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RESEARCH ARTICLE

Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry

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Abstract Many studies demonstrated a higher accuracy in perception and action when using more than one sense. The maximum-likelihood estimation (MLE) model offers a recent approach on how perceptual information is integrated across different sensory modalities suggesting statistically optimal integration. The purpose of the present study was to investigate how visual and proprioceptive movement information is integrated for the perception of trajectory geometry. To test this, participants sat in front of an apparatus that moved a handle along a horizontal plane. Participants had to decide whether two consecutive trajectories formed an acute or an obtuse movement path. Judgments had to be based on information from a single modality alone, i.e., vision or proprioception, or on the combined information of both modalities. We estimated both the bias and variance for each single modality condition and predicted these parameters for the bimodal condition using the MLE model. Consistent with previous findings, variability decreased for perceptual judgments about trajectory geometry based on combined visual-proprioceptive information. Furthermore, the observed bimodal data corresponded well to the predicted parameters. Our results suggest that visual and proprioceptive movement information for the perception of trajectory geometry is integrated in a statistically optimal manner.

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Introduction

Humans use information from several modalities in everyday life, especially when interacting with objects in their environment. For example, grasping a cup of tea requires a combination of visual, proprioceptive, and tactile information to localize the position of the object and the hand, and to control the arm movement in order to successfully perform a goal-directed action. Simultaneous input from different senses can increase the detectability of external stimuli, disambiguate their discrimination, and speed up responsiveness (Stein and Meredith 1993).

Multisensory integration, referring to the interaction between redundant signals (Ernst and Bülthoff 2004), rests on neural mechanisms which combine redundant information from single modalities into a unitary percept. For example, when integrating vision and proprioception, these inputs are more likely to be combined to a unitary percept when they are spatially coincident (Gepshtein et al. 2005; Sambo and Forster 2008). In this case, both modalities contribute to the same percept. Following the 'ideal observer' model, information from multiple senses is integrated by weighting the single modalities with respect to their reliability, yielding to the most reliable multisensory estimate (Ernst and Banks 2002; Ernst and Bülthoff 2004; Landy et al. 1995; Yuille and Bülthoff 1996). Therefore, senses with small variance, and consequently high reliability, contribute more to a multisensory percept than those with a large variance. An optimal integration occurs if the percept's reliability is maximal, i.e., if its variance is minimal. The maximum-likelihood estimation (MLE) model (Ernst and Banks 2002; Landy et al. 1995) describes optimal integration under the assumptions that noise in each single modality's estimate follows a Gaussian distribution and that these noise distributions are mutually independent from each other. The MLE model predicts a linear combination of the unimodal information which is weighted proportionally to the modality's relative reliability. Under this combination rule, integration of different sensory information is statistically optimal.

Several studies have reported evidence for optimal integration of different cues within a single modality. In vision, for example, disparity and texture cues (Hillis et al. 2004; Knill and Saunders 2003) seem to be optimally integrated in order to perceive surface slant. Regarding the haptic domain, the integration of force and position cues for shape perception has been shown to follow predictions from optimal integration (Drewing and Ernst 2006; Drewing et al. 2008). The MLE model has been successfully applied to the integration of redundant information across different modalities as well. Optimal integration has been demonstrated for visual and haptic information of size (Ernst and Banks 2002; Gepshtein et al. 2005; Helbig and Ernst 2008) and shape (Helbig and Ernst 2007). Furthermore, there is evidence that position information provided by vision and audition (Alais and Burr 2004b), or by vision and proprioception (van Beers et al. 1996, 1999) is also integrated in an optimal way (for an exception see Rosas et al. 2005).

So far, little is known about the integration of vision and proprioception for the perception of path geometry. To this end, unimodal and bimodal stimuli following a movement trajectory are required, thus, providing sensory information which changes along space and time. A few studies have examined integration of moving auditory and visual stimuli showing improved motion detection when audition and vision are presented simultaneously (Alais and Burr 2004a; Meyer et al. 2005; Wuerger et al. 2003).

The present study investigates how visual and proprioceptive movement information for the perception of trajectory geometry yields a unified percept. More precisely, we quantitatively tested whether visual and proprioceptive movement information of angular trajectories is integrated in a statistically optimal fashion according to the MLE model. Participants received sensory information about a moving light dot (vision) and their moving limb (proprioception) through either one modality alone (unimodal condition) or both modalities (bimodal condition). They were asked to indicate whether an angle consisting of two consecutive trajectories felt more like an acute or an obtuse movement path.

We fitted psychometric functions for all conditions. Therefore, we determined the angle that each participant judged as being acute or obtuse with equal frequency, or in other words, their estimate of a right angle. Previous results of Lakatos and Marks (1998) indicate that there is a natural discrepancy between visual and proprioceptive biases for perceived angularity. They showed that participants perceived angles as being more acute-angled in the proprioceptive than in the visual condition. Since our task is comparable to the one of Lakatos and Marks (1998), we suppose a natural discrepancy between the single estimates, i.e., proprioceptive bias should be shifted more toward acute-angularity than visual bias. Such natural discrepancy between both modalities would enable us to test whether the multisensory percept (measured by the bimodal bias) can be predicted as a weighted average of the single unimodal estimates, with weights that depend on the reliability of each input (first prediction from MLE model). We hypothesize that the observed bimodal biases would be similar to the predicted bimodal biases. According to the MLE model, these combined (bimodal) estimates should be more reliable than either of the unimodal estimates (inverse of the percept's variance; Landy et al. 1995). To examine this second prediction, we measured the variance for each unimodal and bimodal estimate from the response probability functions. If visual and proprioceptive movement information is integrated in a statistically optimal fashion, the reliability of the bimodal percept of a right angle should be greater than those from the unimodal conditions, i.e., the bimodal percept should be more precise (less variable) than either the visual or proprioceptive percept. The amount by which this variability should decrease when combining visual and proprioceptive information should be similar to that predicted by the MLE model.

Our results confirmed both predictions made by the MLE model, suggesting that integration of visual and proprioceptive movement information for the perception of trajectory geometry follows the optimal observer model.

Methods

Participants

We recruited 15 female participants (mean age: 22.07 years, range: 20–26 years) who voluntarily took part in this experiment. However, we eliminated three participants that produced outliers greater than two standard deviations from the mean for each condition and included

12 participants in the statistical analyses. They were naïve to the purpose of the study and were paid for participation. All participants had normal or corrected-to-normal vision and were right handed as assessed by a German translation of the Edinburgh Handedness Inventory (mean ± standard deviation: 86.37 ± 14.00) (Oldfield 1971). The experiment lasted approximately 70 min, and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (2000).

Apparatus and experimental conditions

The experiment took place in a completely darkened room, where participants sat in front of a table on which an apparatus was mounted. We used two programmable servomotors controlled by LabVIEW (http://www.ni.com/labview/) for driving the device of the apparatus. Movements of the device had two degrees of freedom (x and y plane) and occurred across a horizontal workspace (1.3 m × 1.7 m). Here, the handle pursued only straight movements with an acceleration of 0.3 m/s^2; reaching a maximum velocity of 0.2 m/s. For each and every trial, the hand started at a location 25 cm in front of the chest, aligned to the participants' body midline. The movement path consisted of two consecutive trajectories, each 15 cm long (Fig. 1a), which were accomplished within 3,000 ms. The first trajectory started in the middle of the participants' chest and moved to the right with an inclination angle of 35° referring to the horizontal edge of the table. The second trajectory was oriented to the first one with an inclination angle varying between 35° and 145°, thereby building an acute- or obtuse-angled movement path, respectively. An LED was mounted on top of the handle and was turned on during the movement depending on the experimental condition. Thus, the apparatus allowed us to present visual, proprioceptive, or bimodal information along trajectories. The participants' task was to indicate whether they perceived an acute- or obtuse-angled movement path, for each of three sensory conditions. To this end, we presented two single-cue conditions and one double-cue condition. In the unimodal proprioceptive condition, participants were blindfolded and instructed to hold the handle with a precision grip using the thumb and index finger of their dominant right hand. The handle passively moved the participants' right arm inducing changes in muscles, tendons, and joints (i.e., proprioceptive input). Since the proprioceptive information was acquired by the moving limb, visual stimuli were presented as a dot of light moving along the same trajectories as the hand in the proprioceptive condition. In this unimodal visual condition, participants saw the moving LED while their right hand remained on the table top in front of their chest in a comfortable resting position across trials. In the bimodal visual-proprioceptive condition, participants saw the movement of the LED while their right arm was simultaneously moved by the handle and thus they were provided with

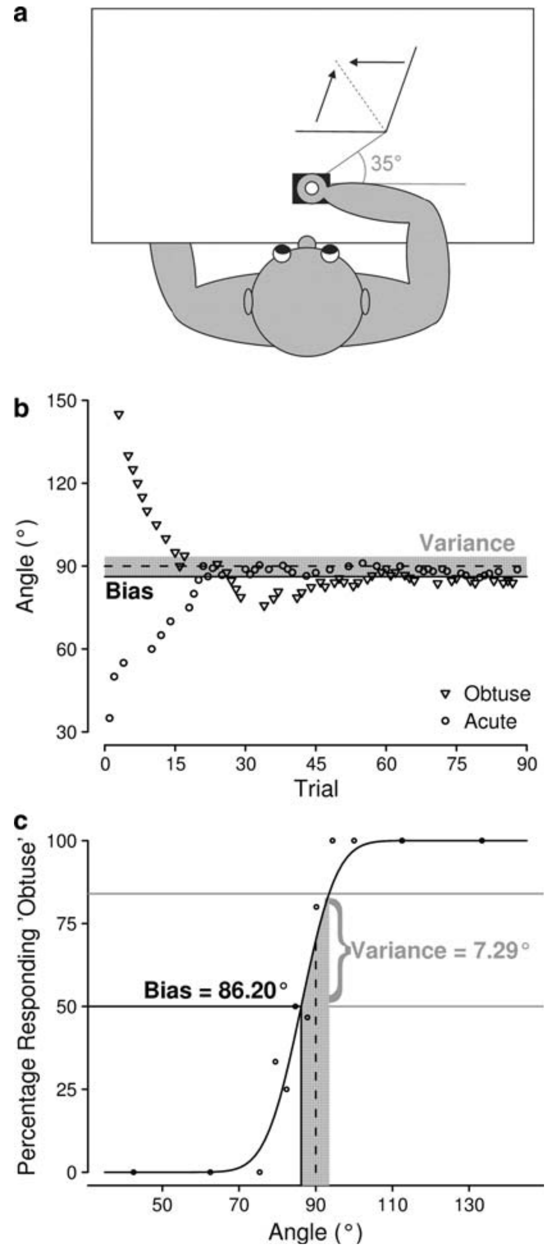

Fig. 1 Presentation of stimuli. **a** The angular movement of the handle started at the body's midline with a right-tilted trajectory followed by a second trajectory, whose angle varied from 55° to 145°. Participants had to decide if the trajectories formed an acute or an obtuse angle. **b** Data of one participant showing 44 obtuse-angled and 44 acute-angled trials (summed to a total of 88 trials), which were randomly presented. *Triangles* depict the obtuse-angled staircase starting with an angle of 145°. *Circles* represent the acute-angled staircase starting with an angle of 35°. **c** Psychometric function of one participant (Gaussian fit to data from Fig 1b). The right-angled reference is marked by the *dashed line*, the bias by the *black solid line,* and the variance by the *shaded area* (**b** and **c**). The bias is defined as the 50% point (μ) of the psychometric function, and variance as the difference between the 50 and 84% point (σ) of the psychometric function

information from both modalities. Each participant performed the three conditions in randomized order.

Procedure

Prior to the experiment we aligned the starting position of the handle to the body midline of each participant. Furthermore, we used an immoveable but adjustable chair and a chin rest to ensure constant body posture throughout the experiment. The height of the chair, the chin rest, and the placement of the button box were adjusted for each individual for a comfortable seat position.

At the beginning of each experimental condition participants positioned their left hand on the response box and started the experiment by pressing the enter key when they were ready to start. Each experimental condition consisted of 88 trials and each trial proceeded in the following way. A high-pitched tone (duration: 500 ms) was presented through the headphones indicating the start of the movement (duration: about 3,000 ms). After movement completion, a low-pitched tone (duration: 500 ms) occurred. This second tone prompted the participants to judge whether the path geometry was acute- or obtuse-angled, i.e., participants should discriminate between 'yes, this path geometry exceeded 90°' (i.e., obtuse), and 'no, this path geometry was less than 90°' (i.e., acute). We used a single interval to rule out any memory component. Moreover, we instructed the participants to focus on the whole movement, i.e., path geometry. Indeed, evaluation of used strategies validated that they really proceeded in this way. Participants indicated their judgments by pressing one of two response buttons with the index or the middle finger of the left hand. After the participants' response, the handle immediately returned to the start position and the next trial was initiated.

We generated the trajectories by two randomly interwoven adaptive staircase procedures (see Treutwein 1995, for a review), one beginning with an obvious acute angle (35°) and the other with an obvious obtuse angle (145°). Each staircase consisted of 44 steps, resulting in a total of 88 trials (Fig. 1b). In the first two trials we applied the stochastic approximation by Robbins-Monro (Robbins and Monro 1951):

$$X_{n+1} = X_n - \frac{c}{n}(Z_n - \phi) \tag{1}$$

where n is the number of the current trial, X the value of the stimulus, and c the initial step size (set at 15°). Z defines if the response was correct (1) or incorrect (0), referring to the corresponding staircase (e.g., 'acute' is correct for the acute- and incorrect for the obtuse-angled staircase). ϕ is the probability of responding in a correct or incorrect way with respect to the corresponding staircase (0.5 in a yes–no-design). For the following trials we used the accelerated stochastic approximation by Kesten (1958):

$$X_{n+1} = X_n - \frac{c}{2 + m_{\mathrm{shift}}}(Z_n - \phi) \tag{2}$$

which additionally includes m_{shift} for the number of shifts in the response category, i.e., m_{shift} increased by one when the response switched from obtuse- to acute-angled along one staircase. For each staircase, the angular path became less acute or obtuse (i.e., closer to being a right angle) when the response was consistent with the previous response for the same staircase and increasing if it was not. The adaptive staircase procedure enabled us to reliably determine the bias and the variance because the stimuli were mainly presented around these parameters. Averaged across all participants, about 38% of all trials consisted of trajectories close to the bias (between the 40 to 60% point of the psychometric function), and about 44% of trajectories occurred around the 10–40% and 60–90% range of the psychometric function. These values were crucial for our variance estimate computed as the difference between the 50 and 84% point on the best fitting psychometric function.

Before the experiment, we assured that participants were familiar with the geometrical concepts of acute, obtuse, and right angles. In addition, participants performed a short training session prior to each of the three experimental conditions, where the reference trajectory (right angle) and the most deviating acute- and obtuse-angled trajectories were presented alternately. The training sessions were implemented to ensure that all participants were familiar with the movements of the device, and that they had a concrete idea of the internal reference of a right angle and the first acute- and obtuse-angled stimuli.

Data analysis

We collected angular data on a circular scale which can be analyzed by circular statistics using specialized models, e.g., the wrapped normal distribution (Fisher 1993; Jammalamadaka and SenGupta 2001). However, for our results for the range of angles tested (discrepancy between modalities <35°; variances <20°), the wrapped normal distribution is nearly identical to the Gaussian distribution which we chose for simplification and comparability to previous results (e.g., Chen and Levi 1996; Helbig and Ernst 2007; Lakatos and Marks 1998; Regan et al. 1996; Voisin et al. 2002).

Applying the adaptive staircase algorithm, we acquired 88 values of the presented angles and the corresponding responses per participant and experimental condition (Fig. 1b). In order to obtain estimates for perceptual variability and bias, we determined individual psychometric functions for each condition. We then fitted cumulative

Gaussian functions to the psychometric functions using the psignifit toolbox for MATLAB (see http://www.boostrap-software./org/psignifit/; Wichmann and Hill 2001), which implements maximum-likelihood estimation methods. The bias was defined as the point where the angle was judged to be acute or obtuse with equal frequency. Thus, the bias is equal to the mean of the Gaussian distribution (50% point of the psychometric function; Fig. 1c) and corresponded to the angle which was perceived as right-angled. To measure the variance of the percept, we calculated the difference between the bias and the 84% point of the psychometric function. This difference corresponded to one standard deviation of the Gaussian distribution (Fig. 1c). Hence, the variance determined how much an angle had to deviate from a trajectory perceived as right-angled to reliably discriminate this angle as obtuse or acute. We calculated these two variables (bias and variance) for each participant, for each condition. These values were used to test the MLE model across all participants.

Results

Predicting bimodal movement discrimination of angular trajectories

The purpose of this study was to investigate whether visual and proprioceptive movement information along angular trajectories is integrated in a statistically optimal fashion. To this end, we calculated the perceptual bias and variability for each experimental condition (unimodal visual, unimodal proprioceptive, and bimodal visual-proprioceptive). The visual and the proprioceptive biases differed significantly from each other and from the bimodal bias. As predicted, the proprioceptive modality showed a clear bias in the acute direction compared to the visual modality ($t_{(11)} = -3.48$; $p < 0.05$; one-sided t test; Fig. 2a), i.e., angles which were perceived as right-angled were more acute in the proprioceptive than in the visual condition. The bimodal bias lay between the unimodal biases and differed significantly from both unimodal estimates (from vision: $t_{(11)} = 2.02$; $p < 0.05$; from proprioception: $t_{(11)} = -4.00$; $p < 0.05$; one-sided t tests; see Fig. 2a). We used this natural discrepancy to predict the bimodal performance from both unimodal estimates according to the MLE model of optimal integration. The MLE predicts the bimodal percept (i.e., the bias, $\hat{S}_{vp}$) by a weighted average of the unimodal estimates (bias of vision $\hat{S}_{v}$, and proprioception $\hat{S}_{p}$):

$$\hat{S}_{vp} = w_v \hat{S}_v + w_p \hat{S}_p \quad (3)$$

The weights are chosen according to the unimodal reliabilities:

$$w_v = \frac{r_v}{r_v + r_p} \quad (4)$$

and correspondingly for w_p. That is, the optimal visual (w_v) and proprioceptive weights (w_p) are formed by their reliability (visual reliability r_v; proprioceptive reliability r_p), standardized at the total reliability. Thus, less reliable percepts contribute to a combined bimodal percept with a lower weight. The reliability (r) is the inverse of the variance (σ^2):

$$r = \frac{1}{\sigma^2} \quad (5)$$

The variance in the present study corresponded to the standard deviation σ. Consequently, this parameter could be used to compute the reliability for each modality.

Furthermore, the MLE model predicts (given that noise distributions are independent and follow a Gaussian distribution) that the reliability of the bimodal percept is the sum of the unimodal reliabilities:

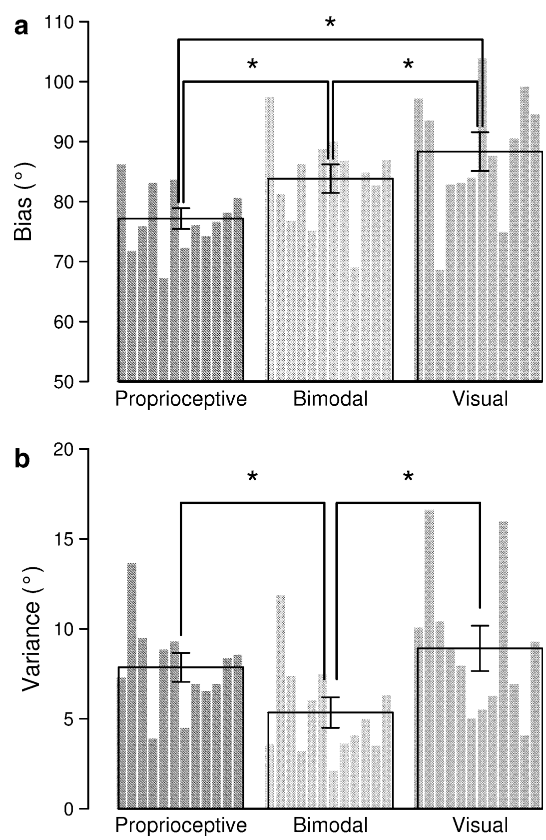

Fig. 2 Results of paired t tests for the biases (**a**) and variance (**b**) of the unimodal and bimodal estimates for all participants (*thin bars*). *Thick open bars* show these estimates averaged across participants for the bimodal visual-proprioceptive, the unimodal proprioceptive, and the unimodal visual perception. Significant differences of means are marked by an *asterisk*. *Error bars* are standard errors of the mean

$$r_{vp} = r_v + r_p \quad (6)$$

Correspondingly, the variance of the bimodal percept (σ^2_{vp}) should be reduced compared to those of the single modalities:

$$\sigma^2_{vp} = \frac{\sigma^2_v \sigma^2_p}{\sigma^2_v + \sigma^2_p} \quad (7)$$

As predicted, the variance for proprioceptive estimates ($t_{(11)} = 8.12$; $p < 0.05$) and for visual estimates ($t_{(11)} = 3.52$; $p < 0.05$) was significantly larger than that for bimodal-based estimates (Fig. 2b). This indicates that the unimodal information was less reliable than the bimodal information about angular path.

Following the MLE rule, we computed the predicted bias and variance for the bimodal percept according to Eqs. 3–7. The mean and standard deviation of the bias and the variance across participants are presented in Table 1. Figure 3a illustrates the psychometric functions of the observed data for the three experimental conditions (unimodal visual, unimodal proprioceptive, and bimodal visual-proprioceptive), and the predicted bimodal percept for two representative participants. The percentage of obtuse responses was plotted as a function of the angle between the trajectories. At the 50% point of the psychometric function, participants equally responded obtuse- or acute-angled, whereas at the 84% point ($\mu + \sigma$ in Gaussian function), they reliably judged the perceived angle as obtuse. Figure 3b shows the corresponding density functions for the observed visual, observed proprioceptive, and observed and predicted bimodal spatial perception for the same two participants. The means of the density curves correspond to the biases, whereas the height and width represent the variance. A curve which is higher and narrower indicates a lower variance and vice versa.

Predicted versus observed bimodal movement discrimination for angular trajectories

Next, we compared the observed and the predicted parameters for the bimodal percept in order to determine whether visual and proprioceptive movement information is integrated in a statistically optimal way. We first compared the bias and the variance between observed and predicted parameters of a combined percept and then conducted regression analysis to quantify how well these predicted and observed values correlated with each other.

Table 1 The means and standard deviations (SD) for the bias and the variance

	Bias		Variance	
	Mean	SD	Mean	SD
Proprioceptive	77.14	5.52	7.86	2.54
Visual	88.32	10.25	8.91	3.98
Bimodal (obs.)	83.80	7.54	5.35	2.68
Bimodal (pred.)	82.79	6.44	5.53	1.97

The results are listed separately for the unimodal proprioceptive, unimodal visual, observed (obs.) bimodal, and predicted (pred.) bimodal movement perception for angular trajectories

As shown in Fig 4a, there are no significant differences between the bimodal parameters predicted by the MLE model (mean of bias = 82.79°; mean of variance = 5.53°) and those observed (mean of bias = 83.80°; mean of variance = 5.35°), for the bias ($t_{(11)} = 0.65$; $p = 0.53$) or the variance ($t_{(11)} = -0.44$; $p = 0.67$). Thus, the mean observed and mean predicted bimodal parameters (bias and variance) seem to be comparable.

The correlations between the predicted and the observed integration of vision and proprioception are demonstrated in Fig 4b. The regression analyses revealed significant R-squares for both the bias ($R^2 = 0.50$; $F_{(1,11)} = 9.94$; $p < 0.01$) and the variance ($R^2 = 0.69$; $F_{(1,11)} = 25.97$; $p < 0.01$). This indicates that the observed and the predicted bimodal perception performances across participants are strongly correlated. Furthermore, regression lines do not differ significantly from a slope of one (bias: $t_{(11)} = -0.66$; $p = 0.52$; variance: $t_{(11)} = 0.70$; $p = 0.50$) nor an intercept of zero (bias: $t_{(11)} = 0.71$; $p = 0.50$; variance: $t_{(11)} = -0.80$; $p = 0.44$), i.e., they are aligned with the identity.

Discussion

The aim of this study was to investigate whether visual and proprioceptive movement information used for perception of angular trajectories is integrated in a statistically optimal way into a unified percept. The MLE model makes two predictions for optimal integration: first, different sensory information is optimally integrated by a weighted average of the unimodal information and second, this integration results in a reduced multisensory variance compared to the corresponding unimodal variances. According to the prediction, visual and proprioceptive movement information is combined into a bimodal percept by a weighted average of single modalities, comparable to the observed bimodal bias. Second, the bimodal percept should be less variable (more precise) than the unimodal percept and more comparable to the variance predicted by the MLE model. As required for testing the first prediction, our data showed natural discrepancies between the visual and proprioceptive biases. The present results revealed similar predicted and observed bimodal biases confirming the first prediction of the MLE model. We further observed higher variance for visual and proprioceptive percepts compared to bimodal percept and a strong correlation between observed and

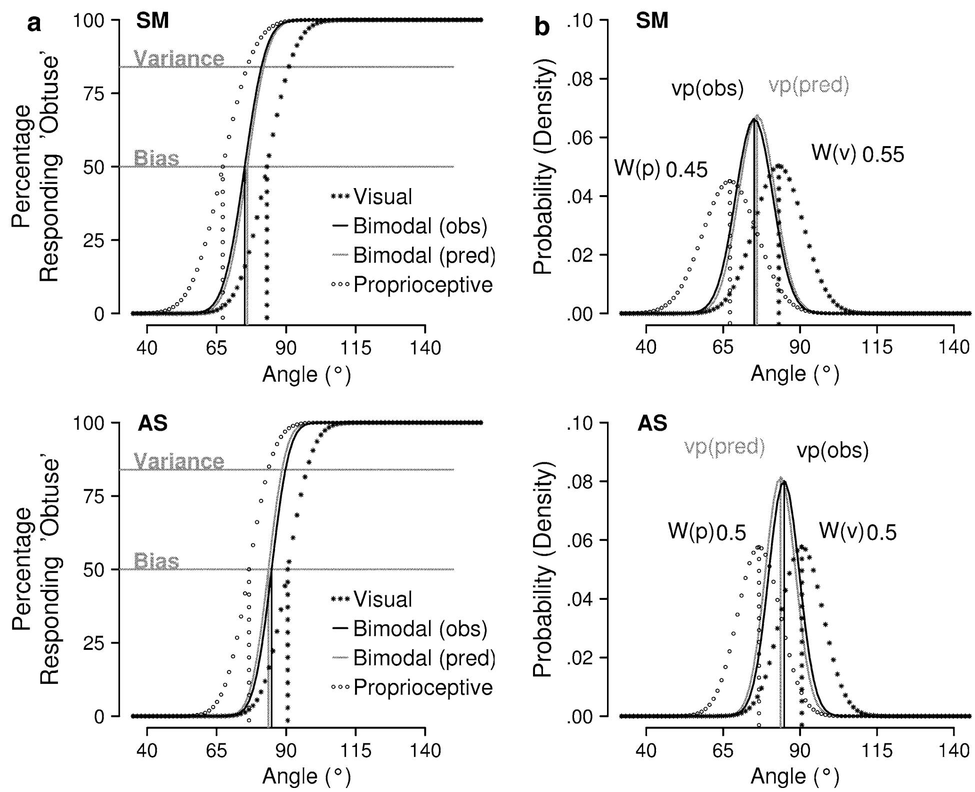

Fig. 3 Psychometric functions (**a**) and density curves (**b**) of two participants (SM and AS), showing the bias and the variance for the proprioceptive (*gray dotted line*), visual (*black dotted line*), observed (obs.) bimodal (*black solid line*) and predicted (pred.) bimodal percept (*gray solid line*). **a** Psychometric functions. The bias (single estimate) is defined as the 50% point (μ) of the psychometric function, and the variance as the difference between the 50 and 84% point (σ) of the psychometric function. **b** Density functions. The bimodal percept is signed as visual-proprioceptive (vp). The means of the density curves reflect the bias, and their width and height reflect the variance (higher and narrower shapes reflect a lower variance). The variance defines the weights of the single modalities that correspond to their contribution to a unified bimodal percept. W(p) is the weight of the proprioceptive perception and W(v) is the weight of the visual perception; both are used for predicting the bimodal bias

predicted bimodal variances, consistent with the second prediction by the MLE model. Overall, our results confirm the predictions from the MLE model suggesting that visual and proprioceptive movement information of trajectory geometry is optimally integrated.

The results of the present study fit well with recent research on integration of multisensory information. It has been shown that the integration of unimodal information perceived by the same sensory system (vision: Hillis et al. 2004; Knill and Saunders 2003; haptics: Drewing and Ernst 2006; Drewing et al. 2008), as well as information perceived from different senses (Alais and Burr 2004b; Ernst and Banks 2002; Helbig and Ernst 2007, 2008; van Beers et al. 1996, 1999) are optimally integrated. Our results confirm the predictions of the MLE model and thus extend previous findings to the integration of visual and proprioceptive movement information for the perception of trajectory geometry. Van Beers et al. (1996, 1999) first investigated integration of visual and proprioceptive sensory information for perception of position by having participants match the position of proprioceptive, visual, or visual-proprioceptive targets with their index finger. Examining the visual-proprioceptive integration of position information they found that visual localization was more precise in the azimuth than in the radial direction (depth) and that proprioceptive localization was more precise in the radial (depth) than in the azimuth direction (van Beers et al. 1999). Furthermore, the authors (van Beers et al. 1999) convincingly showed that mechanisms integrating visual and proprioceptive position information efficiently take into account these direction-dependent reliabilities predicted by optimal integration. We extended the results of multisensory integration of spatial position information (van Beers et al. 1996, 1999) to multisensory integration of movement information of path geometry. Thus, we quantitatively validated the MLE model for moving visual and proprioceptive spatial information. To this end, we used purely visual and purely proprioceptive stimuli in the unimodal conditions and used the same stimulus presentation in the bimodal condition as well.

In the present study, participants underestimated angular trajectories in the unimodal proprioceptive condition,

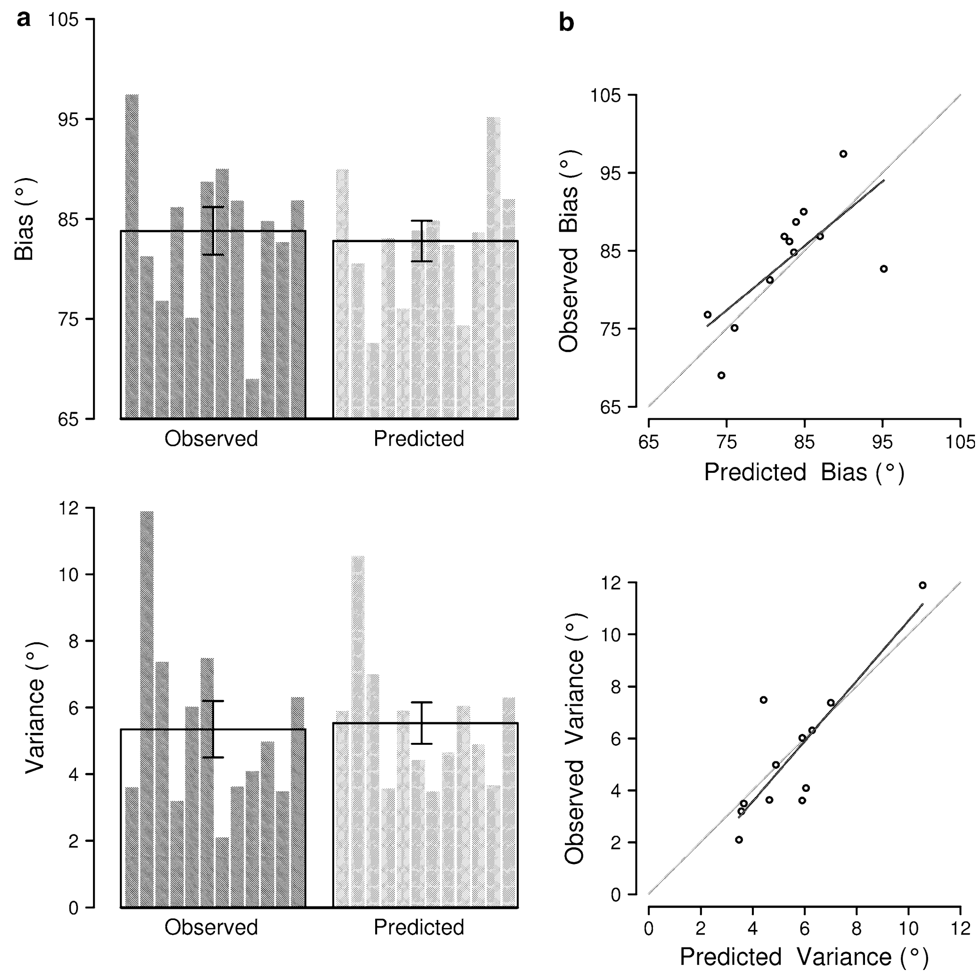

Fig. 4 Comparison of observed and predicted parameters. **a** *Thin bars* represents the bias (*top panel*) and variance (*bottom panel*) for each participant while the *thick bars* represent the averages across participants. *Error bars* are standard errors of the mean. **b** Scatter plots of the bias (*top panel*), and variance (*bottom panel*): observed bimodal values of each participant are plotted as a function of predicted bimodal values. The relationship between observed and predicted bimodal values is illustrated by the regression line (*black solid line*). The identity with an intercept of zero and a slope of one is depicted by the *gray solid line*

overestimated angular trajectories in the unimodal visual condition, and showed a nearly unbiased perception in the bimodal (visual proprioceptive) condition. The observed values for the visual, proprioceptive, and visual-proprioceptive biases are comparable to previous findings of Lakatos and Marks (1998), who investigated the accuracy with which angles are perceived. Their results differed from ours by about 2° for the proprioceptive bias, and 1° for the visual and visual-proprioceptive biases.

We found a higher variance in vision and proprioception compared to the bimodal percept. The variability of proprioceptive estimates of hand path angles were similar to those of Voisin et al. (2002) when we applied the same mode of variance calculation (the difference between the 50 and 75% point of the psychometric function; Voisin et al. 2002: mean of 7.16° versus present data: mean of 5.33°). In the study by Voisin et al. (2002), participants ran their index finger along two edges of a triangle constructed from Plexiglas after the finger had been anaesthetized, i.e., judgments were based on proprioceptive information only, not tactile information. However, other studies have suggested that people are more sensitive to detecting angular deviation for visual stimuli (in the order of 1°–2°; Chen and Levi 1996; Kennedy et al. 2006; Regan et al. 1996) than that which was suggested by our own results. This is likely because these other studies used whole lines while we used a sequential presentation of a moving dot. A lower variance of vision and therefore a higher weight of vision compared to other sensory information were observed in non-conflict conditions of several integration studies as well (Alais and Burr 2004b; Ernst and Banks 2002; Helbig and Ernst 2007). However, in the present study, proprioception and vision contributed to the bimodal percept nearly to the same extent, i.e., vision and proprioception were equally reliable. This may be due to some experimental factors. First, participants perceived trajectories in two-dimensional space, including not only azimuth but also depth information. Previous experiments on space perception (Gepshtein and Banks 2003; van Beers et al. 2002) have shown that in depth direction proprioception is more heavily weighted than vision. Second, visual information was presented sequentially rather than simultaneously: this made the angle along which the dot moved much more difficult to decipher than if the visual stimuli showed the complete movement path, i.e., an angle with two visible lines. This is why we attempted to make the stimuli presentation similar across the modalities. So, given the greater difficulty in detecting the angle of a moving dot, it is not surprising that the reliability of this visual information be poorer and therefore more equivalent to that of proprioceptive information, and thus leads to equal variance of both proprioception and vision.

The results of the present study together with previous MLE findings give some indication of putative underlying brain mechanisms responsible for multisensory integration. Recent studies propose several brain areas involved in multisensory integration. The primary sensory cortices (Martuzzi et al. 2007), subcortical structures, like the superior colliculus (Calvert et al. 2001), and cortical convergence zones, like the superior temporal sulcus (STS) (Beauchamp et al. 2004), or the intraparietal sulcus (IPS) in the posterior parietal cortex (PPC) (Calvert et al. 2001), have been discussed as neural substrates of multisensory integration (for a review see Amedi et al. 2005). Consistently, electrophysiological studies in monkeys (Duhamel et al. 1998; Schlack et al. 2005) and in humans (Gobbelé et al. 2003; Gondan et al. 2005), and functional imaging studies in humans (Macaluso et al. 2003; Ricciardi et al. 2006; Fiehler et al. 2008), have found activation in the PPC during spatial processing using different sensory modalities. Polymodal neurons responding to self movements and motion stimuli in peripersonal space irrespective of the sensory modality have been identified in monkey IPS, in particular within the ventral intraparietal area (VIP) (Duhamel et al. 1998). Accordingly, neuroimaging studies suggest a putative human homologue of the macaques' polymodal area VIP which is responsive to visual, tactile, and auditory motion stimuli (Bremmer et al. 2001; for a review see Grefkes and Fink 2005). Furthermore, studies in humans have found that brain regions which are usually activated during visual motion perception [human middle temporal/V5 complex (MT/V5)], were also active during tactile (Blake et al. 2004) or auditory motion perception (Alink et al. 2008).

However, it remains unclear whether the discussed brain areas integrate multisensory input in a statistically optimal fashion. A recent study in monkeys investigated the neural mechanisms underlying multisensory integration by using combined electrophysiological and psychophysical methods (Gu et al. 2008). While monkeys had to integrate visual and vestibular tilt information, neuronal activity was recorded in the monkeys' dorsal medial superior temporal (MSTd) area—located near area MT and sensitive to movements in space. The response of MSTd neurons was highly correlated with behavioral performance, i.e., firing rates reflected the response pattern predicted by MLE based on the behavioral data. The approach of combining different techniques could advance our understanding of brain functioning, and thus provide direction for future research.

In conclusion, the present results suggest that movement information of trajectory geometry perceived by vision and proprioception is integrated in a statistically optimal fashion, following the MLE.

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