one forelimb alternates with the other to advance the downward movement of the string, with both forelimbs featuring characteristic upper arm, lower arm, and hand movements in each phase of the action. Similar arm and hand movements were used for target-based string-pulling and for the memory-based string pulling that occurred immediately following target-based trials. Figure 1 illustrates string-pulling movements in a representative participant. A video of a target-based string-pull sequence is shown in Video 1 and a memory-based sting-pull sequence is shown in Video 2. Table 1 summarizes the following component movements of string-pulling that were common to both types of string-pulling.

1. *Release* Release of the string by the pulling hand occurs by extension of the lower arm, upper arm, and the fingers, with slight abduction of the hand as the release is completed.
2. *Lift* The hand is lifted to the midpoint of the torso on the way to initiate a new pull by flexion of the lower arm at the elbow, with the hand carried to a horizontal position with the digits slightly flexed, and with the distal ends of the digits aligned to the body midline.
3. *Advance* The hand is carried in an upward motion toward the string, first by extension of the upper arm at the shoulder followed by extension of the lower arm at the elbow, with a slight adduction of the hand so that palm of the hand is aligned with the body midpoint and with the string.

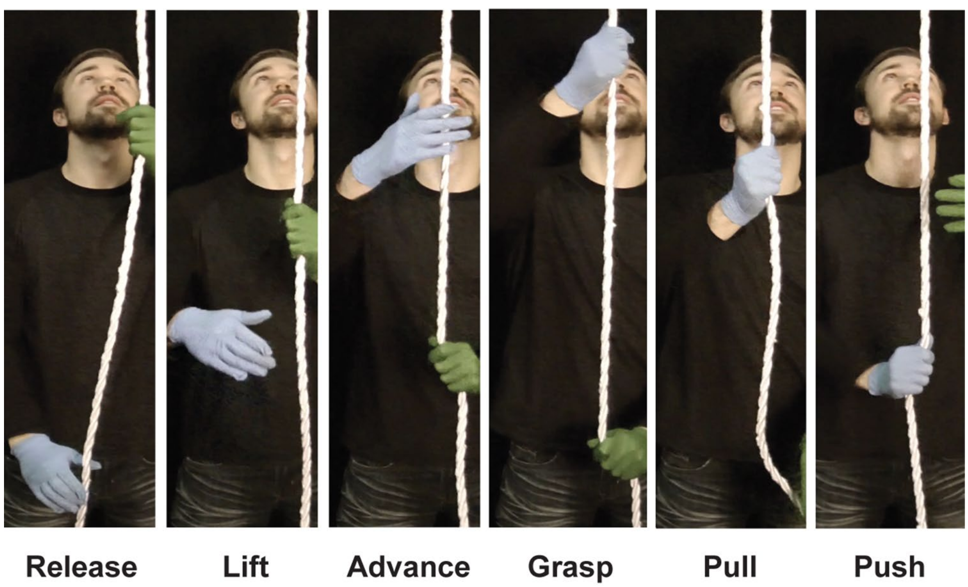


**Fig. 1** The five movements of string-pulling illustrated for the right hand of a participant making a target-based string-pulling movement. *Release* fingers open and extend to release the string, *Lift* the hand is raised to the midpoint of the torso largely by flexion of the lower arm, *Advance* the hand is raised to grasp the string largely by extension at the shoulder and elbow, *Grasp* the fingers are closed and flexed to grasp the string, *Pull* the string is lowered largely by flexion at the shoulder and the lower arm, *Push* the continued movement of the string is produced largely be extension of the lower arm. Note: gaze is directed to the string at a point above the grasp point on the string

**Table 1** Main arm and hand movements of target-based string pulling

| Movement | Hand | Lower arm | Upper arm |
|---|---|---|---|
| Release | Fingers extend/open Arpeggio 5-1 | Abduct, extend | Abduct extend |
| Lift | Fingers partially closed | Flex at elbow | May extend |
| Advance | Fingers extend | Extend at elbow | Extend |
| Grasp | Fingers flex/close Arpeggio 5-1 | Begins to close | Begins to flex |
| Pull | Fingers grasp | Flex at elbow | Flex |
| Push | Fingers grasp | Extend at elbow | Flex, abduct |

4. *Grasp* To grasp the fingers more fully extend and open to purchase the string with a whole-hand grasp, and with contact with the string made as the hand begins to descend.
5. *Pull* For the pull the hand is advancing toward the midpoint of the torso with the upper arm flexing at the shoulder, the lower arm flexing at the elbow, and the hand dorsiflexing at the wrist.
6. *Push* For the push, the hand moves downward toward the hips by extension of the lower arm at the elbow and by pronation of the hand, such that the digits are directed downward.

### Different grasp and release for target-based and memory-based tasks

The hands closed to grasp and opened to release at roughly the same temporal points in target-based string-pulling and memory-based string-pulling but the way in which they opened and closed in the two conditions was different. Figure 2 gives an example of hand movements for release and grasp in the target-based and the memory-based string-pulling conditions. The initiation of the movements (grasp or release) is shown in the A-panels, the midpoint is shown in the B-panels, and the completion shown in the C-panels.

*Target-based grasp and release* To grasp a real string, the hand supinates so that the palm of the hand is aligned with the string, which is in turn aligned with the body midline. The fingers fully open and extend before the grasp and then fingers 5 (pinky) and 4 usually make first contact with the string and gather the string and move it toward the palm of the hand. As the hand begins to make a downward movement, the digits close in a sequence of 5 through 1 (thumb) until the string is held in a whole-hand grasp.

To release the string in the target-based condition, the palm is directed toward the body, the fingers extend downward as they open, and they open in the sequence 5 through 1, with fingers 1 and 2 being the last to release the string. When the string is fully released the fingers are fully extended with the palm facing inward toward the body and the digits directed downward.

*Memory-based grasp and release* The grasp for memory-based string pulling was different from that of the target-based grasp. First, as the hand approaches the "string", the digits do not fully extend or open. Second, the fingers usually close in the order, 1 through 5, a sequence that is the opposite of that of a target-based grasp. Third, hand closing sometimes occurs when the hand is paused at the end of the upward movement and is sometimes closed as it continues upward, as contrasted with a target-based grasp that is always associated with a downward hand movement.

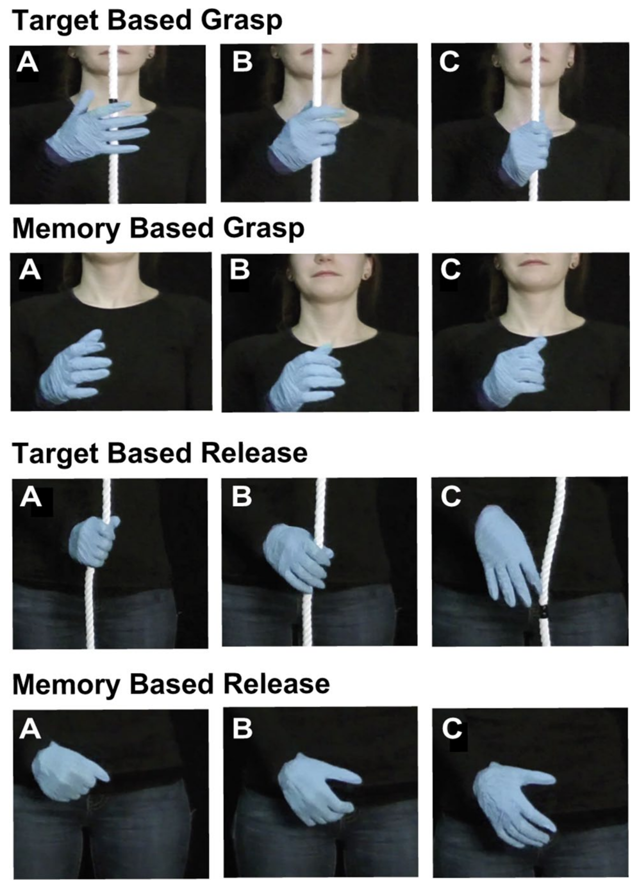


**Fig. 2** Hand shaping movements to grasp and release the string in target-based string-pulling and memory-based string-pulling. **a** The point of movement initiation, **b** midpoint of hand shaping to grasp and release, **c** the point the string is grasped or released. Note: (1) to make a target-based grasp of the string the fingers are closed in the order 5 through 1 (pinky first, thumb last) and to make a real release of the string the fingers are opened in the order 5 through 1. (2) To make a memory-based grasp, the fingers close in the order 1 through 5 and open to release the string in the order 1 through 5. Note (2): the grasp is likely made through touch cues from fingers 5 and 4; and Note (3) the pulling hand is signalling to the other hand the location and movement of the string

### Rating of target- vs memory-based grasp and release

Figure 3 illustrates the rating scores obtained from five hand release and hand grasp movements for each participant in each of the four string-pulling groups performing the target-based and memory-based task. A 3-point rating scale was used to describe the sequence of finger closing for the grasp and opening for the release with the sequence of finger movement 5 through 1 = "0", concurrent opening and closing of all fingers = "0.5" score, and finger opening or closing in the sequence of fingers 1 through 5 = "1".

As is illustrated in Fig. 3, there was almost no overlap in the scores of target-based grasp and release vs memory-based grasp and release. That the scores reflect a significant

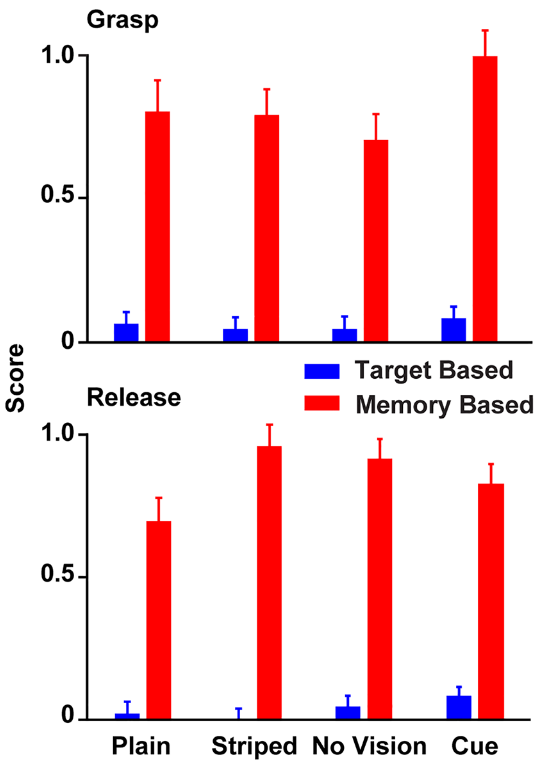


**Fig. 3** Scores (mean ± SE) for target-based and memory-based string release and grasp. Scores were "0", the fingers open or close in the order 5 through 1, "0.5", the fingers open or close concurrently, "1", the fingers open or close in the order 1 through 5. Note: the 5 through 1 order of finger movement of target-based pulling is reversed to 1 through five for memory-based string-pulling

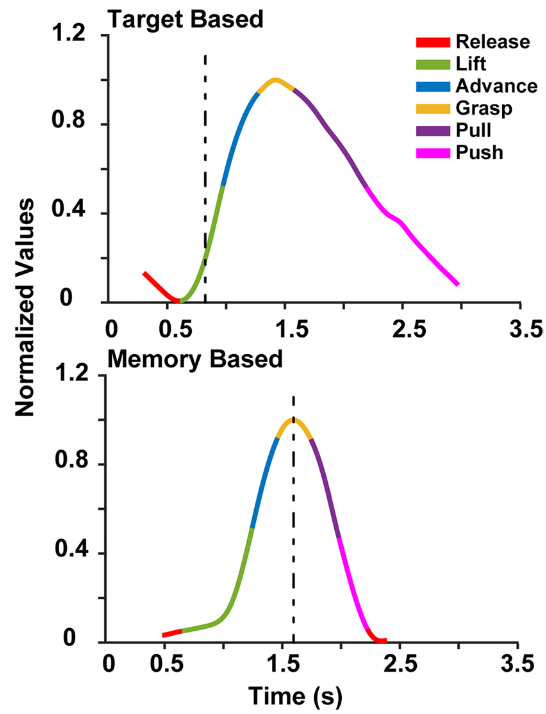


**Fig. 4** A representative Cartesian plot of hand movement in the y-direction (up/down) for a target-based string-pull (top) and a memory-based string-pull (bottom) that is color coded to reflect successive movements. Note (1) the up/down movement ratios of 1:2 for target-based and 1:1 for memory-based string-pulling. The vertical lines represent the point prior at which the hand fully opens. Note (2): for target-based string-pulling, the hand fully opens at the point of initiation of the lift, whereas for memory-based string-pulling, the hand has its greatest opening at about the point that grasping is initiated. Note (3) that a greater portion of the release and grasp occurs on the down movement for target-bases vs memory-based string pulling

difference with the target-based condition featuring finger sequence of 5–1 and the memory-based condition featuring finger sequence 1–5 was confirmed by a significant condition effect for grasp, Condition $F(1,40) = 223.23$, $p < 0.001$, and a significant condition effect for release, Condition $F(1,40) = 357.8$, $p < 0.001$. The difference in finger sequence occurred for all of the groups and for both sexes, as the group and sex effects were not significantly different and the interactions between groups and sexes were also not significantly different.

### The timing of hand opening to grasp

The y-trajectory of a target-based string-pull and a memory-based string-pull is shown in Fig. 4. The trajectory is color-coded to show the timing of movements during the pull. For the target-based reach the duration of the down movement is twice as long as the duration of the up movement (i.e., 1:2) and it is on the down movement the grasp and release hand movements occur. For the memory-based reach the ratio of up-to-down is 1:1 and hand opening and closing may occur as part of the up sequence.

Frame-by-frame inspection of the video of hand opening and hand closing showed hand movement were also attenuated in the memory-based condition relative to the target-based condition. All of the memory-based participants had a more closed hand throughout the reach. Indeed, with the hand opening that they displayed they would not have been able to grasp or release a real string. The hand opening was also temporally different for target- vs memory-based reaches on the up-movement. Maximum hand opening for target-based string-pulling occurred with release of the string whereas maximum hand opening for memory-based string-pulling occurred just before the grasp.

The differences in timing of hand-opening were reflected in the video-based surface measures of the hand taken throughout the reach and are also summarized in Fig. 4. Relative to the movement that comprises the y-trajectory profile, the mean maximum hand opening for target-based reaching, as indicated by the vertical dotted line, occurred after the string was released and at about the time the lift of the hand began. Relative to movements that comprise the y-movement profile, the mean maximum hand opening for memory-based hand opening occurred as the string was grasped. In short, maximum hand opening for target-based string-pulling occurred just after Release and maximum hand opening for memory-based string-pulling occurred just before the grasp. An ANOVA on the time to maximum opening before the apex of the up-movement was calculated for 5 cycles for each subject in each condition showed that there was a significant difference between the timing of target-based and memory-based reaches, Condition $F(1,40) = 7.81$, $p < 0.01$, but no group, sex, or interaction differences.

## Sensory control of string-pulling

### Head and gaze orientation for target-based and memory-based string-pulling

For the unmarked string group of participants, who pulled the unmarked string but were given no instructions on where to look, inspection of the video record suggested that they did not reliably look at the point on the string that they grasped. Of the 12 participants, five directed their gaze onto the string at point above their grasp point on the string, three directed their gaze onto the string at the location that they grasped the string, two directed their gaze to a point below the location on the string that they grasped, and two looked in a direction well away from where the string was located. There was little change in the gaze of each participant throughout a string-pulling sequence except for only one "look away" participant who shifted head orientation throughout the string-pulling sequence. Thus, although the participants did look in the direction of the string as they were pulling, they did not reliably look at a point on the string at which they grasped. When asked where he was looking, one participant who looked well above the grasping point on the string replied, "It is like driving a car, you look way down the highway not directly in front of you."

To assess the relationship between head orientation and grasp points, head orientation and grasp location relative to the plane of the participants' visual horizon was rated on a 3-point scale and a correlation between head orientation and grasp location for target-based and memory-based string-pulling groups was determined. The correlations were: (1) unmarked string ($r = 0.0329$ and $r = -0.094$, not significant); (2) marked string ($r = 0.192$) and $r = 0.0242$, not significant); (3) visual-occlusion ($r = 0.603$ and $r = 0.680$; $p < 0.5$ for both values); (4) visual cue ($r = 1$ and $r = 0.98$, $p < 0.05$ for both values). In short, the participants in the first two groups did not reliably orient their gaze to location on the string that they were grasping. The visual-occlusion group participants all oriented their head straight forward and this was a location at which many of them grasped the string, thus producing a significant correlation between head orientation and the grasping point even though they could not see the string. In contrast, all of the visual-cue group participants looked directly at the cue target for which they reached.

### Gaze and pupil responses related to target-based and memory-based string pulling

Experiment 2 was performed to confirm that participants did not target their gaze to grasp points on the string when no instructions were given. Two groups of participants of ten participants each reached for a marked string with only one group instructed to grasp the string at cue points. The participants wore eye-tracking and pupil-diameter-sensitive glasses.

*Non-visual cue condition* In the nonvisual condition for target-based reaches, only one participant consistently looked at the string at the grasp point, but the participant did not shift gaze as if tracking the string and did not display changes in pupillary response as the grasp occurred. Of the remaining participants, five looked above their grasp points and four looked below their grasp points and there was no obvious relationship between gaze and grasping or pupillary responses and grasping. Gaze and pupil response in relation to grasping were similar in their memory-based string-pulling task.

*Visual-cue condition* In the visual-cue condition, all ten participants directed their gaze to the marker on the string as the reaching hand moved up. They then tracked the marker to about the point that the hand grasped the string at the marker, following which gaze was directed upward to the location of the next marker. In addition to visually tracking the marker on the string, the diameter of the pupil increased as the hand approached the cue, reached maximum diameter at about the time of the grasp, and decreased as the hand grasped and pulled.

In the memory-based visual-cue condition, all of the participants directed their gaze upward, with four participants directing their gaze above the location where they pantomimed a grasping movement and six participants directing their gaze to roughly the same location that they pantomimed a grasp. Only one of the participants in the visual-cue condition displayed gaze-tracking movements similar to the cue-tracking movements displayed in the real string-pulling condition. There were no changes in pupil diameter in association with hand grasping on the pretend string for any of the participants.

Figure 5 illustrates these main findings for a representative target-based and memory-based reach for one participant. For the target-based task, gaze is shown to track the cue (downward green trace) and the pupils dilate (upward black trace) at about the point of the grasp. For the memory-based task there is no evidence of cue tracking or pupil response at the point of the grasp.

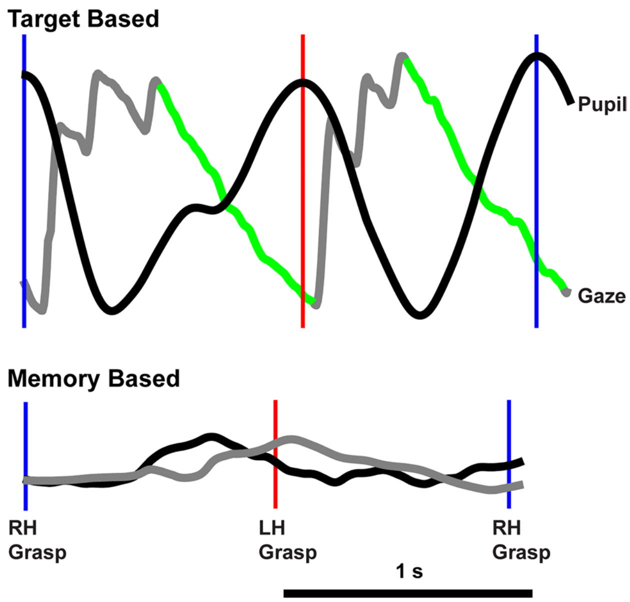


**Fig. 5** Eye movement and pupil response. The upper panel shows the eye movement tracked the cue to which the participants reached (green portion of the eye movement trace that moves downward) and then disengaged to search for the next cue. Associated with visual tracking, pupil diameter increased to reach a maximum at about the time that the string was grasped (shown as movement to apex of the black trace). The lower panel shows that there was no associated eye tracking or pupillary dilation associated with memory-based grasping. *LH* left hand, *RH* right hand

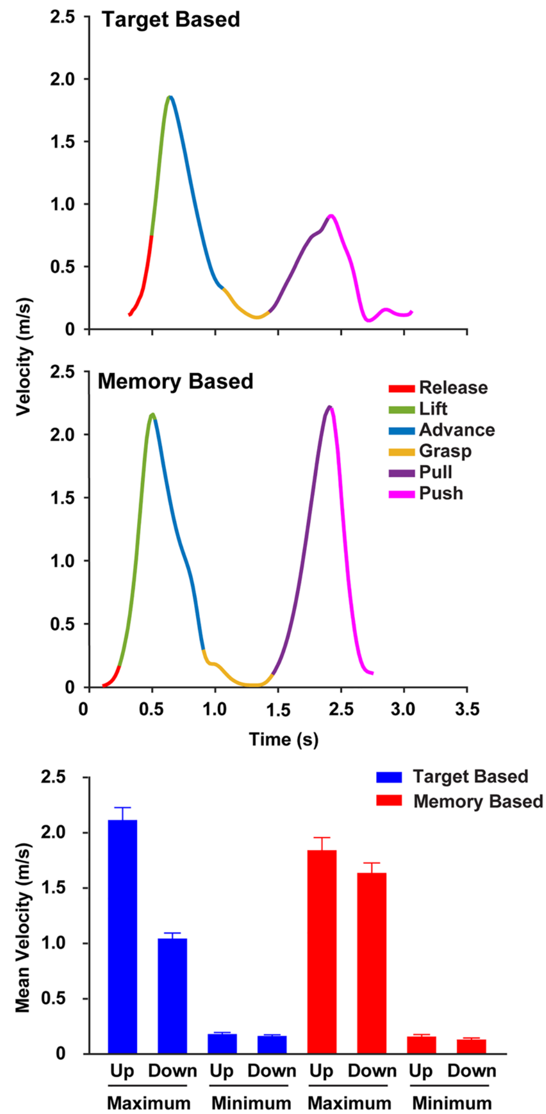


**Fig. 6** Representative velocity profiles for a target-based string pull (top) and a memory-based string pull (middle) and group values (mean ± SE) for target-based and memory-based maximum and minimum velocity. Note: (1) maximum velocity occurs at the midpoint of the torso at about the transition of the lift and advance movements; (2) the maximum velocity of the down movement occurs at the midpoint of the torso at about the transition between the pull and the push. Maximum downward velocity is lower than the maximum velocity of the up movement for target-based string-pulling, whereas up and down velocity is equivalent for memory-based string-pulling; (3) minimum velocity occurs at the grasp point for the up movement and at the release point for the down movement for both target-based and memory-based string-pulling

## Kinematic measures of string-pulling

### Target-based and memory-based velocity profiles

Figure 6 shows a representative velocity profile of a single target-based cycle (top), a memory-based string-pulling cycle (middle), and group values (bottom). The velocity profile of the target-based string-pulling cycle features two high-velocity peaks, a highest velocity peak occurs for the up movement whereas a lower velocity peak occurs at the midpoint of the down movement. Both peaks occurred at about the point that the hand passes the midpoint of the torso, and at this point the two hands were juxtaposed at the midpoint of the torso. The velocity profile of a target-based reach also features two points of minimum velocity, the first as the fingers close to grasp the string and the second as the fingers open to release the string, and the minimums occurred sequentially for the two hands, the release by one hand always following the grasp by the other hand.

The profile of a memory-based string-pulling cycle also features high-velocity peaks for upward and downward movement except that they are equivalent, and both occur as the hands are juxtaposed passing through the torso midpoint. The memory-based velocity profiles also feature two minimums, one at the pantomime grasp and one at the pantomime release, the minimums frequently feature a pause in motion, and the release by one hand and the grasp by the other occur almost simultaneously.

The ANOVA of the maximum and minimum velocities for the up and down movements confirmed the description of the differences in velocity of target-based and memory-based reaches by featuring a three-way interaction between maximum/minimum, direction and condition, MM × direction × condition $F(1,40) = 118.69$, $p < 0.001$. There was a significant difference in maximum/minimum velocity for the comparison of target-based vs memory-based conditions, condition $F(1,40) = 418.58$, $p < 0.001$, and a significant difference in the measures for the direction of hand movements, Direction $F(1,40) = 102.884$, $p < 0.001$. There was a significant interaction between maximum/minimum velocity and direction, velocity × direction $F(1,40) = 90.992$, $p < 0.001$, and between target-based vs memory-based conditions and direction, condition × direction, $F(1,40) = 98.956$, $p < 0.001$. There were no differences in the maximum, and minimum velocities as function of group or sex, and none of the interactions featuring group or sex were significant.

### Frequency and amplitude of target-based and memory-based string-pulling

Figure 7 gives a summary of the measures of frequency (number of cycles per/s) and amplitude (apex to apogee of the upward/downward distance), of string pulls for the target-based and memory-based conditions. Overall, both the frequency and amplitude of pull cycles were similar for target-based and memory-based conditions for each of the four groups of subjects. Both the amplitude and frequency were also similar for the conditions that did not involve visually tracking the markers on the string. The visual-cue group displayed a lower frequency and higher amplitude cycle. These conclusions are supported by the following statistical analyses.

*Frequency* A summary of string-pulling frequency is displayed in Fig. 7a. There was a significant group effect, Group $F(3,40) = 9.16$, $p < 0.001$. Bonferroni follow-up tests indicated frequency by the group in the vision-cue condition was lower than in the other groups, which did not differ from each other (vision-cue vs no vision, $p = 0.001$, vision-cue vs control plain, $p = 0.002$, vision-cue vs control striped, $p < 0.001$). The comparison between string-pulling frequencies for the target-based vs memory-based conditions gave no significant difference, Condition $F(3,40) = 0.41$, $p = 0.24$. There was no significant sex difference or significant interaction between group and sex.

*Amplitude* A summary of string-pulling amplitude is displayed in Fig. 6b. There was a significant group effect, Group $F(3,40) = 8.857$, $p < 0.001$. Bonferroni follow-up tests indicated the string-pulling amplitude by the group in the vision-cue condition was higher than that of the other groups (vision-cue vs novision, $p = 0.003$, vision-cue vs strip $p = 0.006$, vision-cue vs plain, $p = 0.033$), which did not differ from each other. The comparison between string-pulling amplitudes also gave a significant difference, with the amplitude of reaches in the memory-based condition being slightly higher than the amplitude for reaches in the respective target-based conditions for all groups, Condition $F(1,40) = 13.71$, $p < 0.001$. The slight amplitude difference may have been due the fact that in general participants in the memory-based task did not display the same hand lowering during the grasp as did the participants engaged in target-based reaching. There was a significant sex difference, Sex $F(1,40) = 10.179$, $p = 0.003$, in which the amplitude for the male participants was higher than that for the female participants. This difference is not surprising as females were shorter than the males. None of the interactions involving hand and sex were significant.

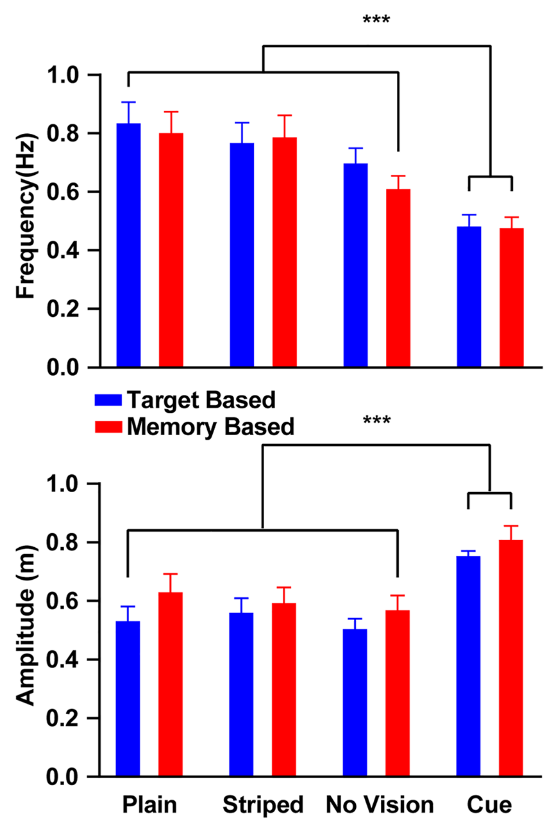


**Fig. 7** Frequency (top) and amplitude (bottom) (mean ± SE) for target-based and memory-based string pulling. Note: (1) frequency does not differ in target-based and memory string-pulling but amplitude is slightly larger for memory-based string pulling. (2) Frequency is lower and amplitude is higher for both target-based string-pulling and memory-based string-pulling in the vision task in which participants were required to grasp the string at markers to 30 cm intervals

### Independent and concurrent string-pull movements

During part of the string-pulling cycle the left hand and the right hand moved independently in that they moved in different directions. But for a part of the string-pulling cycle, both hands moved together in the same direction, as one hand engaged in a pull and the other engaged in a push. A distinguishing difference in target-based and memory-based string pulling is that the combined movement had a longer duration for target-based vs memory-based string-pulling. The difference is illustrated in Fig. 8, which shows velocity profiles of representative right-hand (solid line) and left-hand (dotted line) string-pulling cycle of one participant making a target-based string-pulling movement (top), and a memory-based string-pulling cycle (middle). The dotted vertical lines for both conditions demark the period of the cycle during which the hands moved in synchrony. It can be seen that in the target-based cycle (Fig. 8, top) the duration was longer than it was for the memory-based cycle (Fig. 8, middle). Descriptively, the difference occurs because in the memory-based condition the two hands simply move up and down with little attention to the details of advancing the string.

The statistical analysis of the duration for the combined movement confirmed that the target-based combined movement duration was longer than the memory-based combined movement duration of the string-pulling cycle. The group measures showed that the total time making combined movements for the target-based string-pulling test condition was significantly longer than that of the memory-based condition, Condition $F(1,40) = 86.155$, $p < 0.001$. In addition, there was an overall group effect, Group $F(3,40) = 2.955$, $p = 0.045$. The combined durations were slightly longer for the participants in the visual-cue condition. This was likely related to the overall longer duration of string-pulling movements made by participants in the visual-cue group. There was no effect of sex or interactions between sex and conditions or groups.

## Bimanual coordination of left and right hands

Figure 9 (top, left) shows the relationship between a complete cycle of a series of left- hand string-pulling movements and right-hand string-pulling movement for target-based and memory-based string-pulling. Overall, for the target-based condition there was a slight lag between left- and right-hand movements. For the memory-based condition, movements were mainly synchronous, when the left hand was going up the right hand was going down. The raw y-data from the left and right hands were used to evaluate the correlation of the hands (Fig. 8, right). Repeated measures ANOVA conducted on initial correlation revealed a significant main effect of condition, Condition $F(1, 44) = 19.308$, $p < 0.001$, but no significant effect of group or group by condition interaction or effects of sex. These results suggest either that the two hands are making slightly different movements in the target-based conditions or the two hands have a slightly different phase (e.g., one hand leading the other) in the target-based condition, relative to the memory-based conditions.

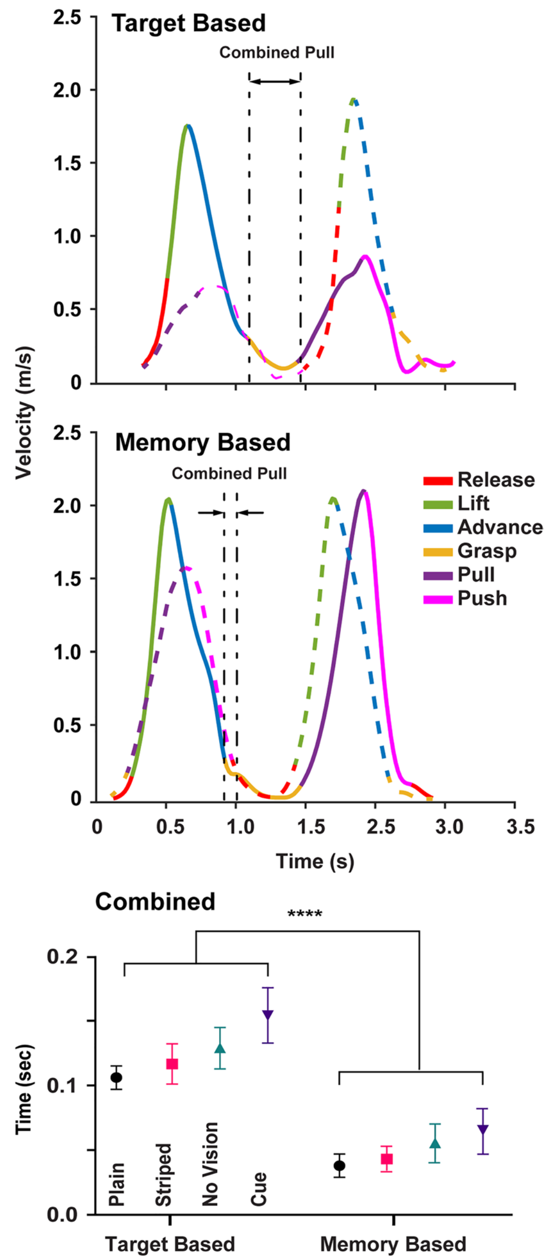


**Fig. 8** Representative right (sold line) and left (dotted line) velocity curves for target-based (top) and memory-based (middle) string-pulling and values (mean ± SE) for concurrent movements of the right and left hands. The period between the vertical lines represents the time that the two hands are moving in concurrently (downward as both advance the string). Note (1) for target-based string-pulling the concurrent movement occurs as the right-hand grasps and pulls and the left-hand pushes; note (2) for memory-based string pulling the concurrent movement is shorter and occurs as the right-hand grasps and the left-hand releases the string; note (3) concurrent hand movements are longer for all groups engaged in target-based string-pulling than in the corresponding memory-based groups

To assess whether the movements of the right and left hands were equivalent, the raw y-data for the right hand was shifted frame-by-frame until the maximum correlation

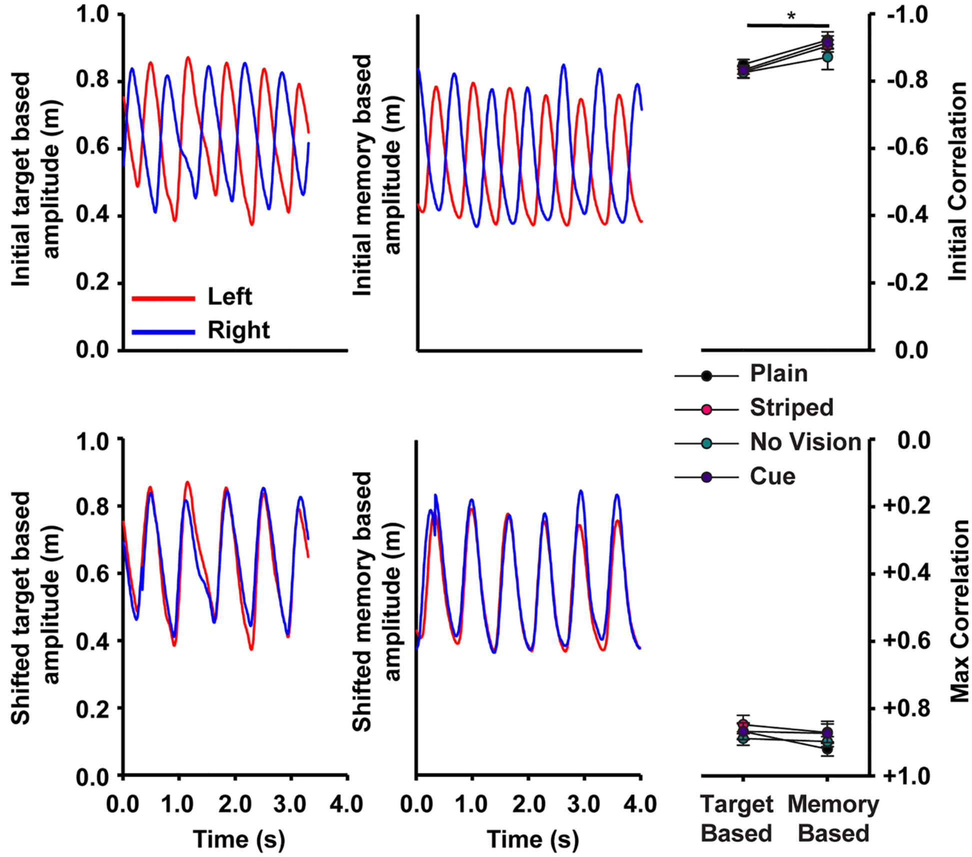


**Fig. 9** Relationship between left- and right-hand string-pulling movements. **a** Change in *y* values for left- and right-hand movements for sequences of string-pulling for target-based and memory-based string-pulling. **b** Correlations between left- and right-hand movements provide a greater negative correlation for memory-based than target-based movements. **c** Change in *y* values for target-based and memory-based reaches is shifted to the position of maximum correlation. *d* Correlations between left- and right-hand movements are highly positive, showing that for both target-based and memory-based movements, the left and right hands are making very similar movements in string-pulling

was achieved between the left and right raw y-data for each participant (see Fig. 8, bottom, left). Repeated measures ANOVA conducted on the maximum correlation (Fig. 8, bottom, right) failed to reveal a significant main effect of Group $F(3, 42) = 1.310$, $p = 0.284$, Condition $F(1, 42) = 1.360$, $p = 0.250$, or Condition by Group $F(3, 42) = 0.384$, $p = 0.765$. Thus, the analyses show that the left and the right hands are making the same, but reciprocal movements, but with a slight phase lag between the hands as if one hand is leading the other.

### Asymmetry and spatial occupancy

Spatial occupancy refers to the extent of the excursion made by the hands on a string-pulling cycle. The main finding made from the analysis of spatial occupancy is that the presence of the string constrained the hands to more up/down movement than side/side movement. This conclusion is illustrated in Fig. 10, which gives a Cartesian representation of the topography and velocity (indicated by color coding) of string-pulling movements made by a representative subject engaged in target-based string-pulling (top) and memory-based string-pulling (bottom). The cartoons of the left- and right-hand spatial occupancy of movements also show the degree to which the movements of the two hands are symmetric. For this participant, the movements of the right and the left hand in target-based string-pulling are symmetric as they were for other participants in the target-based string-pulling conditions. The movements of memory-based string-pulling were quite asymmetric for the same participant, with one hand having a higher rise time and greater spatial occupancy than the other hand. Similar asymmetries were found in the memory-based condition for other participants. The spatial occupancy asymmetry was not lateralized, however, and was about equally represented in the left or right hands of the participants.

Figure 11 summarizes group values for the parameters of spatial occupancy and symmetry. Figure 11a gives values for spatial occupancy. An ANOVA showed that there was no hand effect with respect to spatial occupancy, Hand $F(1,40) = 0.104$, $p = 0.749$, so for some subjects, spatial occupancy was just as likely to be larger for the right hand as for the left hand. There was an effect of test condition, however, in which the spatial occupancy of target-based string-pulling was smaller than the spatial occupancy of memory-based string-pulling, Condition $F(1,40) = 4.929$, $p < 0.001$. There were also effects of group, Group $F(3,40) = 10.125$, $p < 0.001$, and sex, Sex $F(1,40) = 10.025$, $p = 0.003$. The group and sex effects are in themselves likely secondary to the amplitude of string-pulling movements. Females being

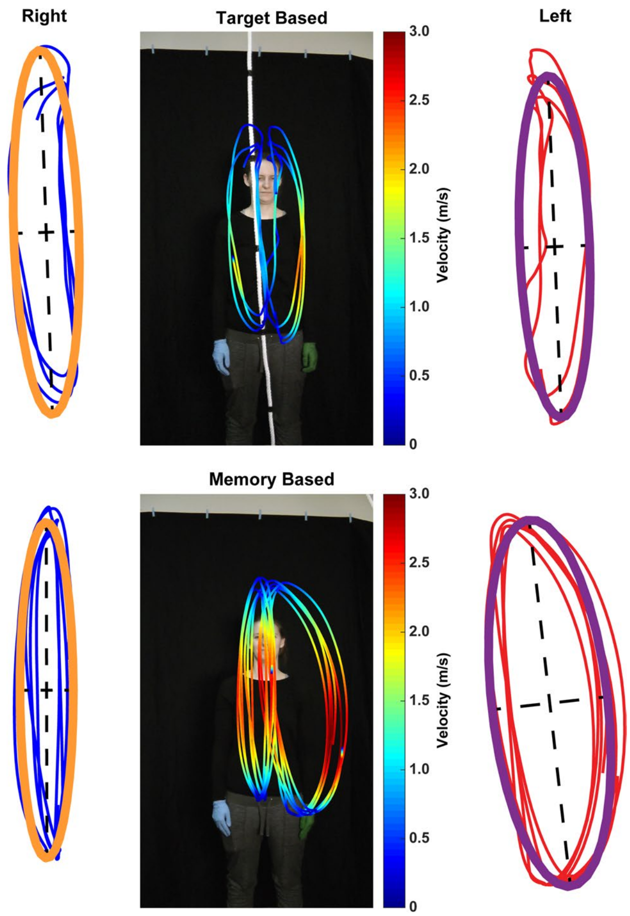


**Fig. 10** Representative Cartesian trajectories of right- and left-hand for target-based sting-pulling (top) and for memory-based string pulling (bottom). In the trajectory plots of the hand movements, the thin lines represent each cycle of movement and the thicker lines represent the average cycle. Note: the symmetry of the target-based string-pulling vs asymmetry of memory-based string pulling. Thus, despite more symmetric velocity memory-based reaches have more asymmetric trajectory

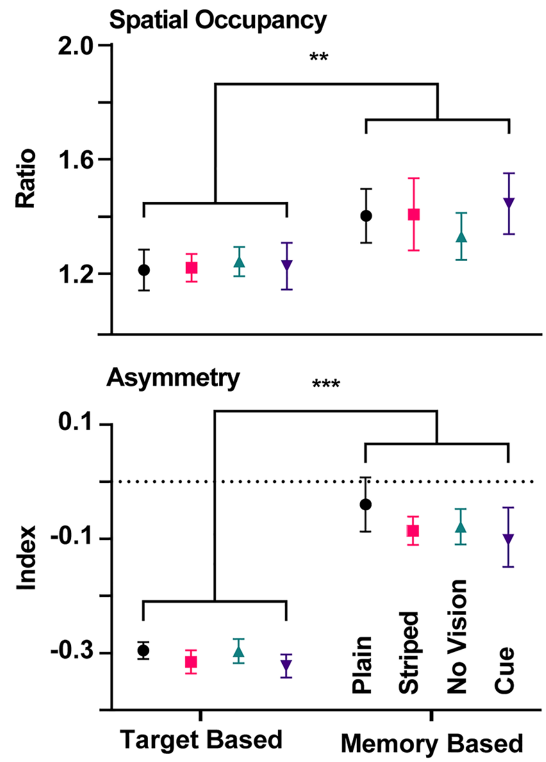


**Fig. 11** Spatial occupancy (top) and asymmetry (bottom) of trajectory values (mean ± SE) for target-based and memory-based string-pulling. Note: (1) spatial occupancy (trajectories are less expansive) for target-based string-pulling than for memory-based string-pulling; (2) trajectories are more symmetric for target-based than for memory-based string-pulling

smaller had overall smaller amplitude cycles. The group effect was due to the larger amplitude movements made by the participants in the vision-cue group.

Figure 11b shows the values for the asymmetry index, the difference in space occupied by the movement of one hand vs the space occupied by the other hand. Thus, for target-based string-pulling, the excursions of the two hands were quite similar, whereas for memory-based string-pulling, the excursions of the two hands were different, without evincing a bias for one hand or the other. An ANOVA confirmed this difference, giving a significantly lower index for target-based string-pulling compared to memory-based string-pulling, Condition $F(1,40) = 103.517$, $p < 0.001$. There were no significant differences as a function of group or sex and there were no significant interactions. The reason for the greater asymmetry in memory-based string pulling is unclear because there must be a velocity/distance trade off that still maintains symmetrically out of phase movement of the two hands.

## Discussion

The results of this string-pulling study show that the participants advanced a real string with one hand following the other for part of the movement and with combined hand movement for another part of the movement. A virtual string was advanced mainly with alternating hand movements. Participants did not appear to use vision in that they did not direct their gaze to their grasp point on the string unless cued to do so. When asked to reach for a cue on the string, they anchored gaze on the marker, tracked the marker, and with dilating pupils grasped the string. These visual events did not occur with memory-based cued reaches. Although the participants did show a bell-shaped kinematic profile associated with a fast movement for the reach and a slowing movement for the grasp, they used a whole hand, but with different whole-hand grasps for target- vs memory-based reaches.

Target-based string-pulling featured asymmetrical cycling of arm/hand movement unlike the symmetrical movement cycle of memory-based string-pulling. The results highlight the information that can be obtained by a novel approach to reaching afforded by bilateral string-pulling. They confirm that real and pantomime hand actions can involve different movements as evidenced by the changes in the reach and the grasp in memory-based and target-based reaching. The results also confirm previous studies that show that bilateral hand movements can be quite different from unilateral hand movements.

The movements of string-pulling were assessed using movement description, eye tracking, and frame-by-frame inspection of the video record and kinematics using a Matlab procedure that tracked the movement of the arm/hand. The accuracy of the Matlab procedure was confirmed by manually digitizing the 60 f/s video record using PhysicsTracker. These procedures reliably identified arm and hand movements, identified the sensory control of string-pulling, and distinguish target-based and memory-based movements. Nevertheless, one weakness in the procedures is that only a frontal view of string-pulling was recorded, thus limiting analysis to the x–y dimensions. One justification for the procedure is that most of the movement of string-pulling is up/down with lesser side-to-side movement and with very little in/out movement, although the hand did make greater rotational movements than did the arm. The accuracy of the present results could be improved by two-camera recording and three-dimensional analyses. Another weakness of the study is that the details of hand/finger movements were scored using a rating scale and Matlab surface analysis and the results of this scoring could be improved by three-dimensional tracking of the hand and fingers, such as can be obtained by using a kinematic glove (Jarque-Bou et al. 2019). Nevertheless, the description of string-pulling provided here is more detailed than has been obtained in previous work and provides insights into differential use of somatosensation and vision, hands used, the structure of reaching movements, and species differences in string-pulling.

The prediction that string-pulling would be under visual control was not supported by the finding that vision was not essential for performance unless the task was cued. Many studies that describe reaching or pointing to target objects also report that gaze is fixed or anchored on the target from the point of movement initiation to movement completion (Prablanc et al. 1979; Neggers and Bekkering 2001; de Bruin et al. 2008; Sacrey and Whishaw 2012). Here gaze anchoring to the location on which the hand contacted the string was usually absent as participants were frequently not looking where their hands were going. Eye tracking and measures of the participants' head orientation confirmed that when they did look at the string, they often did so at a point above or below their hand contact point. Visual guidance was not used for string-pulling hand placement as was confirmed by the identical movement and kinematic results obtained when participants were blindfolded. When the task was cued, however, with participants instructed to grasp the string on cues spaced at 30 cm intervals, gaze was directed to the cues in advance of each reach, the cue was then visually tracked, and the pupils dilated to maximum at the time of the grasp. Thus, sting-pulling can be a mainly somatosensory-based task or a visually-cued task.

The prediction that participants would use a precision grasp was not supported by the finding that they used a whole grasp although with different grasp patterns between target-based and memory-based conditions. Inspection of the participants' grasp indicated that as the hand approached the string in a fully open posture, the more lateral fingers were used to contact/gather the string toward the palm at which point it was grasped with finger closing from finger 5 through 1 in a whole-hand grasp. In the absence of direct visual control, it seems likely that effective grasping occurred because the participants knew something of the string's location because they always had one hand on the string, the string was typically located on the body midline, and they used an open hand grasp and they used touch cues. In short it appears that the hand holding the string during the pull signals enough information about the location of the string to direct the other hand to an effective grasp point. String grasping with an open hand in turn provides another example of grasping based on touch cues, as occurs when reaching when blindfolded (Karl et al. 2012) or reaching into peripheral vision (Hall et al. 2014), tasks in which participants use an open hand to find the target and then use touch to guide their grasp. String pulling features another example of touch-based grasping supporting the idea the reach and the grasp can be dissociated as argued by Jeannerod's dual visual channel theory (Jeannerod 1981; Jeannerod et al. 1994; Kuntz and Whishaw 2016). That the grasp pattern was reversed for memory-based reaches is also surprising and suggests that the participants were substituting a completely different grasp movement rather than attempting to pantomime the previously used hand grasp.

The prediction that memory-based string-pulling movements would be largely altered from target-based movements was largely supported. Hand movements, however, were seemingly more changed than arm movements. In studies of memory-based single-handed pantomime both reach and grasp kinematics are reported to be changed (Goodale et al. 1991, 1994; Westwood et al. 2000; Milner et al. 2001; Fukui and Inui 2013; Holmes et al. 2013; Kuntz and Whishaw 2016; Freud et al. 2018; Kuntz et al. 2018). For string-pulling, the amplitude and frequency of reaches were largely similar for target-based and memory-based conditions. In contrast, for a target-based grasp and release of the string, the finger movement sequence was 5 (pinky) to 1 (thumb), whereas for the memory-based hand movements, the order was reversed to 1 to 5. In addition to a change in finger order for grasping in memory-based string-pulling, finger opening and closing were attenuated, with participants only slightly opening and closing the hands or sometimes not opening or closing at all. In previous studies that compare target-based vs memory-based grasp patterns, finger shaping and movement for grasping is also reported to be smaller as assessed by kinematic features (Goodale et al. 1994; Kuntz and Whishaw 2016). That the memory-based hand movement of string-pulling is not an inaccurate version of a target-based movement but a different movement supports the action/perception theory that pantomime movements may be different because they are mediated by memory/perceptual networks of the ventral stream rather than by online networks of the dorsal stream (Goodale et al. 1991, 1994). Perhaps participants are substituting verbal-related gestures for the pantomime grasp and release action (McNeill 1992; Kendon 2004).

Although the two hands made cycling movements at the same speed and with the same amplitude in target-based and memory-based string pulling, the up/down movements of pantomime were much more symmetrical in velocity and duration. For target-based string-pulling, the ratio of up-to-down phases approximated 1:2 whereas for pantomime the ratio approximated 1:1. Thus, it seemed that in removing the hand shaping and grasping movement from string-pulling, the arm synchrony of the movement began to resemble that of a pure oscillator. Similar shifts in movement ratios occur in a wide range of human real and pantomime movements (Wannier et al. 2001). It is suggested that the kinematics of limb movement represent two influences, that of a pattern generator that produces the movement and that of control mechanisms that puts the limb to a specific functional use (Perry 1992; Marder and Bucher 2001; Swinnen 2002). Thus, in pantomime, the string-pulling movement appears to reflect mainly the action of the pattern generator, whereas the modification in the rhythm associated with target-based reaching reflects the addition of a control mechanism that performs the grasp, etc. This could provide a reason that the arm movements of target-based and memory-based movements preserve greater similarities than the hand movements.

In comparative studies, an analysis of string-pulling similar to that presented here has only been made for the mouse and the rat (Blackwell et al. 2018a, b, c), species in which the form of the target-based action is similar to that described here for humans. These animals also use tactile cues, but from the snout, to track the string. The movement cycles are also faster for rodents, which might be expected from their small size. A marked species difference is in the ratio of the up-to-down movement, which is about 1:4 for the rat and 1:5 for the mouse, rather than a 1:2 ratio as described here for humans. The ratio difference suggests that the down movement, in which the hand movements of grasping, holding, and releasing occur, may be more difficult for rodents than for humans. This speculation seems borne out by the observation that for the mouse, the hand pauses between the pull and push of the downward movement whereas for humans this transition features the highest velocity of the downward movement. In general, that the downward movements are slower than the upward movements is consistent with Fitts's law (1954) that more complex movements will be performed more slowly. Species comparison provides a novel application of the law. In future studies, more direct species comparisons of string-pulling might provide insights into the evolution of forelimb skills, as have studies of walking and single-handed reaching movements (Sacrey et al. 2009; Whishaw et al. 2010; Karl and Whishaw 2013).

In conclusion, this analysis of string-pulling provides the first detailed description of a bilateral movement in which the two hands engage in both sequential and concurrent movement. The study shows that many aspects of the string-pulling movement including, visual tracking, grasp/release of the string, the amplitude and frequency of arm movements, and the temporal relations between the two limbs, is somewhat different from that predicted from single-handed reaching, supporting other studies that note differences between one and two-handed reaching (Kelso et al. 1979). In addition, the differences in target-based and memory-based string-pulling provide insight into the organization of reaching movements. Because human string-pulling movements have some similarity to those displayed by other animals including rodents, the string-pulling task is useful for comparative studies that investigate the neural basis of bilaterally coordinated movements and could also prove useful as a diagnostic and therapeutic tool related to brain injury.

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