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When more is less: Increasing allocentric visual information can switch visual–proprioceptive combination from an optimal to sub-optimal process

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ABSTRACT

When reaching for an object in the environment, the brain often has access to multiple independent estimates of that object's location. For example, if someone places their coffee cup on a table, then later they know where it is because they see it, but also because they remember how their reaching limb was oriented when they placed the cup. Intuitively, one would expect more accurate reaches if *either* of these estimates were improved (e.g., if a light were turned on so the cup were more visible). It is now well-established that the brain tends to combine two or more estimates about the same stimulus as a maximum-likelihood estimator (MLE), which is the best thing to do when estimates are unbiased. Even in the presence of small biases, relying on the MLE rule is still often better than choosing a single estimate. For this work, we designed a reaching task in which human subjects could integrate proprioceptive and allocentric (landmark-relative) visual information to reach for a remembered target. Even though both of these modalities contain some level of bias, we demonstrate via simulation that our subjects should use an MLE rule in preference to relying on one modality or the other in isolation. Furthermore, we show that when visual information is poor, subjects do, indeed, combine information in this way. However, when we improve the quality of visual information, subjects counter-intuitively switch to a sub-optimal strategy that occasionally includes reliance on a single modality.

1. Introduction

When reaching to an object in the environment, healthy individuals usually have access to multiple redundant sources of sensory information upon which to base their action. The most straightforward example is direct vision of the object, which we refer to as *egocentric* visual information because it provides knowledge of the target object's spatial location relative to a part of the self. Another cue to a target object's location comes from visual landmarks. In principle, knowing a target location relative to some other landmark in the visual field provides additional indirect information about that location relative to the self. This latter type of information, known as *allocentric* visual information, has been shown clearly to improve reaches to actual and remembered target locations (Byrne, Cappadocia, & Crawford, 2010; Krigolson, Clark, Heath, & Binsted, 2007; Krigolson & Heath, 2004; Obhi & Goodale, 2005; Redon & Hay, 2005), likely via combination with egocentric visual information (Byrne & Crawford, 2010). Although numerous studies have investigated how egocentric visual information combines with information from other sensory modalities (e.g., for vision–audition see Battaglia, Jacobs, & Aslin, 2003; or for vision–proprioception see van Beers, Sittig, & Gon, 1999), the interaction of allocentric visual information with these modalities remains unexplored. Here we are interested in how the brain combines allocentric visual information with proprioceptive information about a target location for the purposes of reach.

It is not known why allocentric information is relied upon even in the presence of direct, egocentric visual information about a clearly visible target. Perhaps the added precision in reach is necessary in extreme circumstances (e.g., one cannot afford to miss the handrail if they begin to fall down the stairs), or for efficiency in repetitive tasks (e.g., more calories collected when picking berries for many hours). However, given that the frequent movements of our gaze often shifts the targets of action into the visual periphery (e.g., Hayhoe, Shrivastava, Mruczek, & Pelz, 2003), such reliance makes more sense. For example, when a subject foveates a reach target and then looks away before reach initiation, they must complete the reach using either low quality peripheral visual information, memory, or both. Indeed, it has been shown that remembered egocentric visual information is

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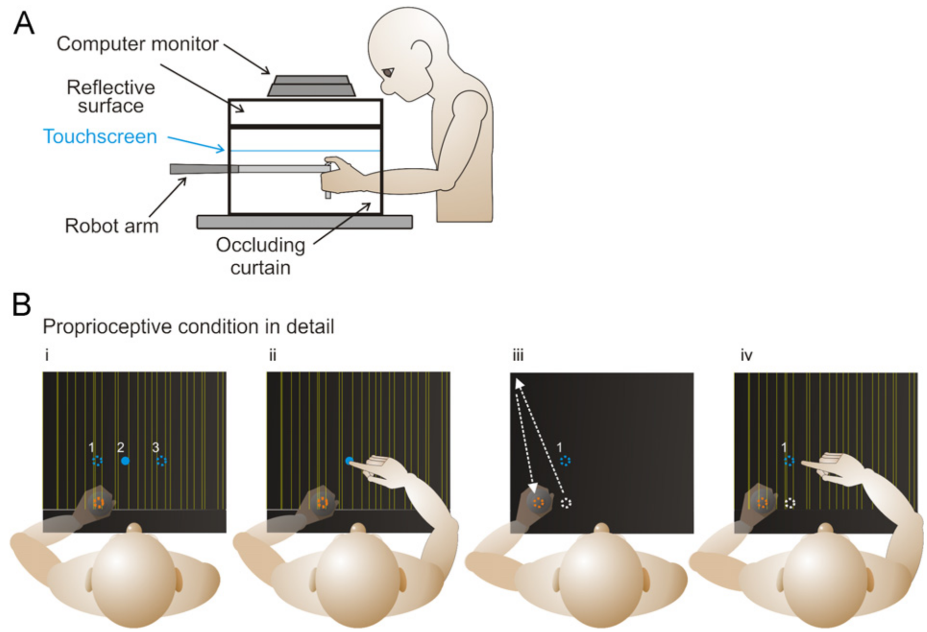

Fig. 1. (A) Side view of the experimental setup. Participants gripped the handle of a robot manipulandum with their unseen left hand. Visual stimuli were projected by an LCD monitor onto a reflective surface so as to appear at the same height as the unseen left hand. At encoding/response, subjects reached to the visible initial/inferred final target location with their illuminated right index finger. A horizontal touch screen panel recorded all reach endpoint locations. (B) Detail of proprioceptive condition. In panel (i), the randomly spaced yellow line background is shown with no embedded visual landmark, along with the three possible reach target locations, labeled 1, 2 and 3. In this case the subject sees a target at *pos2*. The orange dashed circle represents the location of the subject's left hand. In panel ii the subject performs an encoding reach and returns the reaching hand to their chest. In panel (iii), the yellow lines and target have disappeared and the robot moves the left hand to a new location that is the same distance from its original location as *pos1* is from *pos2*. In panel iv, the yellow lines reappear and the subject must reach to the new, left-hand relative target location. Unbeknownst to the subject, a perfect reach would bring their fingertip to *pos1*.

combined with lower quality peripheral visual information to improve reaches (Brouwer & Knill, 2009). Given that reaches to remembered visual targets based purely on allocentric visual information are as precise as reaches based purely on egocentric visual information (e.g., Byrne & Crawford, 2010; Chen, Byrne, & Crawford, 2011), it seems likely that remembered allocentric visual information could play a similarly important role, especially if landmarks remain relatively near the fovea.

There are a variety of circumstances in which allocentric visual information could be combined with sensory information from other modalities in order to facilitate goal-directed action. As a clear example involving *proprioception*, consider driving along a busy street in a car with a manual transmission. At some point the driver must shift gears, but cannot see the gearshift clearly unless he or she takes their eyes off the road (the layout of PB's car is like this). Since the driver has previously seen interior views of the car, and has seen where the gearshift is relative to the dashboard, the steering wheel, etc., he or she can use allocentric visual information from these still visible landmarks to estimate the gearshift location. Moreover, just as visual memory allows one to reach for previously seen target objects, numerous studies have shown that subjects are able to remember and reproduce accurately previous joint angle configurations purely from proprioceptive memory (e.g., Chapman, Heath, Westwood, & Roy, 2001; Darling & Miller, 1995; Goble & Brown, 2008; Goble, Mousigian, & Brown, 2012; Goble, Noble, & Brown, 2010; Jones & Henriques, 2010; Laabs, 1973; Marteniu, 1973). Therefore, since the driver has likely changed gears in the recent past, he or she can replicate the previous joint configuration to bring their arm within reach of the gearshift. Thus, allocentric visual information and proprioception provide two redundant, but independent cues to the gearshift location.

Studies of multisensory integration have demonstrated that the brain usually combines two (or more) independent, unbiased estimates using an optimal linear combination (Battaglia et al., 2003; Byrne & Crawford, 2010; Deneve & Pouget, 2004; Ernst & Banks, 2002; Knill, 2007; Niemeier, Crawford, & Tweed, 2003; Reuschel, Drewing, Henriques, Rosler, & Fiehler, 2010; Scarfe & Hibbard, 2011; van Beers et al., 1999; Vaziri, Diedrichsen, & Shadmehr, 2006) that is unbiased and minimum-variance. In cases where individual cues are biased, the brain still often uses the same maximum-likelihood estimator (MLE) combination rule (Scarfe & Hibbard, 2011), possibly because the combination is still minimum-variance. In order to investigate interactions between proprioceptive and allocentric visual information, we employed a reaching task in which subjects had to rely on estimates of target location derived from a visual landmark (allocentric vision) and/or proprioception in order to respond appropriately. With this task we confirmed that the brain combines remembered proprioceptive and allocentric visual information using an MLE rule, but *only* when visual information is relatively poor. Surprisingly, we confirmed via simulation that increasing the quality of visual landmarks actually causes subjects in our task to switch to a sub-optimal combination strategy.

2. Methods

In this study subjects completed three experimental conditions. In the *proprioceptive condition* (shown in detail in Fig. 1B), subjects had to encode the location of a reach target *relative* to their unseen left hand (i.e., the target was not any part of the left hand, nor at the same location as the left hand, but the left hand served as a sort of landmark), while in the *visual condition*, subjects had to encode the target location *relative* to a visual landmark. In both conditions, subjects then had to reach to the left hand/visual landmark-relative location of the remembered target after the left hand/visual landmark had shifted to a new location. By examining reaching performance in these single cue control conditions, we were able to predict subjects' performance in a *combined condition* in which both sources of information were available.

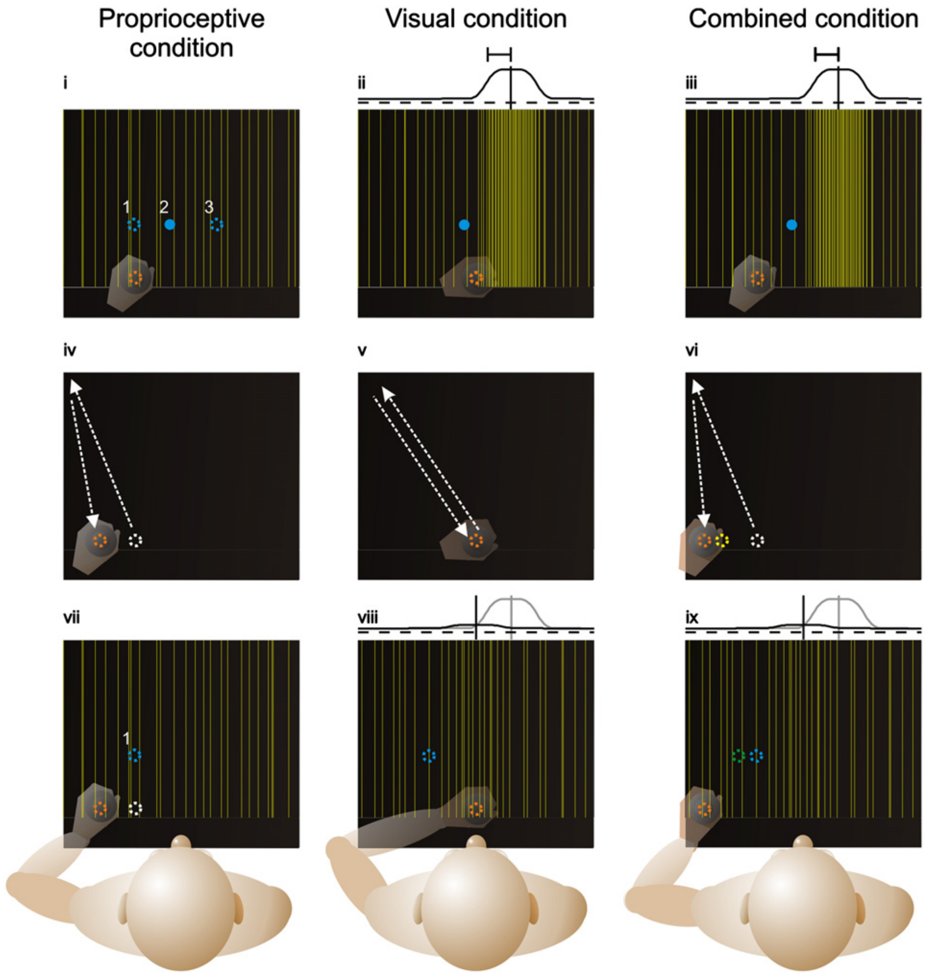

Fig. 2. Paradigms. *Left column*: proprioceptive control condition. Identical to Fig. 1B, but with reaches not shown. *Middle column*: visual control condition. This condition is similar to the proprioceptive condition except that a local increase in line density serves as a visual landmark. In panel (ii), a highly visible landmark is presented along with the reach target at *pos2*, while the subject's left hand is held at midline regardless of target location. The curve above the panel indicates relative line density, while the horizontal bar indicates the range over which the landmark could be centered for a target at this location. In panel (v), the visual stimuli disappear and the robot generates an irrelevant movement of the left hand away from and back to its initial location. In panel (viii), the visual landmarks reappear at a new location, but with a degraded signal-to-noise ratio (the gray curve represents the original line density, while the black curve represents the degraded density). The subject must reach to the correct landmark-relative target location, *pos1* in this case. *Right column*: combined condition. The top panel (iii) is simply the summation of the control conditions: both the left hand and visual landmark are available for a target at *pos2*. In panel vi, the robot moves the left hand to a new location that is 0.88 cm further to the left than the position that would be consistent with the target moving to *pos1* (latter position indicated by the yellow dashed circle). In panel (ix), the degraded visual landmark reappears at a location exactly consistent with the target having been moved to *pos1* (blue dashed circle). When the subject reaches, they should reach to *pos1* only if they are relying entirely on vision, but further to the left of *pos1* if they are relying on a combination of proprioceptive and visual information. They should reach to the green dashed circle if they are relying purely on proprioception.

2.1. Subjects

Twelve right-handed young adults (mean age = 29, SD = 6.1, 6 female) were recruited from York University and volunteered to participate in the experiments described below. Subjects were pre-screened verbally for self-reported handedness and any history of visual, neurological, and/or motor dysfunction. All subjects provided informed consent in accordance with the ethical guidelines set by the York University Human Participants Review Sub-Committee.

2.2. Apparatus

A side view of the set up is provided in Fig. 1A. Subjects were seated in a height-adjustable chair so that they could comfortably see and reach to all visually-presented targets. These targets, as well as visual landmarks (see below), were projected by an LCD monitor (Samsung 510N, refresh rate 72 Hz, screen width of 30 cm, set to a resolution of 1024 × 768 pixels) placed face-down on an acrylic glass tray 13 cm above a horizontally-oriented, semi-opaque reflective surface. When subjects looked at this reflecting surface, the visual stimuli appeared to lie in a horizontal plane 13 cm below it, at exactly the height of a horizontally-oriented, pressure-sensitive touch screen panel (Keytec Inc., Garland, TX; resolution of 4096 × 4096 pixels, 43 cm (length) × 33 cm (width), 3 mm thick), which was used to record the position of the right index finger when reaching to a remembered target location. In all conditions, subjects grasped the vertical handle of a two-joint robot manipulandum mounted in the horizontal plane (Interactive Motion Technologies) immediately below the touch screen with their left hand. More specifically, the subject would place their left thumb on a nut that secures the vertical handle to the robot arm. In the proprioceptive/combined conditions, subjects were instructed to remember a target location *relative* to this thumb (see below), although for simplicity we will refer here only to their "left hand". The room lights were dimmed and subjects' view of their left hand was blocked by the reflective surface and a black cloth draped between the experimental set up and the subjects' shoulders. A white LED was affixed to the subject's right index finger and illuminated only during reach movements in order to provide visual feedback from the reaching hand through the semi-opaque reflective surface.

2.3. Visual stimuli

On any given trial the subject's task was to remember the location of a visually-presented reach target relative to either their left hand or to a visual landmark, or both. The visual stimuli (target and visual landmark) were presented on an otherwise black background. The target was a blue disc with a diameter of 1.17 cm (40 pixels) situated at one of three possible locations: 6 or 1.5 cm to the left of the subject's midline, or 4.5 cm to the right (see Fig. 1B-i). These will be referred to as *pos1, 2* and *3*, respectively. Subjects were never informed that there were only three possible target locations and often expressed surprise when informed of this at the end of the experiment. Visual landmarks were generated in the visual and combined conditions by locally varying the horizontal density of a set of randomly-spaced yellow lines (see Fig. 2ii and iii). During target presentation, the peak density of these lines was very high relative to the background density so that the visual landmark was clearly visible and the target's landmark-relative location could be encoded easily. However, during the test phase, when the landmark appeared at a new location and the subject had to reach to the new landmark-relative target location, the peak density was substantially lower (see Fig. 2viii and ix). For consistency, lines were also presented at these two time epochs in the proprioceptive condition, but in this case the lines were uniformly distributed (i.e., no embedded visual landmark). More specifically, the horizontal density of lines was chosen to be

$$D(x) = \frac{1}{30}\left(25 + A\,\exp\left\{-\frac{(x-x_l)^4}{2(3)^4}\right\}\right), \tag{1}$$

where $D(x)$ is the density of lines in lines/cm at horizontal position x, A is the landmark amplitude ($A=200$ for initial landmark/target presentation, $A=12.5$ for low-reliability visual landmarks at test, $A=25$ for high-reliability visual landmarks at test, and $A=0$ for no landmark), x_l is the location of the landmark peak, and x is horizontal screen location in cm. The peak of the visual landmark was chosen randomly on a trial-by-trial basis to be between 3 and 6 cm to the right of the current target location. Each of the lines comprising the visual landmark spanned the entire depth dimension (normally this would be the vertical dimension if the screen were upright) of the LCD screen and had a width of 2 pixels.

2.4. Procedure

2.4.1. Overview

In all three experimental conditions (shown in the three columns of Fig. 2) subjects had to encode the position of a reach target *relative* to some other location—either their left hand in the proprioceptive condition (Fig. 1B and the left column of Fig. 2), or a visual landmark (described above) in the visual condition (center column of Fig. 2). In the combined condition (right column of Fig. 2), both types of encoding could be useful because the left hand and the visual landmark were present and were informative about final target location. Following encoding, the left hand/visual landmark would be shifted to a new location and subjects were required to indicate via reach with their right index finger where the now invisible target would be relative to the shifted left hand/visual landmark. All three conditions began with subjects viewing and reaching to touch the visible target at a location randomly selected from *pos1, 2,* or *3*. (row 1 of Fig. 2). After encoding target location relative to the appropriate entity (left hand, visual landmark, or both), the target would disappear (row 2 of Fig. 2) along with the visual landmark in the visual and combined conditions, and the left hand would be passively shifted to a new location in the proprioceptive and combined conditions (or just back to the midline in the visual condition). Shortly after target disappearance, the visual landmark would reappear at a new location in the visual and combined conditions. During the test phase (row 3 of Fig. 2) subjects had to reach to the updated left hand/visual landmark-relative location of the target (row 3).

2.4.2. Proprioceptive condition

In the proprioceptive condition (Fig. 1B and left column of Fig. 2) subjects were able to encode the location of a target relative to their left hand, allowing us to measure the reliability and biases associated with purely proprioceptive encoding of location. Each trial began with the placement of the left hand relative to one of the three randomly-selected target locations (*pos1, 2* or *3*). Placement of the left hand was accomplished using a robot manipulandum to passively move it to a location 4.4 cm (150 pixels) to the left of the target site on 90% of trials and 4.4 cm to the right on 10% of trials. These latter 10% of trials were intended to ensure subjects did not generate some default encoding and they were not included in final analysis. In all cases the final left hand location was 7 cm closer in depth than the selected target location. This relatively large distance between presented target and the left hand in the irrelevant depth direction was employed in order to ensure that subjects did not unintentionally come to believe that the target was located directly above their hand, as was the case in previous experimental studies that some of our subjects might have completed.

Once the manipulandum came to rest at the appropriate left hand location, the reach target was displayed and the background of randomly spaced vertical yellow lines appeared, but without any embedded visual landmark (i.e., A was set to zero in Eq. (1)). The subject then used their right index finger to reach to this visual target and, thereby, was provided an opportunity for direct proprioceptive encoding of the target location *relative* to the unseen left hand; subjects were asked to remember this relative location between target and left hand. During the entirety of this encoding reach both the target and reaching finger were visible, and the subject had as much time as they liked to complete the reach. Therefore, any representational variability resulting from inaccurate reaches should be negligible. At the end of any reach, the subject was instructed to bring their reaching hand to the same location against their chest. Subjects were monitored from time-to-time to make sure they were complying with this instruction.

After completion of the encoding reach, all visual stimuli disappeared and the robot manipulandum passively moved the left hand to a remote intermediate location approximately 15 cm further in depth and 15 cm to the left of the body midline (depicted in Fig. 2iv) before returning it to a new, final location. Once the manipulandum came to rest at this final location, the background of randomly-spaced yellow lines reappeared without any embedded visual landmark and the subject was required to reach to the new, non-visible left hand-relative target location (i.e., the location the target would take if it had shifted with the left hand). The reach endpoint was recorded when the subject pressed the horizontal touch screen at this location. Importantly, subjects were instructed to reach as accurately as possible, with no movement time constraints. With this instruction, subjects should have been able to move their reaching finger arbitrarily close to whatever location matched their internal representation of proprioceptively-defined target location. Subjects received no feedback about their accuracy.

In order to simplify analysis, and to control for any possible hysteresis effects without unduly increasing the number of trials necessary, the final left hand location was always chosen so that a perfect reach to the left hand-relative target location would bring the right index finger to the unselected target location immediately to the left of the initial target location (i.e., *pos3*→*pos2, pos2*→*pos1, pos1*→*pos3*). For example, if the subject touched the presented reach target at *pos 3*, then the appropriate reaching response when the left hand was at its final location would be to *pos 2*. Again, the existence of the three discrete target locations was not known by subjects so they should simply have encoded the location of the target relative to their unseen left hand and reached to the new location based on where they thought the target would be if it had shifted with their left hand.

2.4.3. Visual condition

In the visual condition (center column of Fig. 2) subjects were able to encode the location of a target relative to a visual landmark, allowing us to measure the reliability and biases associated with this type of landmark-relative representation of location. In order to maintain consistency with the proprioceptive condition, the trial began with the manipulandum moving the left hand, this time to an irrelevant location horizontally aligned with the midline. Once the manipulandum came to rest, one of the three reach targets was presented along with a background of randomly spaced vertical yellow lines with a clearly visible landmark (A was set to 200 in Eq. (1)) embedded within. As described above, the location of the center of this visual landmark was chosen randomly to lie between 3 and 6 cm to the right of the target. Subjects were instructed simply to remember where the reach target was *relative* to the visual landmark. In addition, for consistency with the other experimental conditions, they were also required to reach with their right index finger to the visible target and return their reaching hand to their chest.

After completion of the initial reach (irrelevant in this condition), all visual stimuli disappeared and the robot manipulandum passively moved the left hand to the same intermediate location described above (depicted in Fig. 2v) before returning it to the same location at the subject's midline. Once the manipulandum came to rest, the background of randomly-spaced yellow lines reappeared with the peak of the embedded visual landmark shifted to a new, final location. Furthermore, the landmark density was substantially reduced at this new location by setting $A=25$ (*high-reliability visual landmark*) or $A=12.5$ (*low-reliability visual landmark*) in Eq. (1). Subjects were explicitly told that the second, degraded landmark was identical to the initial landmark, just "harder to see". At this point the subject was required to reach to the new, landmark-relative target location with their right index finger. The reach endpoint was recorded when the subject pressed the horizontal touch screen at this location. As in the proprioceptive condition, a perfect final reach would bring the right index finger to the unselected target location immediately to the left of the initial target location. Once again, subjects were instructed to reach as accurately as possible, with no movement time constraint. Given that subjects also had visual feedback of their reaching finger, they should have thus been able to place their right fingertip arbitrarily close to whatever location matched their internal representation of visually-defined target location. Once again, subjects received no feedback about their accuracy.

It is important to note that in the visual condition, the left hand, which was always located at the body midline, provided no information about the original or final target location. Moreover, the visual landmark's final location, like the final target location itself, could not be predicted from any other source of proprioceptive information.

2.4.4. Combined condition

In the combined condition (right column of Fig. 2) subjects were able to encode the location of a target relative to both the left hand and the visual landmark. Each trial began with the placement of the left hand relative to one of the three randomly-selected target locations (*pos1, 2* or *3*), as in the proprioceptive condition. Once the manipulandum came to rest at the initial left hand site, the reach target was displayed at the selected location and the background of randomly spaced vertical yellow lines appeared with a clearly visible embedded landmark (A was set to 200 in Eq. (1)). As in the proprioceptive condition, the left hand was 4.4 cm to the left of the target, and as in the visual condition, the center of the visual landmark was between 3 and 6 cm to the right of the target. Thus, the spacing between the left hand and visual landmark was between 7.4 and 10.4 cm. Subjects then had to reach to this visible target so they could either form a proprioceptive encoding of the target location relative to their left hand, or remember where the target was relative to the visual landmark, or both. Indeed, they were instructed explicitly that they could use either of the cues to target location as they preferred.

After completion of the encoding reach, all visual stimuli disappeared and the robot manipulandum passively moved the left hand to the intermediate remote location (depicted in Fig. 2vi) before returning it to a new, final location (new left hand site). At this point, the background of randomly-spaced yellow lines also reappeared with the peak of the embedded visual landmark shifted to a new, final location (new visual landmark site). The subject was then required to reach to the new, left hand/visual landmark-relative target location with their right index finger. The reach endpoint was recorded when the subject pressed the horizontal touch screen at this location. Subjects were given no feedback regarding accuracy relative to either the left hand or visual landmark.

For the first block of combined trials (*no-conflict*) both the left hand and visual landmark were shifted by an equal amount and the subject could use either one or both to make the correct final reach. As in the visual condition, the second visual landmark presentation was at reduced reliability ($A=12.5$, or 25 in Eq. (1) for low or high-reliability, respectively).

The purpose of the no-conflict block described above was to ensure that subjects understood that they could rely on either the left hand or visual landmark. Since we only collected one block of trials in this condition, the data was not analyzed any further. The remaining three blocks of the combined condition were identical to each other, and similar to the no-conflict block. The only difference was that the left hand was shifted by an additional ± 0.88 cm (± 30 pixels) relative to the visual landmark, thus generating *rightward* vs. *leftward cue-conflict* between both types of target location representation. Pilot work indicated that subjects should not have been able to detect a conflict of this magnitude, and indeed, subjects did not report detecting it in debriefing. Data from these *conflict* blocks was analyzed to examine the cue-combination question in detail.

2.4.5. Calibration

At the end of the last session, subjects were given a short calibration task in order to create a mapping between touch screen coordinates and display screen coordinates that partially accounts for any systematic reach errors that the subject might make to fully visible targets. The subject simply had to reach to touch the displayed targets, which included the three reach targets and one additional location 9 cm to the right of the midline, presented in random order. Based on 25 such responses to these randomly presented targets, a linear mapping was created to convert the touch screen coordinates of reaches into display screen coordinates.

2.4.6. Scheduling

For the three experiment conditions described above, subjects completed a total of nine 100 trial blocks, each lasting approximately 20 min. These blocks, two proprioceptive, three visual and four combined (one no-conflict and three conflict), were spread over three one hour sessions, with each session occurring on a different day, and with all sessions for a given subject occurring within a period of less than two weeks. The order of the blocks was chosen randomly for each subject, within the constraint that subjects had to complete at least one visual and one proprioceptive block before completing any of the combined blocks. This was done to ensure subjects understood how to use each of the landmarks in isolation. Furthermore, the no-conflict combined block had to be completed before the remaining three conflict blocks. In total, subjects completed 900 reach trials each, not including the additional 25 calibration trials.

2.5. Data analysis

After converting all reaching data into display screen coordinates, outliers were removed separately for each conjunction of subject, experimental condition, block, landmark reliability level, and target location if they were more than 2.5 SD from the mean response in either the horizontal or depth directions. We did this because a subject would sometimes report simply forgetting the proper target location between presentation and test. The subject was instructed to touch the right edge of the touch screen in these cases, thus generating a clear outlier. At the 2.5 SD level removed fewer data points than the standard Chauvenet criterion (Taylor, 1997).

Given the nature of the visual landmark, subjects might have occasionally misidentified a random cluster of yellow lines present during reach as part of the shifted landmark. Such misidentifications should be infrequent for most subjects, and the location of these misidentified landmarks should be random over the workspace. In order to account for the effects of these random "reaching mistakes", we modeled the probability of given subject making a particular reaching response to a particular target location in the visual condition as

$$p(x) = p_{\mathrm{err}}U(l,r)+(1-p_{\mathrm{err}})\phi(x;\quad \mu,\sigma), \tag{2}$$

where x is the observed response location, p_{err} is the probability of misidentifying a random cluster of lines as part of the visual landmark, ϕ is the normal probability density function (pdf) with mean μ and variance σ^2, and $U(l,r)$ is a continuous uniform pdf ranging over the interval $[l,r]$. Values for the parameters in Eq. (2) were determined via standard maximum likelihood fitting under the constraints that the interval $[l,r]$ had to contain the three possible target locations, σ was positive, and p_{err} was within the interval [0,1]. After fitting, μ provided a corrected estimate of where the subject perceived a given target location to be on average, while σ provided a corrected estimate of the precision of these location representations. In order to ensure that enough non-mistake trials were available to generate a good estimate of σ, we discarded data from any subject/condition/reliability/target location conjunction in which p_{err} was greater than 0.25. This meant that at least 30 reaching responses for each retained set were "non-mistakes". All data from any subject that demonstrated $p_{\mathrm{err}} > 0.25$ at more than one location were discarded from the main analysis. Given the nature of the proprioceptive landmark, p_{err} should be small for both the proprioceptive and combined conditions. However, for consistency, we applied the same procedure to the data from these conditions as well.

In choosing σ from Eq. (2) as our estimate of representational error we were ignoring execution error, which can be quite large under open-loop circumstances, especially with time constraints (van Beers, Haggard, & Wolpert, 2004). However, our subjects reached to proprioceptively-defined target locations with full proprioceptive feedback, they reached to visually-defined targets with full visual feedback, and they were under no time constraints. Thus, subjects should have been able to bring their reaching fingertip arbitrarily close to whatever proprioceptively or visually-defined target location representation they possessed. Additional reach variability might possibly have arisen from some fluctuating criterion that a subject used to determine when their fingertip location matched their internal representation of target location. Presumably this variability would be quite small—smaller than the fingertip itself. Indeed, we found that estimating this variability from the calibration trials and subtracting it from σ made no qualitative difference to any of our results below (all statistically (in)significant comparisons remained that way regardless of an accounting for this additional variability). Given that the calibration session contained relatively few trials – not likely enough for a precise measure of this "matching" variability – we only present analysis of the uncorrected data below.

With the parameters we have chosen for Eq. (1), the reach target always appeared to be in the vicinity of the left edge of the visual landmark. In order to ensure that subjects did not simply reach to the same landmark-relative location (e.g., the left edge of the landmark) on all trials, we regressed target-relative reaching endpoint (i.e., where subjects reached relative to where they *should* have reached) against the target-relative location of the landmark center. This regression was performed separately for each subject/reliability/target location conjunction in the visual condition. The resulting slopes, which should be equal to one if the subject was reaching to a fixed landmark-relative location, and zero if they were reaching to the correct target location, were then averaged across the three possible target locations and compared to zero and one using standard t-tests.

2.6. Theory and modeling

Within the MLE framework, optimal combination of two or more redundant but independent estimates of a stimulus dimension (usually, but not always, from two different sensory modalities) is linear, with the combination weights being proportional to the reliability of each estimate. Assuming MLE combination occurs in our combined condition, we would expect a subject's mean reaching endpoint to a given target location (e.g., *pos1*) to be

$$\overline{x}_c = \frac{\frac{1}{\sigma_p^2}}{\frac{1}{\sigma_p^2}+\frac{1}{\sigma_v^2}}\overline{x}_p + \frac{\frac{1}{\sigma_v^2}}{\frac{1}{\sigma_p^2}+\frac{1}{\sigma_v^2}}\overline{x}_v, \tag{3}$$

where $\overline{x}_{p/v}$ and $\sigma_{p/v}^2$ are the mean reaching endpoint and reaching variance to that target location in the proprioceptive/visual control conditions. The combined reaching variance should also be

$$\sigma_c^2 = \frac{\sigma_p^2\sigma_v^2}{\sigma_p^2+\sigma_v^2}. \tag{4}$$

This ML estimate of a stimulus dimension is minimum variance, as well as unbiased insofar as the single-cue estimates are themselves unbiased. Should the single-cue estimates be biased, then it follows directly from Eq. (3) that the MLE combination will demonstrate a bias that is less than the most biased cue. This is important because it implies that, even when large biases exist in the single-cue estimates, it is usually better in a certain sense to rely on an MLE combination than it is ever to rely on the most biased modality (discussed further below).

In order to determine whether subjects in our experiments were performing MLE combination, we first used response variability and bias measured from the proprioceptive and visual conditions to calculate the MLE predictions of these

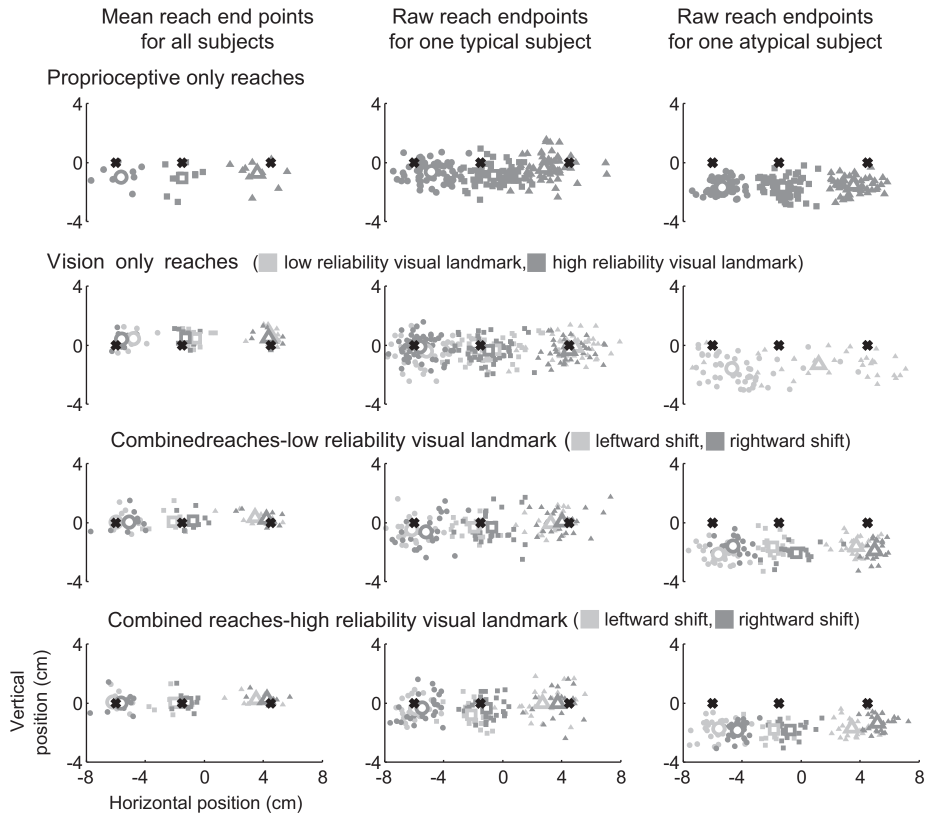

Fig. 3. Reaching data. *Left column*: mean reaches for each subject are shown in each of the experimental conditions. Smaller filled symbols represent each subject's mean reach, while large unfilled symbols are the between-subjects means. Circles are reaches to targets that were initially presented at *pos2*, but which were "brought to" *pos1* (the appropriate response location) by the shifted left hand/ visual landmark. Similarly, squares represent reaches to *pos2* (presentation location at *pos3*), and triangles represent reaches to *pos3*. The black "X"s are the locations of *pos1, pos2,* and, *pos3. Middle column*: raw reach data is shown for one typical subject in each experimental condition, with the larger unfilled symbols representing the means for that subject. *Right column*: raw reaches for on atypical subject. In the visual condition, only data from the low-reliability landmarks are shown, and only for *pos1* and *pos3*. The extensive spread of the responses is evident, indicating that this subject had difficulty using the visual landmarks.

quantities for each subject at each target location and landmark reliability level in the combined condition. After calculating the predictions specifically for each target location, we averaged the observed and predicted variabilities and biases across locations because these locations were relatively close in space, and because we had no location-specific hypotheses. Thus, the proprioceptive condition yielded two data points for each subject: average (across target locations) bias and average endpoint variability. The visual condition yielded two average bias and average variability values per subject because there were two levels of visual landmark reliability (low vs. high). The combined condition yielded 2 (leftward vs. rightward cue-conflict) $\times$ 2 (low vs. high-reliability visual landmark) $=$ 4 values of observed average bias, 4 corresponding values of observed average variability, and the 8 corresponding MLE predictions of these quantities. Observed and predicted variabilities were further averaged across cue-conflict conditions (leftward vs. rightward conflict) because the MLE model predicts no differences here. All remaining analysis was performed on this simplified data set.

To test the MLE hypothesis, we first performed a set of planned comparisons using Holm–Bonferroni corrected *t*-tests in order to compare between-subjects endpoint variability from the combined condition to that observed in the control conditions, and to the predicted values. This was done separately for low and high-reliability visual landmarks, but the *t*-tests were corrected for the entire set of comparisons (six in total). If the MLE model holds, then subjects should show significantly lower endpoint variability in the combined condition relative to either of the control conditions. In principle, the observed and predicted variability values should match not only on average, but for each individual subject. Therefore we also performed two linear regressions (one for low reliability visual landmarks and one for high) of observed variability against MLE-predicted values. These regressions should yield slopes significantly greater than zero if there is a relationship between observed endpoint variability and MLE predictions across subjects. Moreover, the slopes should be equal to one and the intercepts should be zero if perfect MLE combination is occurring. For these regression analyses we employed standard "Model I" regression. Many researchers prefer to use "Model II" regression when there is measured variability in the independent variable (IV) (i.e., when the IV is not fixed by the researcher). However, when the dependent variable (DV) should, in principle, be predictable from the IV (as in our case), and when most of the variability in the IV is "natural" variability and not measurement error, then the use of Model I regression is more appropriate (for details, see Smith, 2009). Model II regression will likely *overestimate* slopes in such a case.

In addition to endpoint variability, the MLE model predicts reaching bias for the combined condition with cue-conflict. In our convention, this bias should be zero if subjects reach accurately based purely on vision, but should be ± 0.88 cm (rightward vs. leftward cue-conflict) if subjects reach accurately based purely on proprioception. Thus, for each subject we calculated the difference in average bias for rightward and leftward cue-conflict trials. We then performed a set of planned comparisons using Holm–Bonferroni corrected *t*-tests to compare these bias differences with zero (pure reliance on vision), 2 times the cue-conflict magnitude $=$ 1.76 cm (pure reliance on proprioception), and the MLE predicted values. As with endpoint variability, MLE-predicted biases should match on a per-subject basis. Thus, a regression of observed bias against predicted bias should yield a slope of one and an intercept of zero. However, considering the possibility of asymmetries between leftward and rightward conflict situations, we first ran an ANCOVA to ensure slopes and intercepts for these two subsets of data did not differ significantly. Following this, we pooled the data and calculated slope and intercept parameters with a standard regression.

Based on our results (described below), which indicate MLE combination of allocentric visual and proprioceptive information in certain circumstances but not others, we developed a highly-simplified model, which we parameterized with data from the proprioceptive and visual controls, that explains our combined data as a mixture of MLE combination and probabilistic cue-switching (PCS) (Serwe, Drewing, & Trommershauser, 2009b)). In order to show that this mixed behavior (MLE + PCS) is not the best thing for the brain to do, we used subjects' individual biases and endpoint variability at each target location from the control experiments to simulate their expected absolute reaching error in the cue-conflict task under various combination rules.

3. Results

Mean reaching endpoints for each subject in each experimental condition at each of the three possible target locations are

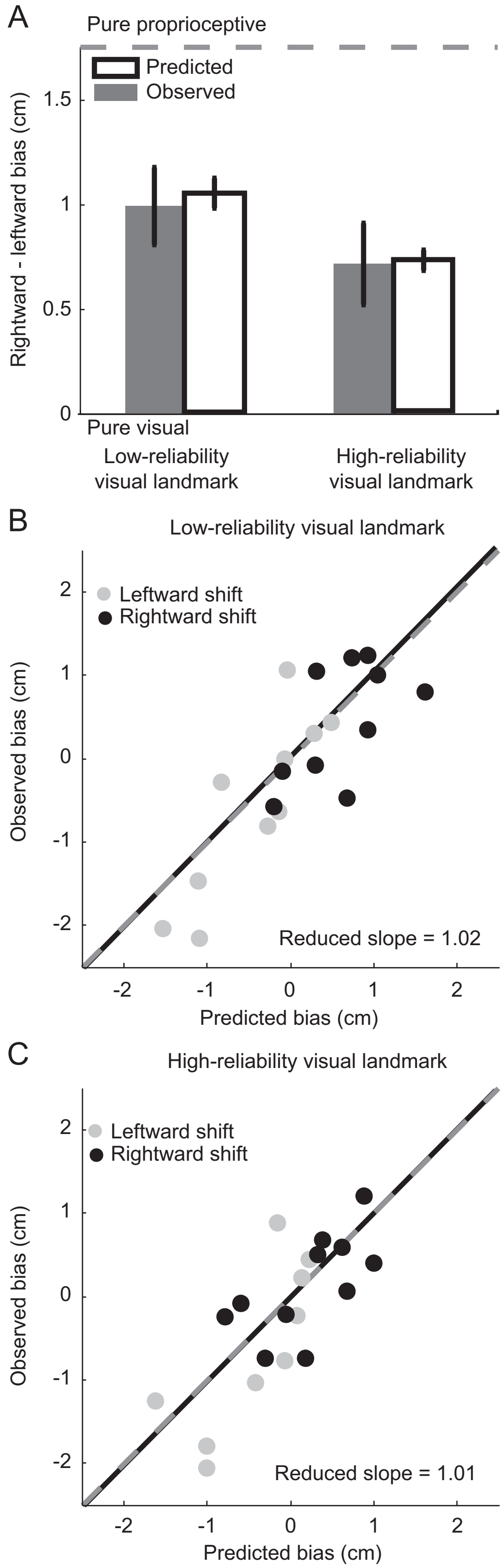

Fig. 4. Reaching endpoint bias. (A) Observed and MLE-predicted between-subjects means for the difference between average reaching bias in rightward cue-conflict trials minus the average reaching bias in leftward cue-conflict trials. (B) Observed vs. MLE-predicted reaching biases for low-reliability visual landmarks. Each light/dark circle is an average bias for one subject in leftward/rightward conflict trials. (C) Observed vs. MLE-predicted reaching biases for high-reliability visual landmarks.

presented in the left column of Fig. 3. In addition, raw reaching endpoints are shown in the center column for one "typical" subject, while raw endpoints are shown at the right for one "atypical" subject. Subjects were classified as typical or atypical based on the p_{err} values from maximum-likelihood fitting of Eq. (2). More specifically, if a given subject produced p_{err} values of greater than 0.25 at more than one location in the visual condition, then that subject was designated atypical. Of twelve subjects, ten were typical, while two were atypical. For one of these two atypical subjects at one location in the low-reliability visual condition, misidentifications reached 80% (i.e., $p_{err}=0.80$). For the other atypical subject, such errors reached 61%. With such large misidentification rates, estimates for σ would likely be poor. Thus, data from these two subjects were not analyzed any further. It should be noted that we have no reason to believe these two atypical subjects were qualitatively any different from the remaining subjects, they just required a higher signal-to-noise ratio stimulus than the others in order to perform our task.

Averaging p_{err} values for each subject in each condition over the three locations yielded between-subjects mean values of $0.03 \pm 0.01 (M \pm SEM)$ for the proprioceptive condition, 0.021 ± 0.009 and 0.002 ± 0.002 for low and high-reliability visual landmarks in the visual condition, and 0.00 ± 0.00 and 0.009 ± 0.006 for low and high-reliability visual landmarks in the combined condition. Thus, in typical subjects reaching mistakes were infrequent.

When target-relative reaching endpoints in the visual condition were regressed against the target-relative location of the landmark center, the between-subjects mean for the low-reliability landmark was 0.39 ± 0.12, while for the high-reliability visual landmark it was 0.35 ± 0.12. These values were significantly less than one ($t(9)=5.28$, $p<0.001$ for low-reliability and $t(9)=5.36$, $p<0.001$ for high) and greater than zero ($t(9)=3.41$, $p=0.008$ for low-reliability and $t(9)=2.91$, $p=0.017$ for high), indicating that subjects did not simply reach to some fixed part of the visual landmark, but they did appear to have been weakly drawn to some part of it. This is consistent with the findings of Diedrichsen, Werner, Schmidt, and Trommershauser (2004), but also implies that subjects were doing the task properly.

The observed average differences between reaching bias for rightward and leftward cue-conflict is shown in Fig. 4A, along with the MLE predictions. Holm–Bonferroni corrected t-tests indicate that the observed values were significantly greater than zero (pure visual reliance) for both low and high-reliability visual landmarks ($p_{corr}=0.003$ and 0.016, respectively), significantly less than 1.76 cm (pure proprioceptive reliance) ($p_{corr}=0.011$ and 0.003) and not different from the MLE predicted values ($p_{corr}=0.70$ and 0.26). Reaching endpoint bias for each subject in the combined condition is plotted against the MLE predictions separately for low and high-reliability visual landmarks in Fig. 4B and C. Given that an ANCOVA analysis revealed no significant interaction between conflict direction (rightward or leftward) and regression slope ($p>0.05$), nor a main effect of conflict direction ($p>0.05$), we pooled data from both conflict directions and performed a standard regression analysis. For low-reliability visual landmarks the regression slope of 1.04 was significantly different from zero ($F(1,18)=36.9$, $p<0.001$), but not from one ($F(1,18)=0.056$, $p=0.82$). The intercept of -0.14 cm was not significantly different from zero ($F(1,18)=1.02$, $p=0.33$). Refitting without the insignificant intercept yielded a reduced slope of 1.02. For high-reliability visual landmarks the regression slope of 0.99 was significantly different from zero ($F(1,18)=24.9$, $p<0.001$), but not from one ($F(1,18)=0.003$, $p=0.96$). The intercept of -0.10 cm was not significantly different from zero ($F(1,18)=0.60$, $p=0.45$). Refitting without the insignificant intercept yielded a reduced slope of 1.01.

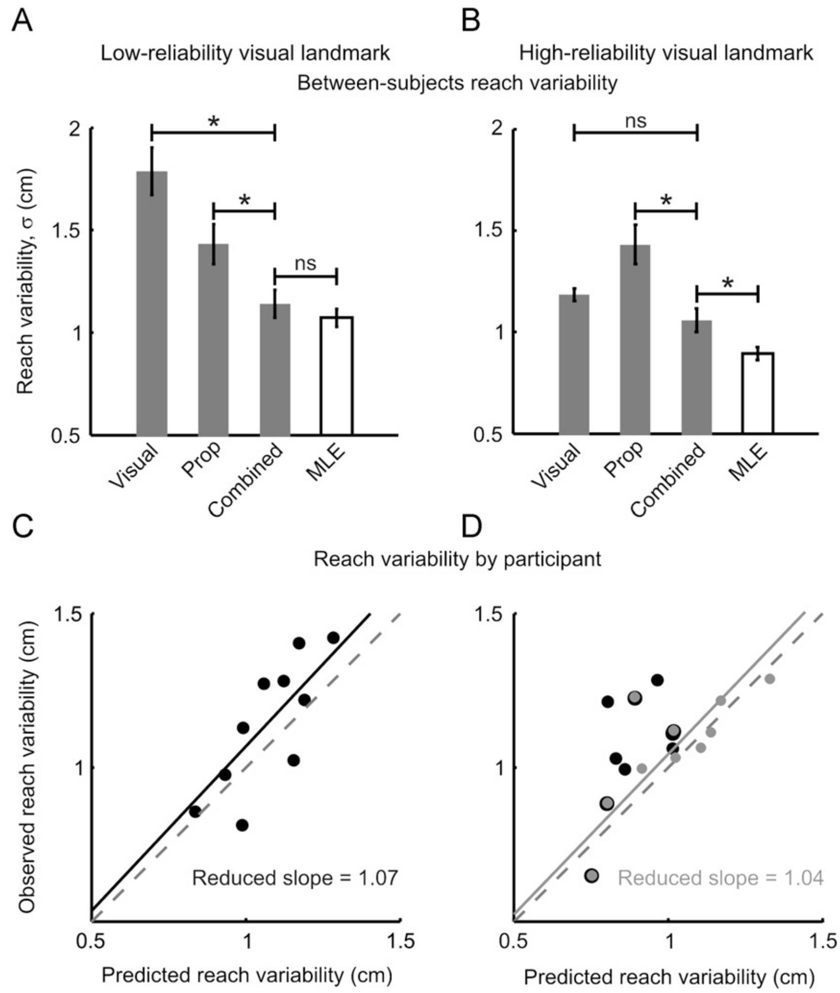

Fig. 5. Reaching endpoint variability. (A) Between-subjects reach variability (σ in Eq. (2)) for low-reliability visual landmarks in each of the experimental conditions, along with corresponding MLE predictions for the combined condition. Error bars are standard error of the mean. (B) Between-subjects reach variability for high-reliability visual landmarks. (C) Observed vs. MLE-predicted reach variability for the low-reliability visual landmarks in the combined condition. The dashed line has unit slope and zero intercept. Each filled circle is data from one subject. (D) Observed vs. MLE-predicted reach variability for the high-reliability visual landmarks in the combined condition. Light gray circles are when variability is predicted from the hybrid model.

Average reach endpoint variabilities (defined based on σ from Eq. (2)), along with MLE predictions, are shown for all experimental conditions in Fig. 5A and B. For low-reliability visual landmarks, Holm–Bonferroni corrected *t*-tests indicate that this endpoint variability was significantly lower in the combined condition (with cue-conflict) than in either single-cue condition ($p_{corr}=0.004$ for visual control, $p_{corr}=0.013$ for proprioceptive control), but not significantly different from the MLE prediction ($p_{corr}=0.15$). For high-reliability visual landmarks, average endpoint variability in the combined condition was significantly lower than for the proprioceptive control ($p_{corr}=0.01$), not significantly different than that from the visual control ($p_{corr}=0.11$), but significantly higher than the MLE prediction ($p_{corr}=0.02$).

Endpoint variability for each subject in the combined condition is plotted against the MLE predictions separately for low and high-reliability visual landmarks in Fig. 5C and D. For low-reliability visual landmarks, standard linear regression yielded a slope of 1.2, which was significantly different from zero ($F(1,8)=13.24$, $p=0.007$), but not from one ($F(1,8)=0.53$, $p=0.49$), and an intercept of -0.2 cm, which was not significantly different from zero ($F(1,8)=0.29$, $p=0.61$). Refitting the linear model without the insignificant intercept yielded a reduced slope of 1.07. For high-reliability visual landmarks, the regression slope was not significantly different from zero $F(1,8)=3.67$, $p=0.09$. Considering the *p*-values obtained for the low-reliability case, this lack of significant correlation for high-reliability landmarks does not seem likely to be related to power.

In summary, the MLE predictions for the combined condition are in full agreement with our observed reaching data for low-reliability visual landmarks. However, although the reaching bias results are consistent with MLE combination of allocentric visual and proprioceptive information with high-reliability visual landmarks, subjects' reaching variability was too high for MLE combination.

4. Modeling

4.1. Probabilistic cue switching?

Probabilistic cue-switching is an alternative model to MLE combination that has been observed to hold in certain circumstances when visual and proprioceptive cues about direction are available to the brain (Serwe et al., 2009b). With PCS the brain still uses information about the reliability of the cues available, but instead of using it to determine the weighting of a linear

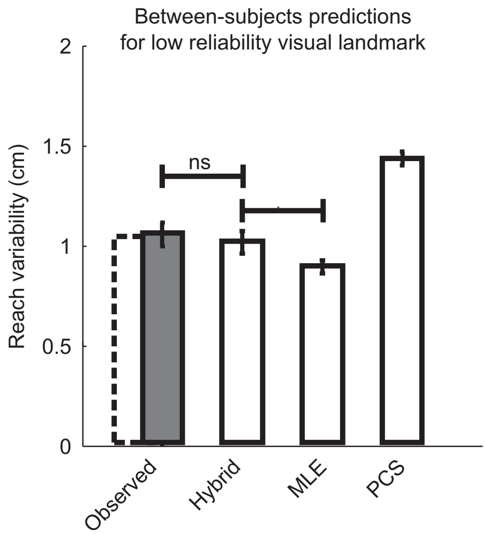

Fig. 6. Between-subjects means for observed and predicted reaching variances under different models in the combined condition. The dashed bar is reaching variance calculated from the un-analyzed no-conflict trials.

combination, it is used to determine the *probability* that one particular cue will be used. More specifically, under PCS the probability of relying on a particular cue is equal to the weight that the cue would have received in the MLE linear combination. Once one cue is chosen on a given trial, the other(s) make no contribution at all. Interestingly, PCS makes exactly the same bias predictions as MLE combination when bias is averaged over trials, but predicts a higher variance than MLE—one that is between what would be observed for reliance on either cue in isolation. Thus, by default, the PCS predictions agree with the biases we observed for the high-reliability visual landmarks, just as the MLE predictions did. In contrast, whereas the MLE predictions of reaching endpoint variance were lower than our observations in this condition, the PCS predictions (see Fig. 6) were significantly higher ($t(9)=7.24$, $p<0.001$). Thus PCS does not explain our data either.

4.2. Sub-optimal combination

Given that the observed reaching variance with our high-reliability visual landmarks fell between that predicted by the MLE and PCS models, and that both predict identical biases, it is clearly possible to create a hybrid model that will fit our data. For example, if we simply assume that on some trials subjects use the MLE rule and on some they use the PCS rule, we can adjust the relative frequencies separately for each subject to perfectly fit each subject's observed endpoint variance. In fact, since the MLE model generates reliability-weighted bias *within* each trial, and PCS generates reliability-weighted bias *across* trials, this hybrid MLE/PCS model appears to be the only reasonable explanation for our results. In principle it is possible that our subjects could have been employing two or more completely novel combination rules, neither of which produces reliability-weighted biases, but which were coincidentally mixed in the correct proportion by our subjects to produce the observed data. However, not only does this possibility seem unlikely in its own right, but in the next section we also present a specific hybrid MLE/PCS model that we fit to our control data, and which quantitatively reproduces our combined data without additional parameters. Thus, we conclude that a hybrid MLE/PCS strategy is almost certainly being used by at least some of our subjects.

The question we wish to address now is whether or not such a hybrid strategy was a sensible thing for subjects to do. For each of our subjects at each target location, we used observed biases and variabilities from the proprioceptive and visual controls to calculate the mean absolute reach error expected at each target location *for any given trial* of the combined condition. We calculated these values separately assuming MLE combination, pure visual reliance or pure proprioceptive reliance in the combined condition. For all 10 subjects with the low-reliability visual landmark, MLE combination gives a lower expected absolute error (averaged over target locations) than pure visual reliance ($M=-0.51$ cm, $t(9)=6.20$, $p=0.0001$) or pure proprioceptive reliance ($M=-0.36$ cm, $t(9)=6.19$, $p=0.0001$). Thus, MLE combination was the most appropriate strategy for subjects to adopt on a trial-by-trial basis in this condition. For eight of 10 subjects with the high-reliability visual landmark, MLE combination gives a lower expected absolute error than pure visual reliance ($M=-0.14$, $t(9)=2.54$, $p=0.032$). For all 10 subjects with the high-reliability visual landmark, MLE combination gave a lower expected absolute error than proprioceptive reliance ($M=-0.57$, $t(9)=7.08$, $p<0.001$). Thus, for any given trial, at least some of our subjects (possibly all) would have a lower expected reach error with the high-reliability visual landmark if they relied on MLE combination rather than purely on vision or purely on proprioception, and should consequently have done so on every trial. However, within a hybrid model, subjects would have engaged in PCS behavior sometimes, meaning they relied purely on vision or proprioception on at least some trials - a suboptimal strategy.

4.3. A quantitative hybrid model

Kording et al. (2007) have shown that subjects combine cues using an MLE rule when they perceive those cues to have arisen from the same stimulus event. When this unitary perception breaks down, so does MLE combination. In our task, such a breakdown might occur if subjects perceived, perhaps unconsciously, that their allocentric visual and proprioceptive estimates of target location were in disagreement with each other. One might wonder if the artificially introduced cue-conflict in our experiment led to such a problem. However, this explanation seems unlikely for three reasons: (1) as is typical of other cue-combination studies, we chose the square of our conflict magnitude to be smaller than the typical response variance seen in either of the single cue controls, (2) the conflict had no such effect with low-reliability visual landmarks, and (3) the response variability in the unanalyzed, no-conflict trials (see dashed bar in Fig. 6) was very similar in magnitude to that observed in the cue-conflict trials (i.e., higher than MLE predictions ($t(9)=5.02$, $p<0.001$)). Instead, we believe any conflict perceived by subjects in the combined condition likely arises from the inherent biases in the proprioceptive modality alone.

Recall that at initial presentation, the reach target typically appeared near the left "edge" of the visual landmark, sometimes outside in the area of low line density, and at other times inside in the area of high line density. Subjects who demonstrate a large rightward proprioceptive bias are therefore likely to experience a situation in which they see the target "outside" the landmark at presentation, but their proprioceptive estimate of its location "pushes" into a region that clearly has a high line density at test. In contrast, subjects with a large leftward proprioceptive bias might have targets that are presented within the high density landmark "pulled" outside at test. However, this "pulling" would not likely be obvious to the subject because of the degraded nature of the landmark at test—it would be hard to tell if there were a conflict, or if the proprioceptive estimate at test just happens to land in a highly degraded area of the landmark. Thus, our model is built on the assumption that subjects who show large rightward reaching biases in the proprioceptive condition are going to demonstrate PCS-like behavior more often in the combined condition than subjects with leftward biases in the high-reliability landmark condition. We assume that the landmark was sufficiently ambiguous in the low-reliability visual landmark that PCS behavior was negligible. Notice here we are not claiming that the brain becomes aware of its own biases – if it knew those, it would likely correct for them – only that, because of the nature of the visual landmark, larger rightward proprioceptive bias might result in the perception of a cue-conflict.

In order to turn our assumption into a simple but explicit model, we note that the effect of rightward proprioceptive bias should be non-linear because of the Gaussian nature of the proprioceptive estimates of target location. That is, the frequency with which a subject should notice a target being "pushed" into the landmark at test should be low for large leftward biases, should increase slowly as bias moves to the right until some critical bias is reached, at which point it should increase rapidly to a maximum for the largest rightward biases. Thus, for our model, we assume that when a subject shows a leftward proprioceptive bias at a given target location in the proprioceptive control, they will always perform MLE combination at that location in the combined condition. In contrast, at any location in which a subject shows a rightward proprioceptive bias, they will engage in PCS with a probability directly proportional to the magnitude of that rightward bias. In order to fully constrain the model, we assume that the largest rightward bias demonstrated by any subject at any location will lead to that subject engaging exclusively in PCS at that location.

As described above, our hybrid model automatically fits the observed high-reliability landmark bias data. Since our hybrid model is probabilistic, predictions from the model were determined by averaging over 100,000 repetitions. This was sufficient to yield values that varied by less than 0.1% across repeated simulations. The between-subjects mean reaching endpoint variability for the hybrid model, which is significantly larger than the MLE-predicted variance ($t(9)=2.56, \quad p=0.03$) and not statistically different from the observed variance ($t(9)=1.25, \quad p=0.24$) is shown in Fig. 6. Endpoint variability for each subject in the high-reliability landmark condition is plotted against the hybrid predictions in Fig. 5D in green. Standard linear regression yielded a slope of 0.82, which was significantly different from zero ($F(1,8)=12.29, \quad p=0.008$), but not from one ($F(1,8)=0.63, \quad p=0.45$), and an intercept of 0.23 cm, which was not significantly different from zero ($F(1,8)=0.96, \quad p=0.36$). Refitting the linear model without the insignificant intercept yielded a reduced slope of 1.04. Thus, our hybrid model well-reproduced our observed data, suggesting that subjects sometimes engaged in MLE combination, while at other times relied solely on one cue or the other—a sub-optimal strategy.

5. Discussion

5.1. General

The brain often combines two estimates of a stimulus dimension using the MLE rule, even when the estimates are biased (Scarfe & Hibbard, 2011; van Beers et al., 1999). Our simulation results demonstrate that subjects in our task should have used an MLE strategy in combining proprioceptive and allocentric visual estimates of target location. Indeed, we observed this for the low-reliability visual landmark condition. However, for the high-reliability visual landmark, subjects employed a hybrid strategy in which they sometimes relied purely on one modality or another—a sub-optimal strategy. We were able to model our subjects' counter-intuitive behavior by assuming that, with a high-reliability landmark, they were more easily able to detect (likely unconsciously) the bias-induced conflict between their estimates of target location, which caused them to resort to a cue-switching strategy during some trials. Thus, we have demonstrated that increasing the quality of information in one modality can lead to suboptimal cue-combination, likely by allowing the brain to detect the presence (but not likely magnitude) of its own inherent biases, which it subsequently interprets as conflict.

A potential alternative explanation for why we observed sub-optimal combination in the high-reliability visual landmark condition is that subjects were simply variable in how they "grouped" the lines in our stimulus to create the visual landmark. Such added variability might hide an underlying optimal strategy. However, given that subjects showed MLE-optimality in the low-reliability condition where the visual landmark was harder to detect (and grouping variability would likely be greater), this explanation seems unlikely.

5.2. Practical implications

It is well-known that performance in tasks involving high cognitive workloads or rapid attention switching between numerous stimuli (e.g., operating room/surgery (Kiefer & Hoeft, 2010), military pilot (Huttunen, Keranen, Vayrynen, Paakkonen, & Leino, 2011), etc.) can be impaired by adding additional relevant stimuli to the work space. To our knowledge, we are the first to show that simply adding information to one already-present sensory cue without obviously increasing cognitive load can also hinder behavioral performance. From our task alone, it is not clear how often this phenomenon has meaningful impact in real world situations, however this unexpected question now appears to be worth investigating further. Indeed, it might turn out to be the case that the best way to improve performance in some specific task is not to add as much information as possible, but rather to add additional information only to the point where it does not allow detection of any real biases, or generate illusions of bias. Furthermore, although a number of studies have failed to find MLE combination of two or more cues to some stimulus dimension (Boulinguez & Rouhana, 2008; Jones & Henriques, 2010; Reuschel, Rosler, Henriques, & Fiehler, 2011; Roach, Heron, & McGraw, 2006; Serwe, Drewing, & Trommershauser, 2009a; Sober & Sabes, 2003), our current work suggests that ruling out underlying MLE combination rule might be premature until it can be demonstrated that the details of a given paradigm have not rendered detectible any conflict generated by single-modality biases, or caused any illusion of bias.

In contrast to our results and those of Scarfe & Hibbard (2011) and van Beers et al. (1999), who find MLE combination even in the presence of single-modality biases (van Beers, van Mierlo, Smeets & Brenner, 2011) have shown that in the presence of performance feedback, the brain will tend to give more weight to the more accurate single cue, irrespective of reliability. Thus, one might argue that our findings, along with those of others who find MLE combination in the presence of single-modality bias, are not necessarily of practical importance because cue-weighting based on reliability is often overridden in real-world tasks by feedback about accuracy. However, van Beers et al.'s task involved repeated trials with highly similar stimuli. In real-world circumstances, it is not clear how long feedback-based reweighting would persist, especially given the rapidity with which van Beers et al.'s subjects engaged in this reweighting. Moreover, it is not clear how large the perceived conflict between estimates from a single sensory modality and from feedback have to be before the kind of reweighting seen by these authors would occur. This is an especially important question because as we have shown in this work, even in the presence of small bias-induced conflict, MLE combination is still better than relying on a single cue alone. As van Beers et al. point out, these important questions require extensive investigation.

5.3. Theoretical implications

Our findings lend support to the idea that the brain generally combines information in a statistically optimal fashion even when it is not acting on direct sensory input, but rather on memory (for similar examples, see Brouwer & Knill, 2009; Byrne & Crawford, 2010; Vaziri et al., 2006). In particular, we did not create any cue-conflict during encoding, but only at test. Thus, subjects appear to have held on to reliability information until a response was required and, only then, used this information to engage in cue combination. Furthermore, our work is consistent with the idea that when MLE combination is not observed, it might typically be because the brain does not perceive the cues involved as arising from the same ''event'' (Kording et al., 2007; Roach et al., 2006). In the particular case where this misperception arises from modality-specific bias, it would be interesting to see if removing the bias via training, or via correction with artificial cue-conflict, could lead to MLE combination where it is not otherwise observed.

Numerous studies have investigated how visual and proprioceptive modalities interact for the purposes of action (e.g., Adamovich, Berkinblit, Hening, Sage, & Poizner, 2001; Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995; Boulinguez & Rouhana, 2008; Jones & Henriques, 2010; Lateiner & Sainburg, 2003; Monaco et al., 2010; van Beers et al., 1999) and perception (e.g., Fiehler, Rosler, & Henriques, 2010; Reuschel et al., 2010, 2011; Rossetti, Desmurget, & Prablanc, 1995; Serwe et al., 2009a), with some finding support for optimal/MLE combination and others not. Some of this inconsistency in the literature arises from the somewhat different questions being asked by the various authors. For example, van Beers et al. (1999) find that proprioceptive and visual information about a reach target's *location* are optimally combined, whereas Boulinguez & Rouhana (2008) show that reproducing *trajectories* from visual and proprioceptive memory is not ''optimal''. Similarly, Sarlegna and Sainburg (2007) argue that the degree of reliance on visual or proprioceptive information about the reaching hand location depends on the reach target modality, as opposed to the relative reliability of these modalities. To be clear, our results apply only to *remembered* reach targets, and we only claim MLE combination occurs with respect to allocentrically-defined reach *endpoints*.

Contributions

PB and DH designed the research, DH provided lab equipment, PB conducted the research, analyzed the data and wrote the manuscript.

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