

# Information and control strategy to solve the degrees-of-freedom problem for nested locomotion-to-reach

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**Abstract** Locomoting-to-reach to a target is a common visuomotor approach behavior that consists of two nested component actions: locomotion and reaching. The information and control strategies that guide locomotion and reaching in isolation are well studied, but their interaction during locomoting-to-reach behavior has received little attention. We investigated the role of proportional rate control in unifying these components into one action. Individuals use this control strategy with hand-centric disparity-based  $\tau$  information to guide seated reaching (Anderson and Bingham in *Exp Brain Res* 205:291–306. doi:10.1007/s00221-010-2361-9, 2010) and use it with sequential information to perform targeted locomotion to bring an outstretched arm and hand to a target; first with eye-centric  $\tau$  information and then hand-centric  $\tau$  information near the target (Anderson and Bingham in *Exp Brain Res* 214:631–644. doi:10.1007/s00221-011-2865-y, 2011). In the current study, participants performed two tasks: locomoting to bring a rigidly outstretched arm and hand to a target (handout), and locomoting to initiate and guide a reach to a target (locomoting-to-reach). Movement trajectories were analyzed. Results show that participants used proportional rate control throughout both tasks, in the sequential manner that was

found by Anderson and Bingham (*Exp Brain Res* 214:631–644. doi:10.1007/s00221-011-2865-y, 2011). Individual differences were found in the moment at which this information switch occurred in the locomoting-to-reach task. Some participants appeared to switch to proportional rate control with hand- $\tau$  once the hand came into view and others switched once the reaching component was complete and the arm was fully outstretched. In the locomoting-to-reach task, participants consistently initiated reaches when eye- $\tau$  specified a time-to-contact of 1.0 s. Proportional rate control provides a solution to the degrees-of-freedom problem in the classic manner, by making multiple things one.

**Keywords** Locomotion · Reaching · Tau · Binocular disparity · Proportional rate control

## Introduction

Locomoting-to-reach to a target is a common visuomotor action that occurs in everyday tasks like opening a door, picking up an object from a table, or turning on a faucet. Both locomotion and reaching have been studied extensively in isolation, but the nested action of reaching to a target while locomoting is more complex and has received little attention. Understanding how locomoting-to-reach behavior is performed requires understanding the visual information that drives it, along with the control strategy that maps this information to action. The reaching component is nested within the locomoting component in the sense that the locomoting component occurs throughout, but the reaching component only comes into play once a certain proximity to the target has been achieved through locomotion. Given this primacy of locomotion, it is natural to start by examining the information and control strategies that are used to guide its execution.

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A classic example of an information/strategy couple is seen in the literature on targeted locomotion. When an observer approaches a target, the optical angle subtended by that target expands. The ratio of this angle to its rate of change at a given moment ( $\tau$ ) corresponds to the time-to-contact with the target if the current velocity of approach was maintained (Lee 1976). There is also a binocular equivalent of this  $\tau$  based on horizontal relative disparity and its rate of change (Regan 2002). These sources of information are especially suitable for controlling approach behaviors like locomotion because they incorporate both position and velocity intrinsically. One control strategy that has been studied for the control of locomotion and other approach behaviors is to guide the velocity of approach such that the first derivative of  $\tau$  with respect to time is maintained at  $-0.5$ . Known as the constant  $\dot{\tau}$  strategy, it results in soft contact with constant deceleration throughout the approach, regardless of initial velocity. Human sensitivity to both  $\tau$  and  $\dot{\tau}$  has been demonstrated (Kim et al. 1993; Regan and Hamstra 1993; Todd 1981). There is evidence that both humans (Yilmaz and Warren 1995) and non-human animals (Lee et al. 1991) rely on a constant  $\dot{\tau}$  control strategy during approach behavior. However, there is also evidence against it (Bardy and Warren 1997; Bootsma and Craig 2003; Coull et al. 1998; Rock et al. 2006).

#### Hand- $\tau$

Such a constant  $\dot{\tau}$  strategy potentially works for bringing the body to a target because  $\tau$  specifies the time-to-contact of the eye and target, but some studies have investigated this strategy in tasks that involve bringing the hand to a target (Wann et al. 1993). Reaching, like locomotion, is an approach behavior with the goal of bringing part of the body to a spatial target with soft contact. However,  $\tau$  information does not relate the hand to the target or eye. Thus, work has been done to identify  $\tau$ -like variables that may specify information about the hand relative to a target in various tasks (Bootsma and Oudejans 1993; Hopkins et al. 2004; Zaal and Bootsma 1995).

Recently, such an optical variable was introduced that specifies the relation of the hand to the target during reaching by exploiting the relative binocular disparities of the hand and target (Anderson and Bingham 2010). Points on the hand have a greater binocular disparity than those on the target during the early portion of a reach because the hand is closer to the eye than the target is. As the hand nears the target, these binocular disparities converge to those of the target and match them upon contact. Thus, the relative disparity between the hand and target converges to 0. Similar to the proportional form of the  $\tau$  information discussed earlier, Anderson and Bingham identified an optical variable that is the proportion of relative disparity to its

own rate of change. This hand-centric disparity  $\tau$  specifies the instantaneous time-to-contact of the images of the hand and target. To differentiate this variable from the  $\tau$  information that was discussed earlier, we call this new variable hand- $\tau$  and the original variable eye- $\tau$ .

#### Proportional rate control

Anderson and Bingham (2010) found evidence for the use of hand- $\tau$  during reaches by stationary participants. However, they did not find evidence for control with the constant  $\dot{\tau}$  strategy. Instead, they found evidence for a different strategy, proportional rate control. Proportional rate, like the constant  $\dot{\tau}$  strategy, maintains a constant value of an optical variable. However, proportional rate control maintains a constant value of the ratio of  $\tau$  to  $\dot{\tau}$  instead of  $\dot{\tau}$  alone. When an observer approaches a target, both  $\tau$  and  $\dot{\tau}$  are relatively large when the observer is at a great distance from the target. As an individual approaches the target, these values both decrease. Proportional rate control guides approach so that these variables decrease while maintaining a constant proportion to each other. Like constant  $\dot{\tau}$  control, proportional rate essentially informs a moving observer how to modulate deceleration. This makes it applicable in a variety of approach behaviors, such as walking, reaching, and braking, despite these tasks having very different velocities, manners of motor control, etc.

Anderson and Bingham (2010) found evidence for proportional rate control with hand- $\tau$  both in the presence and absence of monocular cues, but trajectories changed and reach accuracy declined when the hand and target were viewed in the absence of binocular information. Rather than use a strictly visual control strategy, a person could control a reach using proprioceptive information. However, Anderson and Bingham (2010) found similar results reflecting proportional rate control with hand- $\tau$  when possible mappings from visual to proprioceptive space were ruled out by moving the target out of reach space and having participants move a variable-length slider apparatus to match the depth of a target. Finally, a person might use the perceived distance of a target to control a reach. Anderson and Bingham (2010) used a telestereoscope to alter participants' perception of distance using the available binocular information and found that the reach trajectories behaved in a manner predicted by reliance on proportional rate control with hand- $\tau$ .

An advantage of the proportional rate control strategy is that a range of constant proportional rate values result in soft contact (Anderson and Bingham 2010, 2011; Fath et al. 2013), instead of the single value of  $-0.5$  that is necessary for the constant  $\dot{\tau}$  strategy. The world presents perturbations and limitations that constrain potential actions. Thus, a control strategy that can only utilize a single value

of an optical variable is infeasible if the present conditions make attaining this required value impossible. For example, a person's action capabilities change when he or she walks from pavement onto sand. It may not still be possible to move fast enough to produce  $\dot{\tau} = -0.5$ . Even if it is, greater effort may be required. If the person is not in a hurry, they might prefer to slow down and move at a velocity that is more energetically efficient given the nature of the new walking surface. The constant  $\dot{\tau}$  strategy cannot permit this shift, but proportional rate can. The flexibility of proportional rate control makes it robust to perturbations, resulting in greater stability (Fath et al. 2013).

Anderson and Bingham (2011) extended their original work on reaching to study locomotion-to-reach and they found evidence for the use of both proportional rate control and hand- $\tau$ . However, that study did not investigate full locomotion-to-reach. To see how eye- $\tau$  and hand- $\tau$  evolve over time, they had participants approach targets with their arms extended out in front of them so that both variables were available throughout each trial. Participants were found to use proportional rate control throughout their approach. During the initial portion, they used eye- $\tau$  under this control strategy and then switched to hand- $\tau$  under the same strategy once their eyes were two arm lengths away from the target (i.e., when the hand became equidistant to both eye and target). Under normal conditions, the hand is not visible during the initial approach phase of locomotion-to-reach, so only eye- $\tau$  is available for control. Because it is ultimately the hand being brought to the target, at some point, a switch has to occur to an optical variable that specifies the hand's relation to the target, and indeed, a switch to hand- $\tau$  was observed when the hand neared the target. What was special about a distance of two arm lengths? During approach, hand- $\tau$  values start much higher than eye- $\tau$ , but once the eye is two arm lengths from the target, hand- $\tau$  crosses below eye- $\tau$ . Subsequent analysis revealed this relative evolution of the two variables to be analytic. Because both variables specify a time-to-contact with the target, always relying on the lesser variable means relying on the more conservative value of the time until collision.

#### The degrees-of-freedom problem, coordination, and locomotion-to-reach

This sequential shift from one variable to another under the same control strategy is a form of coordination that solves a degrees-of-freedom problem for the complex, nested locomoting-to-reach behavior. The problem is that it is difficult to perform more than one action at a time. Coordinative solutions turn multiple things into one. In this case, the approach was performed with the arm and hand held out in a rigid relation to the eye. One control strategy was used across optical variables to bring this single, rigid body

to a target. During early approach, control was based on the eye's spatial-temporal relation to the target. The arm's location came for free with movement of the eye to the target. After the information switch, the same rigid body was guided to the target, but the hand was now the locus of control.

However, in normal locomotion-to-reach, the arm and hand are not fixed in position with respect to the eye to form a rigid body. Instead, the action of reaching is nested within the act of locomotion. In the handout locomotion task of Anderson and Bingham (2011), control was centered at the eye during the early portion of approach. Thus, it may not matter that the hand moves during the reach in locomotion-to-reach. Control of the body could continue to be centered at the eye throughout the reach and then switch to the hand once the reach is completed and the hand is close to the target. This is consistent with the understanding that the early portion of a reach is visually feedforward, while the later portion is controlled online with feedback from binocular vision (Bradshaw and Elliott 2003; Servos and Goodale 1994). In this way, the head, eyes, arm, and hand could be treated as a single rigid body for the sake of control, because the hand does not come into play with respect to visual control until it has stopped moving with respect to the trunk, when the two again form a rigid body. This would mean that, when locomoting-to-reach, people do not perform two different tasks with two different means of control. Instead, they perform a single locomoting-to-reach action with a single control strategy. An information switch would still be necessary to shift the locus of control from the head to the hand, reflecting the same solution to the degrees-of-freedom problem that was found by Anderson and Bingham (2011).

Two main components must be investigated to test this possible organization of locomotion-to-reach. As in previous studies, the nature of control during approach must be studied. Some form of sequential proportional rate control is expected, as has been shown in similar tasks. Because this task is similar to but more complex than the handout task, an information switch under a single control strategy would be especially useful. What makes full locomotion-to-reach more complex is the initiation of the reach. It is not known what information is used to initiate reaches in this task. It is possible that reaches are initiated at a given distance from the target, a given value of eye- $\tau$ , or some other informational landmark. To test these possibilities, we performed an experiment in which participants completed a task that was a replication of the handout task of Anderson and Bingham (2011), as well as the full locomoting-to-reach task. We examined which optical variables exhibited invariance during different phases of approach and conducted an analysis of reach accuracy under different conditions.

## Materials and methods

### Participants

Twelve adults (six males and six females), aged 19–54 years, were recruited to participate in this experiment. The participants had normal or corrected-to-normal vision, with stereoacuity of at least 80 arcsec crossed disparity as measured by the Stereo Fly Test (Stereo Optical Company, Inc.). Data from two participants were excluded because they did not properly follow instructions. Of the ten participants included, nine were right-handed and one was left-handed, but the left-handed participant reported no difficulty guiding their right hand to the target. No anomalous behavior was observed from the left-handed participant, neither during testing nor data analysis. All participants gave their informed consent prior to participation in this study. All procedures were approved by and conform to the standards of the Indiana University Institutional Review Board.

### Procedure

Participants were required to perform two visually guided locomotion tasks: (1) reaching to a target while locomoting (locomoting-to-reach) and (2) bringing the hand of an outstretched arm to a target while locomoting (handout). All trials were carried out in a 2.3 m by 30.8 m hallway. A stand was placed at the end of the hallway, against the wall to the left and out of the path of the approaching participant. A rod was projected from the stand to the right at shoulder height. The end of an optic fiber was attached to the right end of this rod to act as the target. For both tasks, half of the trials were performed under fully illuminated conditions. The remaining trials were performed in the dark, with the end of another optic fiber affixed to the thumb of the right hand to indicate its location. Both fibers were lit from the opposite end by battery-powered lights that were out of view, so that the resulting point lights were the only visible elements of the environment during the dark condition. Note that under these conditions, the binocular disparity of these points was still available to participants, so hand- $\tau$  was also available to them. However, this manipulation eliminated optical expansion during approach, preventing the use of monocular eye- $\tau$ , but not its binocular equivalent. Thus, the binocular form of eye- $\tau$  could be isolated and its utility could be tested. Each of the four task  $\times$  lighting condition pairs was performed in a block of 15 trials, resulting in 60 total trials for each participant. The order of these blocks was counterbalanced. For safety, experimenters acted as spotters to make sure the participant would not run into a wall when jogging in a dark hallway.

In the handout task, participants jogged to the target with their right arm fully extended in front of them and their right hand in a “thumbs-up” position. In the locomoting-to-reach task, participants jogged to the same target with their right arm contracted. While locomoting, participants extended their right arm to reach to the target. Reaches were initiated by participants when they saw fit. Participants ended their reaches with the hand in the same thumbs-up position as on the handout trials. The right hand of each participant was Velcroed to his or her chest at the beginning of each trial with the thumb up and the pad oriented toward the target so that the data clearly specified when a reach was initiated. This prevented hand movements that were not directed to the target but allowed participants to easily detach their hand to initiate and perform a reach.

In both tasks, multiple values of the initial distance from the participant to the target were presented in a random order to prevent participants from stereotyping their approach or otherwise relying on artifactual cues resulting from a common initial distance. Magnitudes of this initial distance were 7, 8, or 9 m so that participants would have the room to accelerate comfortably to jogging velocity, as well as the room to decelerate without spatial constraints producing artificially high deceleration. For both tasks, each participant completed ten trials from each starting location (five in each viewing condition), resulting in a total of thirty trials per task for each participant. In both tasks, participants were instructed to place their right thumb directly to the right of the target when bringing their hand to it. This required participants to match the depth of the target with their thumb, but prevented collision with or occlusion of the target. Participants were instructed to approach briskly and were not allowed to correct the position of their hands after coming to a stop.

### Data recording

An Optotrak infrared motion measurement system was used to collect three-dimensional motion data during all trials. The Optotrak camera was placed behind the target, just above the height of the target. Infrared light-emitting diodes (IREDs) were placed on the back of the stand supporting the target, between and just above the participant's eyes, on the right thumb pad (facing the camera), on the right shoulder, and on the sternum to record their spatial location throughout each trial. These IREDs were not visible in the dark. Raw data were recorded for each IRED as three-dimensional spatial coordinates, such that the  $x$ -,  $y$ -, and  $z$ -dimensions corresponded to horizontal, vertical, and depth with respect to the eyes. These data were recorded for each marker at 60 Hz. Recording started approximately 1 s before the participant was instructed to begin moving and concluded approximately 1 s after the participant

verbally indicated that they had reached the target. The initiation and termination of data recording during a trial was controlled by the experimenter through a personal computer integrated with the Optotrak system.

All analyses on the raw data were completed using a MATLAB program written by the authors. These data were transformed from a camera-centered coordinate frame to a target-centered frame, such that the origin was set to be the target position and participants moved along the  $z$ -axis when approaching the target. Because of the limited capture volume of the Optotrak, the entirety of approach trajectories could not be recorded, so the earliest portions were not collected. However, all relevant actions, such as reach initiation, reach termination, and target acquisition, were captured. The entire captured portion of each movement trajectory was recorded, with analyses of full trajectories and end point accuracy. Each movement trajectory was filtered using two oppositely directed passes of a low-pass Butterworth filter with a resulting cutoff frequency of 7 Hz.

For locomoting-to-reach trials, the initiation of a reach was determined to be the first moment at which the velocity of the hand with respect to the head exceeded 15 cm/s. A sufficiently large threshold was needed so that false reach initiations were not chosen due to the jostling and vibration of the hand during approach. As discussed earlier, participants began locomoting-to-reach trials with their right hand Velcroed to their chest in an effort to minimize hand movements that were not directed to the target, but such movements could not be eliminated entirely because oscillations of the body are inherent to locomotion. The end of a reach was determined to be the first moment after reach initiation at which the velocity of the hand with respect to the head dropped below 18 cm/s. A larger threshold was used for reach termination than reach initiation to exclude the sort of fine post-reach adjustments that participants were discouraged from employing. In all locomoting-to-reach trials, forward motion of the hand relative to the head ceased at the end of the reach and then the participant guided a rigid arm/hand to the target, i.e., the reach ended before the target was acquired. Note that this did not occur because of instruction. Participants performed the task as they preferred given the constraints already described. Thus, the conclusion of a locomoting-to-reach trial was very similar to a handout trial, and it was necessary to define the end of the total movement to the target for all trials, as this differed from the end of the reach. This was determined to be the first moment that the velocity of either the hand or the head dropped below 10 cm/s with respect to the target.

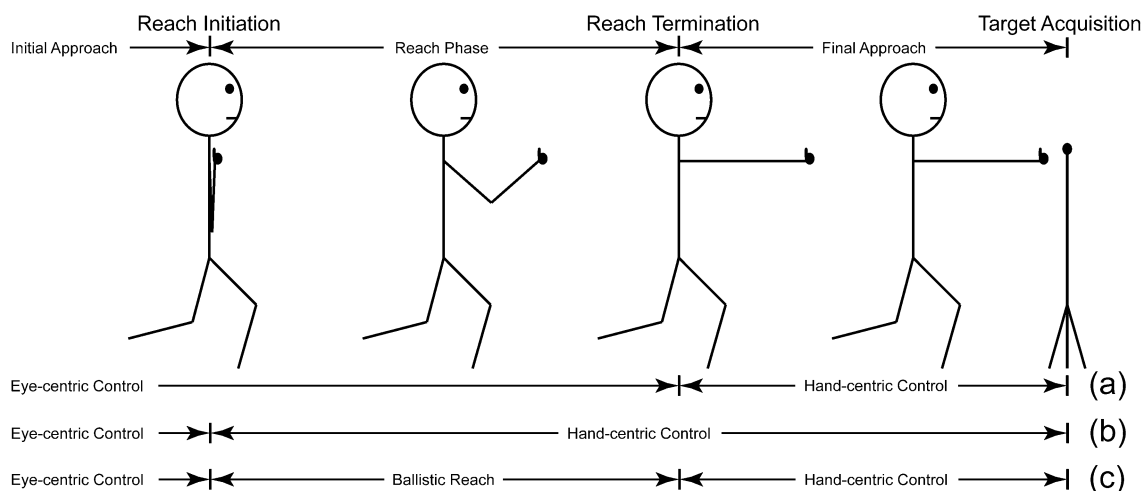
#### Data analysis

First, we performed an analysis of end point accuracy for both the handout and the locomoting-to-reach tasks in both

lighting conditions (dark and lighted). A repeated-measures ANOVA was performed on final distances from the target with task and lighting condition as factors.

Second, we analyzed the information and control strategies used to control the approach of head and eye and then the hand to the target. Two different information variables were analyzed,  $\text{eye-}\tau$  and  $\text{hand-}\tau$ .  $\text{Eye-}\tau$  was expected to be used early in the approach and  $\text{hand-}\tau$  later in the approach. Two different control strategies were analyzed: constant- $\dot{\tau}$  control and constant proportional rate control. For each task, specific landmarks or events were used to divide the entire approach into epochs for analysis. To test whether either  $\dot{\tau}$  or proportional rate ( $\tau/\dot{\tau}$ ) was held constant, the information trajectories in each epoch were analyzed using the “split-half” analysis developed by Anderson and Bingham (2011). The trajectories from each trial were split into half at the median time value, and then an average value was derived for each half. The mean values from the two halves were tested for a potential difference using repeated-measures ANOVA. A significant difference between the halves showed that the information variable tested (either  $\dot{\tau}$  or proportional rate) was not being held constant by participants over the trajectory. Comparisons between lighting conditions (dark and lighted) were also tested.

The trajectories from the handout task were analyzed first. The handout task under dark lighting conditions was a replication of the Bin/Bin condition of Anderson and Bingham (2011). As shown in the previous study, the two  $\tau$  variables reliably exhibited certain regularities used to determine landmarks distinguishing epochs for analysis.  $\text{Hand-}\tau$  began with a much greater value than  $\text{eye-}\tau$  but decreased rapidly during the approach, eventually crossing  $\text{eye-}\tau$  when a participant’s eyes were two times the length of the arm away from the target, i.e., when the hand was equidistant to eye and target. The act of bringing the outstretched hand to the target resulted in the head stopping considerably short of the target, so the rate of change of optical expansion converged to 0, causing  $\text{eye-}\tau$  to increase exponentially. As the hand was brought to the target,  $\text{hand-}\tau$  converged to 0. Anderson and Bingham (2011) used the point at which  $\text{hand-}\tau$  and  $\text{eye-}\tau$  crossed as the landmark for an information switch, where participants stopped using  $\text{eye-}\tau$  information and started using  $\text{hand-}\tau$ . Switching from  $\text{eye-}\tau$  to  $\text{hand-}\tau$  at this landmark results in reliance on the  $\tau$ -variable with the smaller value, that is, the variable that specifies a sooner time-to-contact. This conservative behavior was assumed to reflect a strategy to avoid collisions, as control strategies that incorporate collision-avoiding measures have been observed in a number of domains (Fath and Fajen 2011; Higuchi et al. 2006; Warren and Whang 1987). Thus, the split-half analysis was performed on the  $\text{eye-}\tau$  trajectory before the cross point and on the  $\text{hand-}\tau$  trajectory after the cross point. Again, these analyses were first



**Fig. 1** Illustration of the locomoting-to-reach task. Reach initiation, reach termination, and target acquisition are shown as action landmarks. Potential strategies include *a* eye-centric control until an information switch to hand-centric control at reach termination;

*b* eye-centric control until an information switch to hand-centric control at reach initiation; *c* eye-centric control until a “ballistic” reach with resumption of (hand-centric) control at reach termination

performed on  $\dot{\tau}$  trajectories for the eye and hand, respectively, and then on the proportional rate trajectories for the eye and hand.

To get a better understanding of what participants were doing, we examined the mean form of the handout proportional rate trajectories. We constructed averaged proportional rate trajectories (with error bars) across all participants by binning data points across all trials. This binning aligned the beginning and end of trials, as well as the trajectory cross point, across trials of different lengths. These mean trajectories were compared across participants and used to interpret and illuminate the results of the split-half analyses.

The same analyses were performed on the trajectories from the locomoting-to-reach task, but because of differences in the relative behavior of the eye- $\tau$  and hand- $\tau$  trajectories, different landmarks were identified and used yielding somewhat different epochs. During locomotion-to-reach, the eye- $\tau$  and hand- $\tau$  trajectories did not reliably cross. So, other landmarks were investigated as possible points for the switch of information. Recall that in this task, as participants locomoted to approach the target, they initiated a reach extending the arm and hand outwards from the body (and head and eyes). The reaching movement relative to the body stopped before the target was acquired, so in the final phase of the approach, the arm, hand, and body moved together as a rigid body exactly as in the handout task. Because disparity information about the hand was not available until the reach was initiated, this initiation of the reach was a candidate landmark for information switch. The other candidate landmark was reach termination, after which the movement resembled the handout task in which

the final approach was controlled using hand- $\tau$ . Thus, the trajectories that were tested were eye- $\tau$  before reach initiation, eye- $\tau$  before reach termination, hand- $\tau$  after reach initiation, and hand- $\tau$  after reach termination (Fig. 1).

If participants in this study began to rely on hand- $\tau$  at reach initiation, then this should also be when they stopped using eye- $\tau$ . If use of hand- $\tau$  began at reach termination, then there are two hypothesized points at which control with eye- $\tau$  may have ceased. First, participants might have used eye- $\tau$  to control target approach right up until reach termination, then switched to use of hand- $\tau$ . Alternatively, participants might have used eye- $\tau$  only until reach initiation, then performed a reach that was not visually controlled, and resumed visual control using hand- $\tau$  at the termination of the reach. We applied the split-half analysis to each of the four epochs to determine where given information variables were held constant by participants. First, we analyzed  $\dot{\tau}$  in each of the four epochs, and then, we analyzed proportional rate. In summary, we analyzed  $\dot{\tau}$  for eye- $\tau$  before reach initiation and then before reach termination, and then, we analyzed  $\dot{\tau}$  for hand- $\tau$  after reach initiation and then after reach termination. Then, we did the same but analyzing proportional rate trajectories instead of  $\dot{\tau}$  trajectories.

Again, to get a better understanding of what participants were doing, we next examined the mean form of the proportional rate trajectories during locomotion-to-reach. We constructed averaged proportional rate trajectories (with error bars) across participants by binning data points across all trials. This binning aligned movement landmarks like reach initiation and termination across trials of different lengths. These mean trajectories allowed for regularities

across participants to be observed, and they were used to interpret and illuminate the results of the split-half analyses.

Finally, we performed an analysis to investigate what information might have been used to initiate a reach during the approach. The two candidates that we considered were perceived distance and time-to-contact ( $\text{eye-}\tau$ ). Under the assumption that the same values should be observed in the two lighting conditions, we used  $t$  tests to compare values in the lighted and dark conditions. We also examined the variabilities.

## Results

### End point accuracy

Results show that participants were able to guide movements to the target accurately under both lighting conditions (dark and lighted) in both tasks (handout and locomoting-to-reach). In the handout task, participants overshot the target by an average of 1.67 cm ( $SD = 1.45$ ) in the lighted condition and only 0.03 cm ( $SD = 1.02$ ) in the dark condition. Similar results were found for the locomoting-to-reach task. In the lighted condition, participants overshot the target by an average of 1.86 cm ( $SD = 1.49$ ), but were 0.21 cm ( $SD = 0.88$ ) short of the target in the dark condition. A repeated-measures ANOVA of final distances from target, with task and lighting condition as factors, yielded a significant difference between lighting conditions [ $F(1, 9) = 34.4, p < 0.05$ ] but not between tasks. There was not a significant interaction of task and lighting condition.

Based on these results, it would appear that participants were more accurate in the dark condition. However, there was a difference between lighting conditions that shows that the observed differences are not meaningful. First, recall that the thumb marker was placed on the thumb pad, facing away from the participant and toward the target. Under lighted conditions, participants matched their thumb in depth with the target as instructed. This would result in a slight overshoot of the thumb marker. Typical thickness of the thumb is between 1 and 2 cm, so mean overshoots of 1.67 and 1.86 cm should be interpreted as accurate. In the dark, the position of the thumb was only specified by the point-light that was also placed on the thumb pad. Thus, participants matched the depth of this point, which roughly equaled that of the thumb marker, with that of the target. This means that accuracy measures obtained from the thumb marker in the dark condition were not displaced from true accuracy in the way that they were in the lighted condition. Recall that the mean accuracies for the handout and locomoting-to-reach tasks in the dark were a 0.03 cm overshoot and a 0.21 cm undershoot, respectively. Thus,

we conclude that participants matched the depth of targets accurately in both tasks and in both conditions.

### Approach control

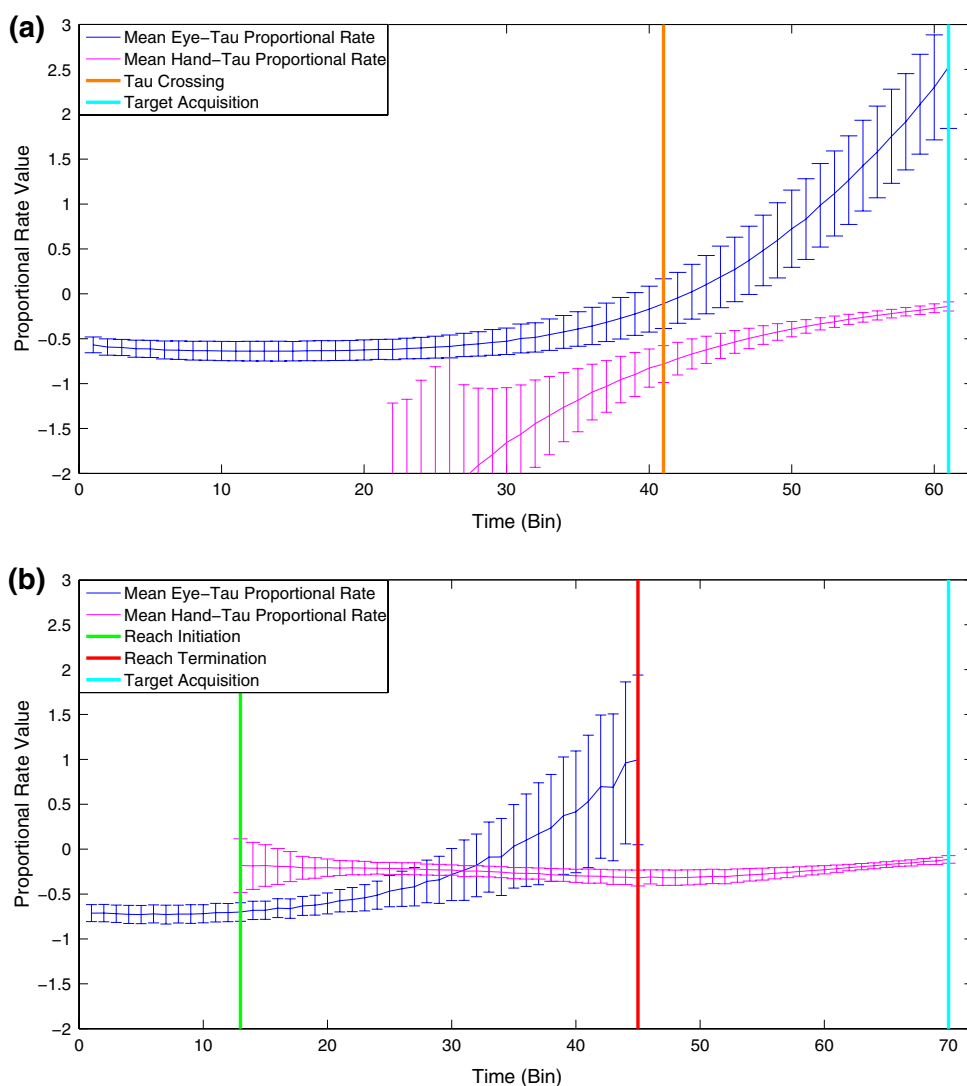
#### Handout

We performed an analysis to determine whether  $\dot{\tau}$  was held constant in the handout task. We first defined the  $\tau$ -crossing to be the first data point at which the value of  $\text{hand-}\tau$  was below that of  $\text{eye-}\tau$ . The portions of the  $\tau$  time series before and after the  $\tau$ -crossing were evaluated separately, yielding four trajectories:  $\text{eye-}\tau$  before  $\tau$ -crossing,  $\text{eye-}\tau$  after  $\tau$ -crossing,  $\text{hand-}\tau$  before  $\tau$ -crossing, and  $\text{hand-}\tau$  after  $\tau$ -crossing. For each of these trajectories, the median time point was identified. This point was used to split each of these trajectories into two components, so that the slopes of the two halves could be compared to determine whether or not  $\dot{\tau}$  changed over the course of the whole trajectory. To determine  $\dot{\tau}$  values, a linear regression was performed on both components of each  $\tau$  trajectory to determine the slopes. If  $\dot{\tau}$  values changed over the course of a trajectory, but proportional rate values did not, this would provide evidence that the participant exhibited a proportional rate control strategy. Given the findings of Anderson and Bingham (2011), the trajectories of interest were  $\text{eye-}\dot{\tau}$  before the  $\tau$ -crossing and  $\text{hand-}\dot{\tau}$  after the  $\tau$ -crossing.

In Anderson and Bingham (2011), mean  $\text{eye-}\dot{\tau}$  values before  $\tau$ -crossing in each condition ranged from  $-0.48$  to  $-0.53$ . In this study, the mean  $\text{eye-}\dot{\tau}$  value before  $\tau$ -crossing for handout trials in the lighted condition was  $-0.59$ , and in the dark, it was  $-0.61$ . This was higher than the previous study, but still within an expected range. A repeated-measures ANOVA was performed on these  $\text{eye-}\dot{\tau}$  values before the  $\tau$ -crossing with lighting and half as factors. A significant difference between halves would indicate a change in  $\text{eye-}\dot{\tau}$  over time. The ANOVA yielded a significant difference between halves [ $F(1, 9) = 587.3, p < 0.05$ ], but not lighting conditions. There was not a significant interaction. Next, we examined the  $\text{hand-}\dot{\tau}$  values after the  $\tau$ -crossing. The overall means for the lighted and dark conditions were  $-1.01$  and  $-0.86$ , respectively. A repeated-measures ANOVA on these  $\dot{\tau}$  values with lighting and half as factors yielded a significant difference between halves [ $F(1, 9) = 17.9, p < 0.05$ ], but not lighting conditions. There was not a significant interaction. These results showed that the  $\text{eye-}\tau$  trajectories before the  $\tau$ -crossing and the  $\text{hand-}\tau$  trajectories after the  $\tau$ -crossing changed in slope over time, providing evidence against a constant  $\dot{\tau}$  strategy in both cases.

Next, we examined the constant proportional rate strategy. The landmarks that were used to determine the beginning and end of  $\dot{\tau}$  trajectories were also used for

**Fig. 2** Averaged proportional rate trajectories. **a** Handout task: averaged trajectory across all participants. In the legend,  $\tau$ -crossing refers to the first instant at which hand- $\tau$  had a lower value than eye- $\tau$ . Note that this does not result in the higher-order proportional rate trajectories crossing. **b** Locomoting-to-reach task: averaged trajectory across all participants who displayed the strategy of switching from eye- $\tau$  to hand- $\tau$  once the eye became visible. This strategy was employed by the majority of participants



proportional rate. Trajectories consisted of the ratios of  $\tau$  to  $\dot{\tau}$  at each time point before or after the  $\tau$ -crossing. A mean proportional rate value was computed for each half of each trajectory of each trial. Again, the relevant optical information was eye- $\tau$  before  $\tau$ -crossing and hand- $\tau$  after  $\tau$ -crossing.

A repeated-measures ANOVA was performed on the proportional rate values for eye- $\tau$  before the  $\tau$ -crossing, with lighting condition and half as factors, to test for constancy of this optical variable. The repeated-measures ANOVA yielded a significant difference between halves [ $F(1, 9) = 31.0, p < 0.05$ ], but not lighting conditions, showing that proportional rate values for eye- $\tau$  changed over time before the  $\tau$ -crossing. There was not a significant interaction. Performing a repeated-measures ANOVA on the hand- $\tau$  proportional rate values after the  $\tau$ -crossing yielded no significant effects or interactions, so there was no indication that proportional rate values with hand- $\tau$  changed after the  $\tau$ -crossing.

These results provided evidence for the proportional rate control strategy with hand- $\tau$  to guide the hand to the target, but they also provided evidence against the proportional rate control strategy with eye- $\tau$  to first approach the target. This latter result was different than what Anderson and Bingham (2011) had found. However, we next examined mean trajectories computed across participants and found both good reliability in the form of the trajectories across participants as well as evidence that constant proportional rate was maintained for eye- $\tau$  despite the split-half result in that case. Because only the hand actually goes to the target in this task and the head and eyes stop at a distance from the target, eye- $\tau$  trajectories always go to infinity during each trial. As shown in Fig. 2a, this causes the proportional rate values to also go to infinity, and this starts to occur before the point at which the eye- $\tau$  and hand- $\tau$  trajectories cross. Nevertheless, it appears that eye- $\tau$  remains constant during the first portion of the trials before it begins to rise. The rise yielded the significant difference in the split-half



analysis because the cross point used to determine the epoch for analysis was inappropriate. Recall that in the locomoting-to-reach task, the  $\tau$ -crossing was not found. It appears that this  $\tau$ -crossing is just a by-product of imposing the constraint of a rigid, outstretched arm. The finding that proportional rate control with eye- $\tau$  is used to guide the approach phase of the handout task was replicated, but it does not appear that the  $\tau$ -crossing is a meaningful landmark for changing optical variables. Finally, judging from the error bars on the mean trajectories, there is a brief ( $\approx 200$  ms) transitional period between the use of eye- $\tau$  and the use of hand- $\tau$ .

#### *Locomoting-to-reach*

First, we performed the split-half analysis on  $\dot{\tau}$  trajectories. A repeated-measures ANOVA was performed on eye- $\dot{\tau}$  values before reach initiation with lighting and half as factors. It yielded a significant difference between halves [ $F(1, 9) = 20.2, p < 0.05$ ], but not lighting conditions. There was also a significant interaction [ $F(1, 9) = 7.1, p < 0.05$ ]. A repeated-measures ANOVA on eye- $\dot{\tau}$  values before reach termination with lighting and half as factors yielded a significant difference between halves [ $F(1, 9) = 44.6, p < 0.05$ ], but not lighting conditions. There was no significant interaction. Both  $\dot{\tau}$  trajectories differed between halves, so we rule out a constant- $\dot{\tau}$  strategy for eye- $\tau$  before reach initiation or before reach termination.

We next examined the hand- $\dot{\tau}$  values. A repeated-measures ANOVA on hand- $\dot{\tau}$  values from reach initiation to target acquisition with lighting and half as factors yielded a significant difference between halves [ $F(1, 9) = 57.0, p < 0.05$ ], but not lighting conditions. There was no significant interaction. A repeated-measures ANOVA on hand- $\dot{\tau}$  values from reach termination to target acquisition with lighting and half as factors yielded a significant difference between halves [ $F(1, 9) = 14.6, p < 0.05$ ], but not lighting conditions. There was no significant interaction. Both of these  $\dot{\tau}$  trajectories differed between halves, so we rule out a constant- $\dot{\tau}$  strategy for hand- $\tau$  from reach initiation to target acquisition or from reach termination to target acquisition. Next, we performed split-half analyses on proportional rate trajectories.

A repeated-measures ANOVA on eye- $\tau$  proportional rate values before reach initiation with lighting and half as factors yielded a significant difference between lighting conditions [ $F(1, 9) = 16.124, p < 0.05$ ], but not halves. There was no significant interaction. Because there was no difference between halves of the eye- $\tau$  proportional rate trajectories, it appears that proportional rate control with eye- $\tau$  was used at least until reach initiation. A repeated-measures ANOVA on eye- $\tau$  proportional rate values before reach termination was performed, with lighting and half as factors,

to determine whether proportional rate control with eye- $\tau$  continued past reach initiation to reach termination. This ANOVA yielded a significant difference between lighting conditions [ $F(1, 9) = 19.4, p < 0.05$ ] and between halves [ $F(1, 9) = 13.4, p < 0.05$ ], but there was no significant interaction, so proportional rate with eye- $\tau$  was not constant through reach termination. Because differences were observed between halves of eye- $\tau$  proportional rate trajectories before reach termination, but not between halves of trajectories before reach initiation, we concluded that proportional rate control with eye- $\tau$  ended at reach initiation, not reach termination.

A repeated-measures ANOVA was performed on hand- $\tau$  proportional rate values from reach initiation to target acquisition with lighting and half as factors. The ANOVA yielded a significant difference between lighting conditions [ $F(1, 9) = 8.4, p < 0.05$ ] and between halves [ $F(1, 9) = 65.6, p < 0.05$ ]. There was also a significant interaction [ $F(1, 9) = 6.0, p < 0.05$ ]. We concluded that proportional rate with hand- $\tau$  was not constant during this phase. A repeated-measures ANOVA was performed on hand- $\tau$  proportional rate values from reach termination to target acquisition with lighting and half as factors. It yielded no significant difference between lighting conditions or between halves, and there was no significant interaction. Because differences were observed between halves of hand- $\tau$  proportional rate trajectories extending from reach initiation to target acquisition, but not between halves of trajectories extending from reach termination to target acquisition, we concluded that proportional rate control with hand- $\tau$  began at reach termination, not reach initiation. Thus, it appears that participants used proportional rate control with eye- $\tau$  until reach initiation, at which point a reach was initiated with a resumption of proportional rate control using hand- $\tau$  at reach termination.

To get a better understanding of what participants were doing, we examined the mean form of the locomoting-to-reach proportional rate trajectories for each participant. This revealed two things. First, the eye- $\tau$  proportional rate trajectory did indeed maintain a constant value until reach initiation and then began to depart from this shortly thereafter. Second, the hand- $\tau$  proportional rate trajectory also maintained a constant value during the latter part of the approach to the target, typically beginning partway through the reach. This made sense because hand- $\tau$  simply would not have been available until the hand was moving in the reach and was brought into view. Thus, control using hand- $\tau$  would be expected to start during the reach. All participants resumed proportional rate control with hand- $\tau$  by reach termination, but a majority (six of the ten participants) did so sooner, that is, shortly after the hand had come into view. For those participants, constant hand- $\tau$  proportional rate reliably began around 200 ms after reach

initiation. Averaged hand- $\tau$  and eye- $\tau$  proportional rate trajectories across the six participants who switched from eye- $\tau$  to hand- $\tau$  once the hand was visible can be seen in Fig. 2b. Others did not exhibit constant proportional rate until reach termination. We identified several factors that might be predictive of which strategy a participant adopted, such as velocity of locomotion or velocity of reaching. However, none were predictive, so it is unclear what drove these differences.

### Initiation of reaches

We investigated the information used to initiate reaches. Participants might have initiated their reaches when they were given distance from the target. Alternatively, participants could have used a  $\tau$ -based time-to-contact threshold at which they initiated their reaches. There was information specifying both distance to the target (e.g., vergence) and time-to-contact (eye- $\tau$ ) in both lighting conditions, so if a preferred value of one of these was used to initiate reaches, that threshold should be robust to any potential differences in behavior across lighting conditions, such as velocity of approach. Comparing lighting conditions,  $t$  tests (two-tailed) were conducted on the eye- $\tau$  values and on the distances from the target, both at the moment of reach initiation. There was a significant difference between mean distance at reach initiation as a function of lighting condition [ $t(9) = 4.6, p < 0.05$ ], but no difference in eye- $\tau$  values [ $t(9) = 0.4, p > 0.05$ ]. Mean distance in the lighted condition was 262.2 cm (SD = 54.6), and in the dark condition, it was 213.5 cm (SD = 52.0). The mean eye- $\tau$  value in both the light and dark conditions was 1.0 (SD = 0.2). These results are consistent with the hypothesis that a preferred eye- $\tau$  value of 1.0 (when eye- $\tau$  specified a time-to-contact of 1.0 s) was used to initiate reaches. Monocular eye- $\tau$  was not available in the dark because the point-light targets did not yield optical expansion during approach, so this result also suggests the use of binocularly specified eye- $\tau$  in this task, at least in the dark condition.

## Discussion

In this study, we investigated the common visuomotor behavior of reaching to a target while locomoting. Our primary concern was identifying the visual information and control strategy that governs this task. Locomotion-to-reach is a complex behavior that involves two distinct, but overlapping components: guidance of the body to within reaching distance of the target and guidance of the hand to the target. We investigated two sources of  $\tau$ -based information, each under two possible control strategies. One strategy maintains a constant value of  $\dot{\tau}$  during approach. The

other strategy, proportional rate control, maintains a constant value of the ratio of  $\tau$  to  $\dot{\tau}$  during approach. The major advantage of the proportional rate control strategy is its robustness to the kinds of perturbations that are common in the world. Using a constant  $\dot{\tau}$  strategy, the only value of  $\dot{\tau}$  that will result in soft contact at the target is  $-0.5$ . Not only is this highly restrictive for such a flexible system, but real-world constraints and perturbations may make it impossible for that particular value to be attained. However, as shown by Fath et al. (2013), proportional rate control enables the use of any of a range of values (see also Anderson and Bingham 2010, 2011), so a new value may be adopted in response to perturbation. This allows for online adjustments to the current proportional rate value, which in turn allows for flexible behavior. This flexibility makes proportional rate control more stable and reliable than a constant  $\dot{\tau}$  strategy. These properties show why proportional rate control should be preferable in principal. Indeed, the evidence from the current study suggests that it is preferable in practice when locomoting-to-reach as well.

A number of studies have argued for or against the use of the constant- $\dot{\tau}$  strategy for the control of various approach behaviors. Other studies have shown the use of proportional rate to control reaching and targeted walking tasks. The results of these latter studies, along with the theoretical considerations just discussed, imply that proportional rate control should be usable, and preferable to constant- $\dot{\tau}$ , in other approach behaviors like locomotion-to-reach and braking. This is the first study to give an account for the control of approach throughout the full locomoting-to-reach behavior and further implies that proportional rate control may be used across approach behaviors.

Results showed that, when locomoting-to-reach, participants' behavior was guided by eye-centric proportional rate control during the pre-reach portion of the behavior and hand-centric control once the hand was extended. During the initial phase of approach, participants used eye- $\tau$  and maintained a constant proportional rate value of about 0.7. When this eye-centric  $\tau$  specified a time-to-contact of 1 s, participants initiated a reach to quickly get the hand in view so that a version of  $\tau$  based on the relative binocular disparities of the hand and target could be used to guide the hand to the target. Participants resumed control with this hand-centric  $\tau$ . Some participants consistently began hand-centric control once the hand came into view and others began once the reach was complete and the arm was rigid. The final phase of approach and target acquisition, with the arm fully extended, was guided by maintaining a new constant proportional rate value in the range 0.25–0.30.

In this study, we showed how visual information maps to action, specifically how an optic regularity is maintained to produce appropriate deceleration. This framework does not describe the manner of control of any individual degree

of freedom. As such, the current findings do not uniquely determine the possibilities for the means of motor control, although they reinforce the importance of synergies, patterns of coordination across multiple degrees of freedom. Locomotion-to-reach is a complex, multistage behavior. Proportional rate control allows for these components to be nested under a single control strategy, which is an effective solution to the degrees-of-freedom problem. It is not necessary to switch the means of control mid-behavior, only the information that a single control strategy exploits.

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

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