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Reach endpoint errors do not vary with movement path of the proprioceptive target

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Jones SA, Byrne PA, Fiehler K, Henriques DY. Reach endpoint errors do not vary with movement path of the proprioceptive target. *J Neurophysiol* 107: 3316–3324, 2012. First published March 7, 2012; doi:10.1152/jn.00901.2011.—Previous research has shown that reach endpoints vary with the starting position of the reaching hand and the location of the reach target in space. We examined the effect of movement direction of a proprioceptive target-hand, immediately preceding a reach, on reach endpoints to that target. Participants reached to visual, proprioceptive (left target-hand), or visual-proprioceptive targets (left target-hand illuminated for 1 s prior to reach onset) with their right hand. Six sites served as starting and final target locations (35 target movement directions in total). Reach endpoints do not vary with the movement direction of the proprioceptive target, but instead appear to be anchored to some other reference (e.g., body). We also compared reach endpoints across the single and dual modality conditions. Overall, the pattern of reaches for visual-proprioceptive targets resembled those for proprioceptive targets, while reach precision resembled those for the visual targets. We did not, however, find evidence for integration of vision and proprioception based on a maximum-likelihood estimator in these tasks.

maximum-likelihood estimator; integration; proprioceptive target-hand

OUR ABILITY TO ACCURATELY localize a hand relative to the other hand is essential to many of our daily activities and our overall quality of life. For example, we might transfer an object of interest from one hand to the other such as when putting on a piece of jewelry, stabilize an object with one hand while manipulating it with the other such as spreading peanut butter on toast, or reach to scratch an itch on our leg or back. Therefore, it is important that we identify and understand how the central nervous system (CNS) processes and uses sensory information about the body.

When reaching to visual or proprioceptive targets, where the reaching hand begins in space can affect reach endpoints (Chokron & Bartolomeo, 1997; Chokron, Colliot, Atzeni, Bartolomeo, & Ohlmann, 2004; Chokron et al., 2002; Farne, Ponti, & Ladavas, 1998; Khoshnoodi, Motiei-Langroudi, Omrani, Ghaderi-Pakdel, & Abbassian, 2006; Sarlegna & Sainburg, 2007). For example, when the reaching hand begins closer to the body (or farther from the body), participants' reach endpoints are also closer to the body (or farther from the body, Sarlegna & Sainburg, 2007). Similarly, the location of a proprioceptive target in space can also affect the accuracy (Adamovich, Berkinblit, Fookson, & Poizner, 1998) and precision (van Beers, Sittig, & Denier van der Gon, 1998) of reaches to that target. Adamovich et al. (1998) reported larger

and more leftward reach endpoints for left final proprioceptive target locations than right ones, and, although van Beers et al. (1998) did not report any accuracy differences across final proprioceptive target locations, these authors found greater reach precision for locations closer to the target-hand's shoulder.

Perhaps more surprising than the effects of final target location and initial reaching hand location on reach endpoints is that starting locations of a proprioceptive target might also affect reach endpoint distribution (Imanaka, 1989; Imanaka & Abernethy, 1992a; Walsh & Russell, 1979; Wrisberg & Winter, 1985). Imanaka and colleagues asked participants to first move a target-hand from one start location to one end location before placing that hand in their lap. When participants reproduced the same end location, but this time began the movement from a second (shifted) start location, reproduction errors shifted in the direction of change of the target's starting location (Imanaka, 1989; Imanaka & Abernethy, 1992a; Walsh & Russell, 1979; Wrisberg & Winter, 1985). These differences in reach accuracy and precision across starting and final target-hand locations may reflect the kind of signals the brain uses to derive the position of the proprioceptive target. Behavioral and neurophysiological research has revealed the existence of both static (i.e., position) and dynamic (i.e., movement) proprioceptive information, and that both types of information can be used separately to determine final limb position (Burke, Hagbarth, Lofstedt, & Wallin, 1976; Edin & Vallbo, 1990; Goble, Noble, & Brown, 2009; Imanaka, 1989; Imanaka & Abernethy, 1992a, 1992b; Lonn, Crenshaw, Djupsjobacka, Pedersen, & Johansson, 2000; Sittig, Denier van der Gon, & Gielen, 1985; Smeets & Brenner, 1995). However, previous research compared localization errors across starting positions of the hand and have not examined if the effect of starting position of the hand on localization errors varies across final target-hand locations. Furthermore, many studies have employed reproduction tasks (in which the participant must reproduce final target-hand location) and have not examined how starting and final target hand locations, together, affect reaches using the opposite hand. For example, the movement path of the proprioceptive target, from a combination of starting and final proprioceptive target locations, might systematically affect the accuracy and precision of reach endpoints to that target. This issue, which has not been investigated in the current literature, will be the main focus of the current study.

In the experiments described below, participants reached to their unseen left target-hand (proprioceptive target) after it was actively moved from one of six sites to one of the five other sites. Thus, on each trial, the left target-hand began at one location, which we will refer to as the starting target-hand

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location, and finished at a second location, which we will refer to as the final target-hand location. The combinations of starting and final target-hand locations resulted in target-hand movement paths from left to right, right to left, near to far, far to near, and on the diagonal from left to right and right to left. We will show that, overall, the movement path of the proprioceptive target does not appear to affect reach endpoints to that target.

A second aim of this study was to determine if the movement direction of the proprioceptive target affects how that information is integrated with visual information about target location. Redundant sensory information about an aspect of a stimulus (e.g., the location of a reaching hand) from two or more sensory sources can be integrated in such a way that a more accurate or precise estimate of that aspect is derived than would be possible with either source in isolation (e.g., Ernst & Banks, 2002; Kording & Wolpert, 2004; Snijders, Holmes, & Spence, 2007; Sober & Sabes, 2005; van Beers, Sittig, & Denier van der Gon, 1996, 1999). If the proprioceptive target moves immediately before a reach, the central nervous system (CNS) could integrate static and dynamic proprioceptive information about the target, forming a reliable estimate of target location based on proprioceptive information (e.g., Goble, Noble, & Brown, 2009). This information might then be used, weighted based on its reliability, along with visual information to determine final target location. As we tested if target-hand movement direction (THMD) would affect reaches to that target, this aim sought to determine if the effect of THMD on reach endpoints would then change in response to the availability of visual information about the target-hand.

To determine the relative reliability of proprioceptive information derived from static and dynamic proprioceptive signals compared with that of visual information about target location, participants reached to static visual targets at one of the same six sites described above. In a visual-proprioceptive condition, participants reached to the unseen left target-hand following both movement (static and dynamic proprioceptive information) and illumination of the target-hand for 1 s in its final location (static visual information). We used individual variabilities in the visual and proprioceptive conditions to predict the variability in the visual-proprioceptive task that would be

expected if vision and proprioception were being combined by the CNS using a maximum-likelihood estimator (MLE) model.

METHODS

Participants

Eleven participants (6 males) with a mean age of 22 yr (range: 16–26 yr) participated in this experiment. One participant's data was excluded from analysis because the variability (as measured by 95% error ellipse area) of their reach endpoints in all conditions was more than four times greater (19.55 cm²) than the average across participants (4.45 cm²). All participants had normal or corrected to normal vision and were right handed (self-reported). Written informed consent was provided by each participant prior to their participation. This experiment was approved by the York University Human Participants Review Subcommittee.

General Experimental Setup

A schematic of the experimental set up is presented in Fig. 1. Participants completed a series of three conditions in which they reached to visual [light-emitting diode (LED)], proprioceptive (left target-hand), or visual-proprioceptive (left target-hand briefly illuminated prior to the reach) targets with the right reaching-hand. The order in which participants completed the experimental paradigms was randomized. Participants sat on a height-adjustable chair in front of a 90-cm-high table so that they could comfortably reach to all areas of a transparent 43 cm (length) × 33 cm (width), 3-mm-thick touch screen panel (resolution of 4,096 × 4,096 pixels; Keytec, Garland, TX) placed on top of a tinted platform (Fig. 1, A and B). The touch screen was used to record all reach endpoints. Six sites served as final target locations in all three conditions and starting target-hand locations in the proprioceptive and visual-proprioceptive conditions (Fig. 1C). These sites were spaced 10 cm apart and arranged in two lines (3 sites/line and 10 cm between the two lines). The closest three sites were located 23 cm from the participant (corresponding to 0° and 23° left and right relative to the cyclopean eye), and the farthest three sites were located 33 cm from the participant (corresponding to 0° and 17° left and right relative to the cyclopean eye). Visual targets consisted of six red LEDs mounted on a box at each of the six sites. The box was placed underneath a pressure-sensitive touch screen held in place by barriers attached to the table (Fig. 1A). For proprioceptive and visual-proprioceptive sessions, participants grasped the vertical handle of a two-jointed robot manipulandum (Interactive Motion Technologies,

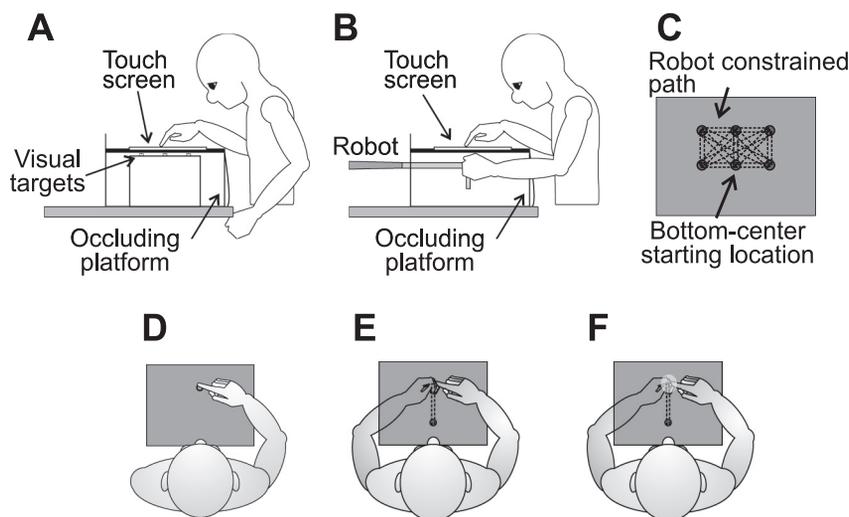


Fig. 1. A schematic of the experimental setup. A: a side view of the experimental set up used in the visually guided reach task. Participants reached with their right hand to the remembered location of light-emitting diodes (LEDs). A horizontally placed touch screen panel recorded all reach endpoint locations. B: a side view of the experimental set up in the proprioceptive and visual-proprioceptive reach tasks. In both tasks, participants gripped the handle of a robot manipulandum with their left target-hand and reached to the target location with their seen right reaching-hand. C: six sites served as start and target positions for the left target-hand in our proprioceptive and visual-proprioceptive conditions. The robot manipulandum restricted participants' active movement of the left target-hand along a straight path from each of these six sites to each of the other five remaining sites. D: in the visual task, participants reached with their seen right hand to the remembered location of visual targets (LEDs). E: in the proprioceptive task, participants reached with their seen right hand to the felt location of the left target-hand. F: in the visual-proprioceptive task, participants reached with their seen right hand to the felt and briefly seen location of the left target-hand.

Cambridge, MA) with their left target-hand in such a way that their thumb rested on top of the robot handle (1.4 cm in diameter); the handle was just above waist level (Fig. 1B). The proprioceptive target was therefore the participants' left thumb, as it rested on top of the handle of the robot manipulandum (Fig. 1B), located at one of the same six sites (Fig. 1C). For convenience, the term target-hand will be used in place of target-thumb. On each trial, the robot manipulandum restricted participants' active movement along a straight constrained path from one of the six starting target-hand locations to one of the five remaining final target-hand locations (dashed slots in Fig. 1C) (See Cressman & Henriques, 2009 for details about active placement of the target-hand). When participants reached to visual-proprioceptive targets, the left thumb was illuminated with three white LEDs for 1 s in the final target-hand location (Fig. 1F), providing visual information about the target-hand prior to the reach on each trial.

The manipulandum was occluded by a tinted translucent Plexiglas platform (on which the transparent touch screen panel was fixed), which was located 2 cm above the height of the target thumb (Fig. 1B) so that once the room lights were turned off, participants were not able to see their target-hand or forearm. A curtain was used to cover the participant's upper arm and shoulder to ensure that no additional visual information concerning hand or arm position could be derived at any point throughout the testing sessions (curtain not shown in Fig. 1). Ambient light from a nearby computer screen allowed participants to see their reaching-hand/arm while reaching.

Conditions

Participants reached to all targets with their right hand. The right reaching-hand began at a comfortable start location on the table to the right of the participants' body, and participants returned their right reaching-hand to this location following each reach. As such, the location that the reaching hand returned to following each reach, although different for each participant, was the same location across all trials for a given participant.

Proprioceptive. In the proprioceptive condition, participants reached to their unseen left target-thumb (Fig. 1E). Each session began with the left target-hand at the bottom-center starting target-hand location (Fig. 1C). Participants first reached to the felt location of the left target-hand in this initial location. A tone signaled contact with the touch screen. Participants then returned their right reaching-hand to the right of their body and actively pushed the robot manipulandum using their left target-hand (guided along a constrained path, Fig. 1C) from this starting location to one of the five remaining target sites. Once the left target-hand reached its final location, a tone prompted participants to once again reach to the left target-hand, making contact with the touch screen (Fig. 1E). Participants then returned their right reaching-hand to the right of their body, and the left target-hand was actively guided to the next final target-hand location. Therefore, the final position of the left target-hand for each trial served as the starting position of the left target-hand for the subsequent trial. To limit proprioceptive drift, the left target-hand began in the bottom-center start location twice as many times as in any other starting position, and the left target-hand was illuminated for 1 s (using three white LEDs) on 50% of these trials (e.g., Brown, Rosenbaum, & Sainburg, 2003; Desmurget, Vindras, Grea, Viviani, & Grafton, 2000; Wann & Ibrahim, 1992). The illumination of the target-hand in this bottom-center location occurred prior to reach onset of the right hand. The left target-hand was not illuminated in any other location in this task. Trials in which the left target-hand was illuminated in the bottom-center start location were not included in the analysis.

Visual-proprioceptive. The same procedure as described for the proprioceptive condition was used in the visual-proprioceptive condition except that participants reached to their left target-hand after it was illuminated (using three white LEDs) for 1 s in its final location (Fig. 1F).

For both proprioceptive and visual-proprioceptive targets, participants made 52 reaches to the left target-hand for each start and final target-hand position combination (35 combinations in total, including those combinations when the target thumb was illuminated in the center-bottom start position). To remove the bias due to proprioception and movement of the right reaching hand, each participant also completed a baseline reaching task at the end of each experimental session. The baseline task consisted of five additional reaches to the continuously visible left target-hand for each start and final target position combination. Horizontal and sagittal reach errors were calculated by taking the reach endpoint, as recorded by the touch screen, for each reaching trial and subtracting this baseline average reach endpoint for each start and target position pairing. Precision (or variability) of reaches was examined by fitting 95% error ellipses around reach endpoints for each start and final target position pairing, for each participant in each condition. The area of the ellipses was used to compare reach precision across the visual, proprioceptive, and visual-proprioceptive target types.

Visual memory. In the visual memory condition, participants reached to the remembered locations of visual targets (red LEDs, shown as open circles above the box in Fig. 1A). A trial began when one of the six red LEDs illuminated for 1 s. When the visual target LED turned off, a tone prompted participants to reach with their right index finger to the remembered location of the visual target (Fig. 1D). A second tone signaled contact with the touch screen and the end of the trial (~3 s in total). Participants then returned the right reaching-hand to a common start location to the right of their body. A new visual target (LED) illuminated to begin the subsequent trial. Participants made 52 reaches to each of the remembered visual target locations (across four sessions). Participants made five baseline reaches to each of the seen target locations at the end of each experimental session (i.e., a reach to each of the LEDs while illuminated). Horizontal and sagittal reach errors were calculated by taking the reach endpoint, as recorded by the touch screen, for each reaching trial, and subtracting the baseline average reach endpoint for each visual target position. Precision was examined by fitting 95% error ellipses around reach endpoints for each final target position pairing, for each participant.

RESULTS

Ellipse Orientation and Target-Hand Movement Path

A custom regression analysis was used to test if ellipse orientation (i.e., the orientation of the major axis of the elliptic fit to reach endpoints) is aligned with the THMD. To begin, we considered two possible limiting relationships between THMD and ellipse orientation. In one case, ellipse orientation could be equal to THMD (possibly plus some small constant offset). This would be equivalent to our hypothesis that the long axis of the endpoint ellipse is aligned with and completely determined by THMD. In another case, ellipse orientation could be completely independent of THMD. We can visualize these two extremes by defining $\Delta\theta$ as the minimum angle between THMD and the major axis of the reach endpoint error ellipse, and θ^{thmd} as the THMD. Thus, $\Delta\theta$ must range between 0° and 90° , and θ^{thmd} ranges between -180° and 180° . In the first limiting case, ellipse orientation equivalent to THMD, $\Delta\theta$ must be a constant function of θ^{thmd} , with a value close to zero. In the second limiting case, ellipse orientation independent of THMD, $\Delta\theta$ must vary as a triangular wave function of θ^{thmd} . An example of this triangular function is depicted by the solid black line in Fig. 2. Specifically, the panels in Fig. 2, A–D, depict the expected difference between THMD (solid black arrows) and ellipse orientation (solid gray line running through

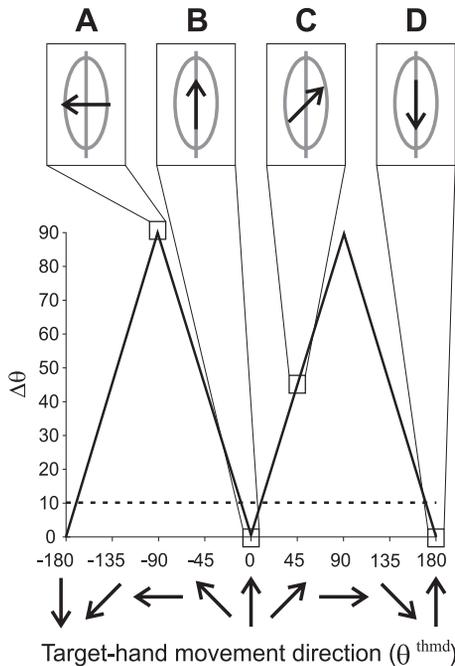


Fig. 2. One way to examine if changes in target-hand movement direction (THMD) result in changes in ellipse orientation is to examine the angular difference between THMD and ellipse orientation ($\Delta\theta$). The solid black line shows the pattern of the differences between THMD and ellipse orientation expected if ellipse orientation is not dependent on THMD. As θ^{thmd} changes from -90 to 0° (A), $\Delta\theta$ (the difference between the solid gray line and solid black arrow) will decrease linearly from 90 to 0° . Next, as θ^{thmd} continues to change to 45° (C), $\Delta\theta$ will grow linearly to 45° (the black arrow is oriented diagonally relative to the gray line in C). Finally, as θ^{thmd} increases to 180° , $\Delta\theta$ once again shrinks down to 0° (the black arrow and gray lines are aligned in D). The horizontal dotted line shows the pattern of ellipse orientations expected if ellipse orientation changes along with THMD. In the case of such a relationship, we can expect a constant difference between THMD and ellipse orientation (i.e., the dotted flat line).

the ellipses) at four THMDs ($\theta^{\text{thmd}} = -90, 0, 45,$ and 180°) assuming no relationship between THMD and ellipse orientation. More specifically, imagine that the major ellipse axis is oriented as in Fig. 2, A-D, for all THMDs. As θ^{thmd} increases from -90 to 0° (Fig. 2, A and B), $\Delta\theta$ [the difference between ellipse orientation (solid gray line) and THMD (solid black arrow)] will decrease linearly from 90 to 0° (the black arrow is perpendicular to ellipse orientation in Fig. 2A, but parallel to ellipse orientation in Fig. 2B). Then, as θ^{thmd} continues increasing to 45° (again with ellipse orientation remaining constant; Fig. 2C), $\Delta\theta$ will grow linearly to 45° (the black arrow is oriented diagonally relative to ellipse orientation in Fig. 2C). Finally, as θ^{thmd} increases to 180° , $\Delta\theta$ once again shrinks down to 0° (the black arrow is parallel with ellipse orientation in Fig. 2D).

The two limiting cases described above, that is, ellipse orientation being equivalent to THMD vs. completely independent of THMD, can be considered limiting cases of the following triangular wave relationship between $\Delta\theta$ and θ^{thmd} :

$$\Delta\theta = T(\theta^{\text{thmd}}; A, \omega, \alpha) = \omega + 2A \left| \frac{\theta^{\text{thmd}} + \alpha}{180} - \left\lfloor \frac{\theta^{\text{thmd}} + \alpha}{180} + \frac{1}{2} \right\rfloor \right|, \quad (1)$$

where ω determines the vertical offset of the function, α is a horizontal offset, A is the amplitude, $\lfloor \dots \rfloor$ indicates absolute

value, and $\lfloor \dots \rfloor$ is the floor function. In the special case of $A = 0$, $\Delta\theta$ is a constant, corresponding to the case in which ellipse orientation is fixed relative to THMD, and therefore completely determined by THMD. The constant angle between ellipse orientation and THMD is ω in this case. Alternatively, if $\omega = 0$, and $A = 90^\circ$, then ellipse orientation is fixed relative to space (this could also mean fixed relative to the body in our case), and is independent of THMD. In this latter case, α simply fixes the value of $\Delta\theta$ at one specific value of θ^{thmd} (e.g., $\alpha = 0$ implies ellipse alignment with THMD at $\theta^{\text{thmd}} = 180$ or 0°).

To determine how THMD affected ellipse orientation in our experiment, we assumed that the probability of participant s producing a given value of $\Delta\theta$ on trial i could be written as

$$P(\Delta\theta_{s,i}) = \phi_F^{[0,90]}[\Delta\theta_{s,i}T(\theta_{s,i}^{\text{thmd}}, A_s, \omega_s, \alpha_s), \sigma_s], \quad (2)$$

where T is the triangular wave function from Eq. 1, and $\phi_F^{[0,90]}$ is a doubly folded normal probability density function (pdf) that is defined over the range $[0^\circ, 90^\circ]$ as

$$\phi_F^{[0,90]}(x; \mu, \sigma) = \phi(x; \mu, \sigma) + \phi(180 - x; \mu, \sigma) + \phi(-x; \mu, \sigma), \quad (3)$$

with ϕ being the normal pdf. Values of A_s , ω_s , α_s , and σ_s were obtained for each participant in both the proprioceptive and visual-proprioceptive experiments using standard maximum-likelihood procedures. Likelihood ratio tests were used to compare A_s with zero (recall $A_s = 0^\circ$ implies ellipse orientation is determined fully by THMD) and 90° ($A_s = 90^\circ$ implies ellipse orientation is completely independent of THMD) separately for each participant. We corrected P values using the stepwise Holm-Bonferroni procedure.

Motivated by the within-participant analysis described above, we also performed an across-participants analysis to determine what our data should have looked like if, indeed, the null hypothesis that $A_s = 90^\circ$ (no dependence of ellipse orientation on THMD) were true. More specifically, for each participant, we used maximum-likelihood procedures to determine the remaining model parameters in Eq. 2 when A_s was forced to be 90° . We then used these restricted models to simulate participant responses for 10,000 repetitions each of the proprioceptive and visual-proprioceptive experiments. For each of these simulated experiments, we calculated the average value of A_s across participants that would have occurred if we had fit Eq. 2 to the simulated data. This led to a distribution of average A_s values that would have been expected if the null hypothesis ($A_s = 90^\circ$) were in fact true. We then compared the average A_s values for each experimental condition calculated from our data with these simulated distributions.

Figure 3, A and B, shows the model-derived $\Delta\theta$ values (calculated by using maximum-likelihood parameters from Eq. 2 in Eq. 1) for each THMD for each participant for proprioceptive (A) and visual-proprioceptive (B) targets. In Fig. 3C, the average model-derived (solid lines) and observed $\Delta\theta$ values (data points with SE of the mean bars) across participants for each THMD are shown. As described below, the observed data for both conditions closely approximated the $A_s = 90^\circ$ null hypothesis model, suggesting strongly that ellipse orientation is not related to THMD.

For proprioceptive targets, Holm-Bonferroni-corrected likelihood-ratio tests indicated that 7 out of 10 participants had A_s values that were significantly greater than zero, suggesting that,

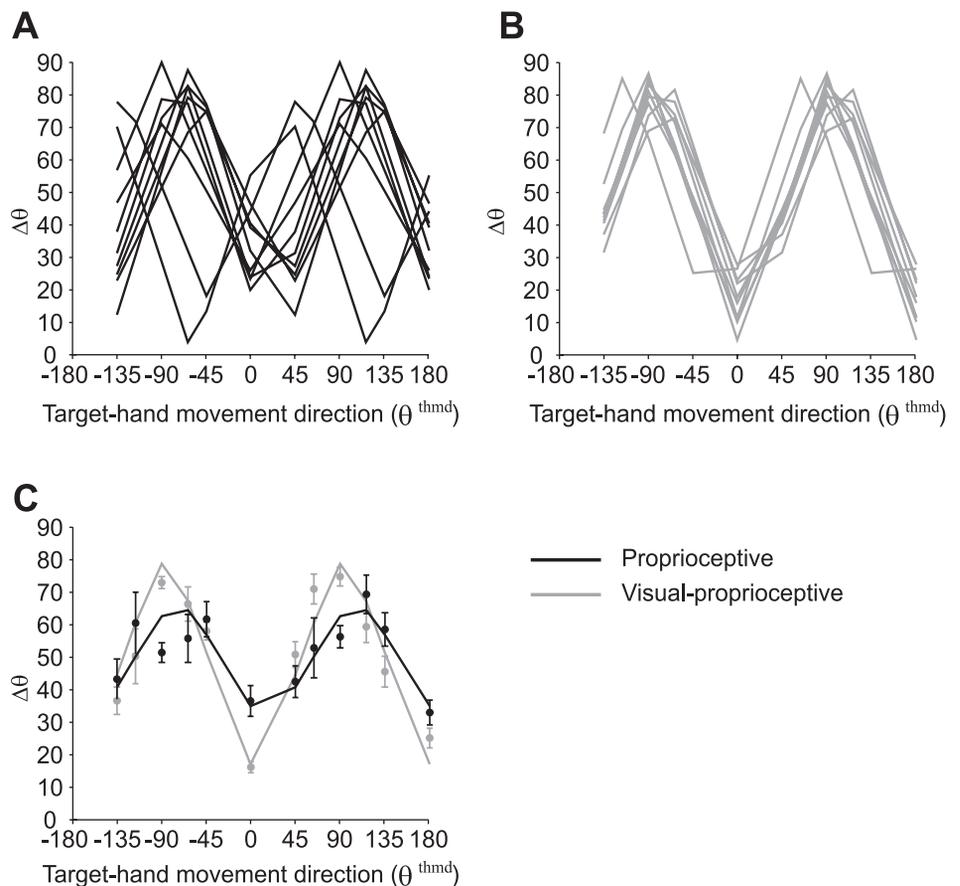


Fig. 3. The model-derived difference between THMD and ellipse orientation ($\Delta\theta$) for each participant for proprioceptive (A) and visual-proprioceptive targets (B). The average model-derived difference between THMD and ellipse orientation for both target types is shown in C. The data points with SE of the mean bars show the observed data.

for most participants, ellipse orientation was not completely determined by THMD. In contrast, A_s values did not differ significantly from 90° for any participant. Under the null hypothesis that $A_s = 90^\circ$ for all participants (space/body-fixed ellipses independent of THMD), our simulated data produced a distribution of average A_s values with a mean of 71.6° {95% confidence interval (CI): [61.8, 80.1]}. The average value of A_s determined from fitting Eq. 2 to our actual data aligned almost perfectly with the mean of this distribution at 72.2° . Ellipse area also did not vary with THMD [$F(11,99) = 1.35$, $P = 0.29$]. Although there was less variability across participants in the visual-proprioceptive condition, similar results were found. Holm-Bonferroni-corrected likelihood-ratio tests indicated A_s values that were significantly greater than zero for all 10 participants, suggesting that ellipse orientation was not completely determined by THMD. Once again, A_s values did not differ significantly from 90° for any participant. For visual-proprioceptive targets, under the null hypothesis that $A_s = 90^\circ$ for all participants (space/body-fixed ellipses independent of THMD), our simulated data produced a distribution of average A_s values with a mean of 80.9° (95% CI: [75.1, 85.7]). The average value of A_s determined from fitting Eq. 2 to our actual data aligned almost perfectly with the mean of this distribution at 78.0° . Once again, ellipse area also did not vary with THMD for visual-proprioceptive targets [$F(11,99) = 1.38$, $P = 0.28$].

Overall, the orientation of the major axis of the elliptic fit (and ellipse area) for proprioceptive and visual-proprioceptive targets does not appear to be associated with the movement direction of that target-hand. We therefore compared the orientation of the major axis of the elliptic fit across starting and

final target-hand locations, separately, using the “circular” package (Jammalamadaka & SenGupta, 2001) in R (version 2.10.0; R Development Core Team, 2009). Due to a violation of von Misesness, a circular analog of linear normality, Watson two-sample tests of homogeneity of the distributions (W; nonparametric analog of the Mann-Whitney U -test data) (Mardia & Jupp, 2000) were used to compare ellipse orientations across starting and final target positions (divided into left, center and right, and top and bottom areas of space; an approximation to Bonferroni correction was used to control for multiple comparisons). Because ellipse orientations did not differ across starting target-hand locations, regardless of final target-hand location or target type (all P values > 0.05), Fig. 4 shows ellipse orientations for each participant and final target-hand location for visual (A), proprioceptive (B), and visual-proprioceptive (C) targets. The lengths of the lines are scaled by the ratio between the major and minor axes of the ellipses, and the solid black circle depicts a one-to-one ratio between the major and minor axes of the ellipse (i.e., a circle). Because the lengths of the lines extend past the perimeter of the solid black circle (greater than a one-to-one ratio), the ellipses are elliptical and not circular. Additionally, we compared the average major and minor axes of the ellipses for each target location for each target type (visual, proprioceptive, and visual-proprioceptive). We found that, regardless of final target location, the major axes of the ellipses are significantly larger than the minor axes of the ellipses (all $P < \text{Bonferroni-Holm corrected } P$ value).

Overall, ellipses were oriented more upright (along the sagittal axis) than horizontally for both unimodal and bimodal targets [visual average orientation (AO) = 20.21° right; pro-

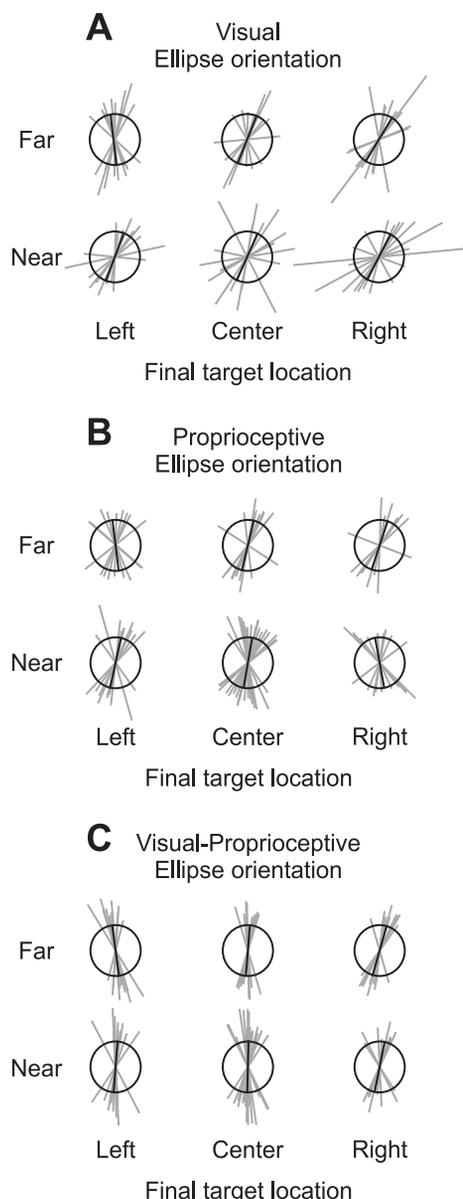


Fig. 4. Ellipse orientations for each participant (gray lines) and final target location for the visual (A), proprioceptive (B), and visual-proprioceptive (C) conditions. The length of each line is scaled by the ratio between the major and minor axes of the ellipse. The diameter of the solid black circle depicts a one-to-one ratio between the major and minor axes of the ellipse. The solid black line is the mean ellipse orientation.

proprioceptive AO = 6.51° right; visual-proprioceptive AO = 3.90° right], but more clockwise for visual and proprioceptive targets (Fig. 4, A and B) than visual-proprioceptive targets [$W = 1.08, P < 0.0167$ (corrected P value) and $W = 2.90, P < 0.0167$; Fig. 4C]. Ellipse orientations also differed across final target-hand locations for proprioceptive (Fig. 4B) and visual-proprioceptive (Fig. 4C) targets, but not for visual targets (Fig. 4A). Specifically, proprioceptive and visual-proprioceptive ellipses were both oriented more clockwise for right final target locations than left final target locations (proprioceptive: $W = 0.46, P < 0.0167$; visual-proprioceptive: $W = 1.37, P < 0.0167$) although proprioceptive ellipses were most clockwise for central final target positions ($P < 0.0167$ for comparisons with left and right final target locations). Proprioceptive el-

lipses were also more clockwise for far final proprioceptive target locations than near final target locations ($W = 0.392, P < 0.025$, corrected P value), but visual-proprioceptive ellipses did not differ across near and far final target locations ($P > 0.025$). In summary, we found that ellipse orientation is not associated with the movement direction of the target hand and that ellipse orientations were overall oriented along body midline with small but significant differences across final target locations. These results suggest that some of the observed errors could be anchored to the body, shoulder, or hand.

Visual and Proprioceptive Integration

While the result that localization was independent of the movement of the target-hand ruled out the possibility of vision playing a role in this (nonexistent) effect, it was still possible that vision could lead to more precise localization of bimodal targets. Many studies of cue-combination have found that two or more noisy estimates of a stimulus property (e.g., target location) are combined by the brain as an MLE (e.g., Ernst & Banks, 2002; Kording & Wolpert, 2004; Snijders et al. 2007; Sober & Sabes, 2005; van Beers et al. 1996, 1999). Within this framework, the variability of a combined (bimodal in our case) estimate can be predicted in a straightforward manner from the individual variabilities measured when responses are made based on the individual cues in isolation (van Beers et al., 1999). In our case, the predicted covariance matrix for two-dimensional reaches made with proprioceptive and visual information can be determined from the observed covariance matrices for reaches made based on proprioception (σ_p) or vision (σ_v) alone as follows:

$$\sigma_{vp} = (\sigma_v^{-1} + \sigma_p^{-1})^{-1} \quad (4)$$

Based upon the eigenvalues of this combined covariance matrix, we predicted the areas that the standard ellipses fitted to our actual bimodal reaching data should take. The light gray bars in Fig. 5 show this average predicted ellipse area for visual-proprioceptive targets, for each participant, as well as the average observed ellipse areas for each target type for each participant. We found that the average observed visual-propri-

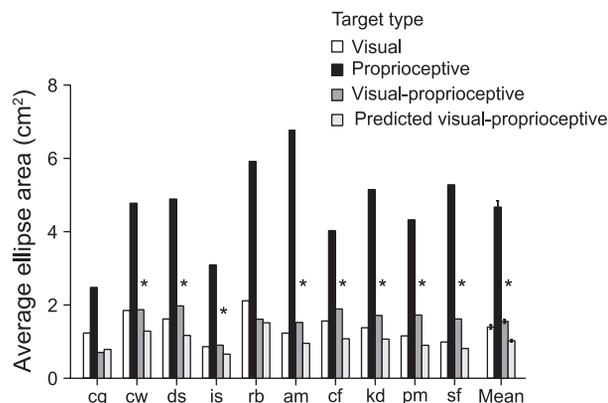


Fig. 5. Average observed ellipse areas (cm²) for each participant and target type (white, visual; black, proprioceptive; dark gray, visual-proprioceptive). The average predicted ellipse area for visual-proprioceptive targets, expected if vision and proprioception are being combined based on a maximum-likelihood estimate (MLE), are shown in light gray. SE of the mean is shown for the average ellipse area across participants. *Significant difference between observed and predicted ellipse area in the visual-proprioceptive condition (at the $\alpha < 0.05$ level).

ceptive ellipse area (dark gray bars) is greater (1.55 cm^2) than that predicted (1.02 cm^2) if vision and proprioception were being combined by the brain as an MLE [light gray bars; $F(1,9) = 25.91, P < 0.05$]. As indicated by the asterisks, 8 out of 10 participants showed this pattern (all $P < 0.05$), whereas two participants showed no difference between the observed and predicted visual-proprioceptive ellipse areas ($P = 0.35$ and 0.48 , respectively). This result suggests that vision and proprioception are not being integrated based on an MLE in this task.

DISCUSSION

We examined if changes in target movement direction would affect reaches to proprioceptive and visual-proprioceptive targets and if visual and proprioceptive information about target position are being integrated in a statistically optimal way. We found that ellipse orientation did not vary with THMD but instead appeared to be anchored to some other reference (e.g., body or space). Overall, the observed ellipse area for visual-proprioceptive targets did not suggest that vision and proprioception are being combined based on an MLE in this task.

Target-Hand Movement Direction

Previous research has suggested that the movement direction of a proprioceptive target may affect reaches to that target in its final location. For example, both starting (e.g., Imanaka, 1989; Imanaka & Abernethy, 1992a, 1992b) and final (Adamovich et al., 1998; van Beers et al., 1998, 1999) proprioceptive target locations, separately, have been shown to affect reaches. Therefore, we asked if various combinations of starting and final target-hand positions also result in systematic changes to reach endpoints. However, we did not find that the direction of target-hand movement (i.e., the interaction between start and final target-hand location) affected reach endpoints in our tasks.

We did find that ellipse orientation varied with final target-hand location. Specifically, we found that reaches made with the right reaching hand to far rightward target locations were deviated more clockwise than reaches to near rightward or leftward target locations (final targets between 23 and 33 cm from the body, located 10 cm to the left or right of body midline). This result is consistent with previous reach paradigms that have found larger reach errors for far and/or rightward or leftward target locations (using the right hand as the reaching hand). For example, previous work in our laboratory (Jones, Cressman, & Henriques, 2010) also found the largest reach errors (right hand reaching) for rightward targets that were farthest from the body (60° clockwise relative to the cyclopean eye). Additionally, Baud Bovy and Viviani (1998) found larger absolute reach errors for right final target locations (when compared with left final target locations), when participants reached with the right hand to the felt position of the left hand (between 30 and 40 cm from the body). Similarly, Chapman, Heath, Westwood, and Roy (2001) found larger errors for right final target locations than targets along body midline (final target locations between 35 and 45 cm from the body) when participants reproduced final target location using a stylus. These researchers also found larger reach errors for left target locations compared with target locations along body midline. These results suggest that participants may be less accurate when localizing a hand on one or both sides of the body or farther in front of the body overall. This seems

appropriate given that many activities that require proprioception involve the manipulation of objects or activities using the hands in a central location (around body midline) that is relatively close to the body (around 20 cm). However, this idea cannot fully account for reach errors across space. For example, Monaco et al. (2010) found no differences in reach accuracy across any of their eight actively or passively placed final proprioceptive targets (arranged radially, 20 cm diameter, centered on body midline, between 15 and 35 cm from the body) and neither did Crowe, Keessen, Kuus, van Vliet, and Zegeling (1987) when comparing reaches across eight final target locations between 30 and 50 cm from the body (arranged in three lines, along body midline, or to left or right of body midline). Hence, while we might be less accurate when localizing a hand that is farther from body midline and farther from the body overall, it is likely that this ability may interact with the context or task.

Combining Vision and Proprioception

Research has shown that redundant sources of sensory information about object properties (Ernst & Banks, 2002) or the location of a reaching hand (Kording & Wolpert, 2004; Sober & Sabes, 2005) can be combined in a statistically optimal manner based on the reliability of the available sensory sources. However, few studies have examined how multiple sources of sensory information about a reach target's final location are integrated (Block & Bastian, 2010; Byrne, Cappadocia, & Crawford, 2010; Byrne & Crawford, 2010; van Beers et al., 1996, 1999; Vaziri, Diedrichsen, & Shadmehr, 2006). In our study, the variability of reaches made to visual-proprioceptive targets was not consistent with that predicted if vision and proprioception were being integrated by the CNS using an MLE model. This suggests that, while visual and proprioceptive information could be integrated in this task, this integration does not appear to be in a way that is strictly based on weighting sources of information as a function of their reliability.

For example, other studies have suggested that probabilistic/Bayesian integration can be dependent on the stages of motor planning, on the context, on the task, or on properties of the stimulus itself (Burns & Blohm, 2010; Byrne & Crawford, 2010; Ernst & Bulthoff, 2004; Knill, 2005; Reuschel et al., 2010; Sober & Sabes, 2005). Knill (2005) found that the weighting of sensory information differed depending on whether the task involved perceptually judging the slant of an object or reaching to the object. In contrast to van Beers et al. (1999) who presented their participants with visual and bimodal targets that were continuously "lit" during reaches with the unseen opposite arm, visual information about target location in our bimodal task was remembered. Perhaps remembered visual information is integrated in a different way overall than what is expected from current visual information. We also used a robot manipulandum for placement of the target-hand, perhaps changing the value assigned to or the way proprioceptive input is used. van Beers et al. (1999) asked their participants to move their target-hand to a position as close to the final target location as possible and then touch the underside of the experimental set up until they found a tactile marker. Previous work in our laboratory (Jones & Henriques, 2010), a reaching task with gaze deviated, using a robot manipulandum for proprioceptive target placement also did not find support

for Bayesian integration of remembered visual information with online or remembered proprioceptive information, nor did previous studies that have employed precise placement of the target-hand using a mechanical apparatus (Monaco et al., 2010; Reuschel, Rosler, Henriques, & Fiehler, 2011). Last, in our study, the last target site was the start of the path to the next target site. This makes it possible that the brain was using proprioceptive information about the target movement to update a (mostly) visual representation of the previous hand-target location (and this was then “reinforced” or recalibrated by having the hand-target light up briefly) (Ren & Crawford, 2009). This form of proprioceptive updating combined with visual representations of target location may be difficult to detect using our task.

In summary, our study systematically examines the effect of movement direction of a proprioceptive target (and thus starting and final target-hand location) on the orientation of the elliptic fit to reach endpoints. We found that THMD did not affect reach endpoints but that ellipse orientations varied with final target-hand locations. However, our results suggest that cue combination based on MLE is not occurring in this task. The use of remembered visual information and placement of the proprioceptive target using a robot manipulandum may have contributed to this result.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: S.A.H.J. and D.Y.P.H. conception and design of research; S.A.H.J. performed experiments; S.A.H.J. and P.A.B. analyzed data; S.A.H.J. and D.Y.P.H. interpreted results of experiments; S.A.H.J. prepared figures; S.A.H.J. drafted manuscript; S.A.H.J., P.A.B., K.F., and D.Y.P.H. edited and revised manuscript; S.A.H.J., P.A.B., K.F., and D.Y.P.H. approved final version of manuscript.

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