Exp Brain Res (2011) 209:619–630
DOI 10.1007/s00221-011-2596-0

RESEARCH ARTICLE

Testing the limits of optimal integration of visual and proprioceptive information of path trajectory

Johanna Reuschel · Frank Rösler ·
Denise Y. P. Henriques · Katja Fiehler

Received: 12 April 2010 / Accepted: 7 February 2011 / Published online: 24 February 2011

Abstract Many studies provide evidence that information from different modalities is integrated following the maximum likelihood estimation model (MLE). For instance, we recently found that visual and proprioceptive path trajectories are optimally combined (Reuschel et al. in Exp Brain Res 201:853–862, 2010). However, other studies have failed to reveal optimal integration of such dynamic information. In the present study, we aim to generalize our previous findings to different parts of the workspace (central, ipsilateral, or contralateral) and to different types of judgments (relative vs. absolute). Participants made relative judgments by judging whether an angular path was acute or obtuse, or they made absolute judgments by judging whether a one-segmented straight path was directed to left or right. Trajectories were presented in the visual, proprioceptive, or combined visual–proprioceptive modality. We measured the bias and the variance of these estimates and predicted both parameters using the MLE. In accordance with the MLE model, participants linearly combined and weighted the unimodal angular path information by their reliabilities irrespective of the side of workspace. However, the precision of bimodal estimates was not greater than that for unimodal estimates, which is inconsistent with the MLE. For the absolute judgment task, participants' estimates were highly accurate and did not differ across modalities. Thus, we were unable to test whether the bimodal percept resulted as a weighted average of the visual and proprioceptive input. Additionally, participants were not more precise in the bimodal compared with the unimodal conditions, which is inconsistent with the MLE. Current findings suggest that optimal integration of visual and proprioceptive information of path trajectory only applies in some conditions.

Keywords Maximum likelihood estimation · Perceptual discrimination · Path trajectories · Vision · Proprioception

Introduction

Many of our daily activities, like grasping a pen from the desk, require us to process information of hand path by using different sensory modalities. Thus, seeing and simultaneously feeling a trajectory enables us to control and optimize goal-directed movements (Goodbody and Wolpert 1999; Flanagan and Rao 1995; Sergio and Scott 1998).

Processing velocity and position information of moving objects are supposed to occur in parallel, but independent of each other, in proprioception and also in vision (Goble and Brown 2009; Proske and Gandevia 2009; Sittig et al. 1985; Smeets and Brenner 1995). This holds for both action (controlling or matching position or velocity) and perception (judging position or velocity) (Sittig et al. 1985; Smeets and Brenner 1995). Hence, the brain is able to use both dynamic and static information, processed parallel and via different sensory channels (e.g., vision and proprioception) for monitoring and controlling movements. However, it still remains unclear how these different sources of information are combined in the brain.

J. Reuschel (✉) · F. Rösler · K. Fiehler (✉)
Department of Experimental and Biological Psychology,
Philipps-University Marburg, Gutenbergstr. 18,
35032 Marburg, Germany
e-mail: johanna.reuschel@staff.uni-marburg.de

K. Fiehler
e-mail: fiehler@staff.uni-marburg.de

D. Y. P. Henriques
School of Kinesiology and Health Science,
Center for Vision Research, York University,
Toronto, ON, Canada

Using different sensory modalities (e.g., vision and proprioception) simultaneously improve perception or localization of stimuli (see Driver and Noesselt 2008 for a review). According to the maximum likelihood estimation (MLE) model, humans weight information from different sensory modalities as a function of the reliability of each of the unimodal estimates and integrate the weighted estimates into a unitary percept (Ernst and Banks 2002; Ernst and Bülthoff 2004; Landy et al. 1995; van Beers et al. 1999; Yuille and Bülthoff 1996). As a consequence, optimal integration occurs when more reliable estimates are weighted higher than less reliable ones; thus, the bimodal percept would be less variable. Several studies confirmed this model by showing that the perception and localization of bimodal stimuli are more precise than that for unimodal stimuli, e.g., when integrating visual and proprioceptive locations (van Beers et al. 1996), visual and auditory position information (Alais and Burr 2004b), or visual and auditory motion information (Alais and Burr 2004a; Meyer et al. 2005; Wuerger et al. 2003), and finally, we recently found optimal integration of visual and proprioceptive path trajectories (Reuschel et al. 2010).

In our previous study, we presented movement trajectories in the center workspace. However, there is evidence that workspace direction could affect visually guided pointing movements. For instance, studies have found systematic directional biases depending on initial hand position (Ghilardi et al. 1995; Goodbody and Wolpert 1999) and kinematic advantages when pointing to targets in the extrapersonal ipsilateral space (especially on the right side) (Carey et al. 1996; Fisk and Goodale 1985; Ishihara and Imanaka 2007). Here, we aim to test whether optimal integration of movement trajectories is dependent on workspace. Therefore, participants perceived a two-segmented path trajectory in the left contralateral, and the right ipsilateral workspace and had to decide whether the two segments formed an acute or an obtuse angle.

Optimal integration of vision and proprioception has been repeatedly demonstrated for stimulus features, such as size (Ernst and Banks 2002; Gepshtein et al. 2005; Helbig and Ernst 2008), shape (Helbig and Ernst 2007), or position (van Beers et al. 1996). Sober and Sabes (2003, 2005) postulated that visual and proprioceptive information is integrated both during movement planning and execution, suggesting a similar combination rule for dynamic information as well. However, some recent studies were unable to find optimal combination across modalities for such dynamic cues, e.g., curvature of path trajectories (Winges et al. 2010), movement direction (Serwe et al. 2009), or remembered location of targets (Jones and Henriques 2010). These studies used one-segmented paths that required a response based on absolute judgments. Thus, our second goal was to examine whether optimal integration of visual and proprioceptive movement information depends on the type of judgment. In our previous study, we found optimal integration of two-segmented stimuli requiring a relative judgment of the movement direction (acute- or obtuse-angled relative to a right angle). In order to test optimal integration of absolute judgments, we presented participants with a straight path in the center of the workspace which they had to judge as being directed left or right (absolute judgment).

In summary, the current study is a follow-up of our previous study (Reuschel et al. 2010) to investigate whether optimal integration generalizes across different workspaces and different judgment types. To this end, we presented proprioceptive, visual, and combined visual–proprioceptive stimuli by moving the participants' hand (proprioceptive target) and/or a green LED (visual target) along path trajectories in the ipsilateral, contralateral, or central workspace while asking participants for an absolute or relative judgment of movement direction.

Methods

Participants

We recruited 46 naïve participants (11 male) aged from 18 to 28 (mean ± standard deviation: 21.17 ± 2.69) who voluntarily took part in this experiment. They were paid for their participation or received course credits. 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: 85.34 ± 13.74) (Oldfield 1971). None of them had a known history of neurological disorder. The experiment consisted of two experimental sessions that were accomplished within one week. It was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Experimental setup

Participants performed the experiment in a completely darkened room, sitting in front of a table on which an apparatus was mounted. Like in previous studies (Fiehler et al. 2009; Reuschel et al. 2010), 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–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. The device has a high spatial resolution with a repetition accuracy of ±0.2 mm and a

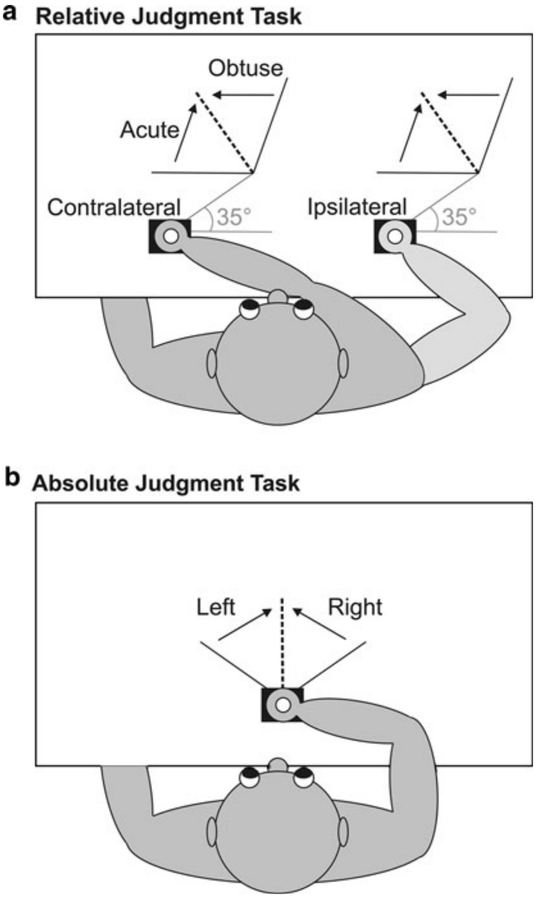


Fig. 1 Presentation of the stimuli started 25 cm in front of the body in both tasks. **a** In the relative judgment task, the angular movement of the handle started 16 cm to the left (contralateral workspace) or to the right (ipsilateral workspace) of the body midline with a right-directed trajectory (35° with reference to the horizontal edge of the table), always followed by a second trajectory at an angle which varied from 35° to 145° (i.e., differed by 55° to the obtuse or acute side of a right angle). Participants had to decide whether the two trajectories formed an acute or an obtuse angle with reference to a right angle, separate for the ipsilateral and contralateral workspaces. **b** In the absolute judgment task, the movement of the handle started at the body midline and moved along a straight trajectory away from the body, while the direction varied from 55° to the left to 55° to the right. Participants had to decide whether this trajectory was directed to the left or to the right, with reference to a straight line along their body midline

limit switch accuracy of <0.1 mm. Furthermore, the movement started about 100 ms after the movement command was sent to the servomotor. The target paths comprised one or two consecutive trajectories, each 15 cm long (black solid lines in Fig. 1), accomplished within 1,500 ms. Visual movement presentation was provided by a green LED mounted on the top of the handle; the experimental condition determined whether or not the LED was turned on. The handle could be comfortably gripped by the participants' right hand, which was passively moved along trajectories for proprioceptive movement presentation. Thus, the apparatus allowed us to present visual, proprioceptive, or bimodal (visual–proprioceptive) targets in a sequential order. Participants indicated their judgments by pressing one of two response buttons with the index or the middle finger of the left hand.

Procedure

The experimental procedure was comparable to the one in our previous study (see Reuschel et al. 2010). Prior to the experiment, we aligned the middle starting position of the handle to the body midline of each participant at a location 25 cm in front of the chest. Furthermore, we used an immoveable, but adjustable, chair and a chin rest to ensure a constant body posture during the experiment. Moreover, we masked the sound of the servomotor using random noise recorded from the movement device in order to prevent participants from auditory stimulus encoding.

Participants started the experimental blocks by pressing a start button. At the beginning of each trial, a high-pitched tone (duration 500 ms) was presented through the headphones indicating the start of the movement. A second low-pitched tone (duration 500 ms) denoted movement completion (movement duration 3,000 ms for the two-segmented trajectory and 1,500 ms for the one-segmented trajectory) and prompted the participants to indicate their response. After the response, the handle immediately returned in a straight course to the start position and the next trial ensued.

Participants performed two different judgment tasks in different sensory modalities. In the relative judgment task (Fig. 1a), they had to decide whether a target path consisting of two linear trajectories followed an acute or an obtuse angular course (comparable to the path trajectory and type of judgment in Reuschel et al. 2010). Both trajectories had a constant length of 15 cm. The first trajectory 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 (black solid lines in Fig. 1a), respectively. Since we were interested whether optimal integration of movement information occurs across different workspaces, the angular stimuli were presented in the ipsilateral (right) and contralateral (left) workspaces. Therefore, the starting position of the first trajectory was shifted 16 cm to the left (contralateral) or to the right (ipsilateral) with respect to the body midline.

For the absolute judgment task (Fig. 1b), the handle moved away from the body along a linear path (black solid line in Fig. 1b) with a length of 15 cm and an inclination angle of 55° left or right of a straight line starting at the middle of the participants' chest (center workspace;

comparable to the location in Reuschel et al. 2010). Afterward, participants had to decide whether the movement trajectory was directed to the left or to the right, i.e., they had to asses the movement direction on the basis of an absolute judgment, compared with the angular movement path that requires a relative judgment. We presented stimuli in the visual, proprioceptive, or bimodal (visual–proprioceptive) domain and varied the sources of movement information in a block-wise manner.

In the visual condition, participants saw the trajectories of an LED placed on top of the handle in a completely darkened room, i.e., they could only see the moving dot of light, but no other environmental information. During visual stimulus presentation, participants' right hand remained on the table top in front of their chest in a comfortable resting position across trials. However, in the proprioceptive condition, participants were blindfolded and instructed to hold the handle like a pen in a precision grip with their right thumb and index finger. In the absence of visual feedback, the handle passively moved the participants' right arm along the trajectories inducing changes in muscles, tendons, and joints, i.e., they received proprioceptive input. For the bimodal (visual–proprioceptive) condition, participants saw the LED, while their right arm was simultaneously moved by the handle, providing both visual and proprioceptive information of the movement path.

In total, each participant randomly performed nine blocks divided into two sessions: three blocks (visual, proprioceptive, bimodal visual–proprioceptive) of the relative judgment task in the ipsilateral workspace, three in the contralateral workspace and three blocks (visual, proprioceptive, bimodal visual–proprioceptive) of the absolute judgment task in the center workspace. Each of the two sessions lasted about two and a half hours.

We adjusted the stimuli using two randomly interwoven adaptive staircase procedures (Fig. 2a) (see Treutwein 1995 for a review), a method already approved in previous studies (see Fiehler et al. 2009; Henriques and Soechting 2003; Reuschel et al. 2010 for details). For each staircase, the target converged to the angle or direction participants perceived as being aligned with the right-angled or the straight path when the response was consistent with the previous judgment and diverged if it was not.

Before the experiment, participants performed a short training session prior to each of the nine experimental blocks.

Data analysis

To measure participants' estimates for perceptual variance and bias, we fitted a psychometric function (Fig. 2b) to the responses of each participant for each task and condition. Specifically, we used the cumulative Gaussian function from the MATLAB psignifit toolbox (see http://www.bootstrap-software./org/psignifit/; Wichmann and Hill 2001) which implements maximum likelihood estimation methods for estimating both parameters; the bias and the variance. The bias is a measure of sensory accuracy defined as the point where participants judge the target being acute- and obtuse-angled (relative judgment task) or left- and right-directed (absolute judgment task) with equal frequency, i.e., the bias is equal to the 50% point of the psychometric function (Fig. 2b). The second parameter, the variance, is also known as the difference threshold and is a measure of the sensory precision. We computed the variance as the difference between the bias and the 84% point of the psychometric function (Fig. 2b), which corresponds to one standard deviation of the Gaussian distribution.

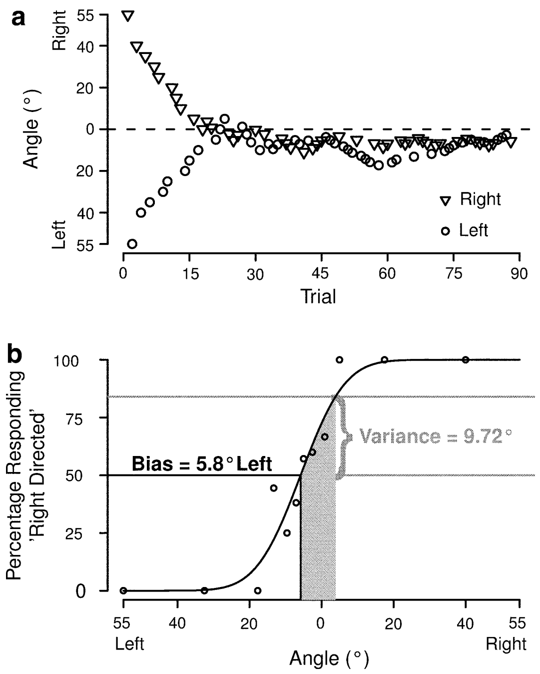


Fig. 2 Data of one representative participant in the proprioceptive condition of the absolute judgment task. **a** Raw data showing 44 right-directed and 44 left-directed trials (a total of 88 trials), which were randomly presented. Triangles depict the right-directed staircase started with a tilt of 55° to the right. Circles represent the left-directed staircase which started with a tilt of 55° to the left. The midline at 0° is marked by the dashed line. **b** Psychometric function fitted to the responses depicted in Fig. 2a. The bias is defined as the straight trajectory that participants would report as being directed left (or right) 50% of the time. The variance is defined as the difference between responding 50% and 84% of the time left-directed (or right-directed)

Finally, we calculated both parameters (bias and variance) for each participant and condition and used these values to test the MLE model across all conditions and participants. For all analyses, we removed outliers (which deviated two standard deviations from the mean within a single condition = 4.47% of all data points across all participants or which deviated obviously from the regular pattern of the data = 0.24% of all data points across all participants).

The first prediction of the MLE assumes that the bimodal percept (i.e., the bias, $\hat{S_{vp}}$) is a weighted average of the unimodal estimates (bias of vision $\hat{S_v}$ and proprioception $\hat{S_p}$):

$$\hat{S}_{vp} = w_v\hat{S}_v + w_p\hat{S}_p \tag{1}$$

The weights for this linear combination are determined by the relative reliabilities of the single modalities:

$$w_v = \frac{r_v}{r_v + r_p} \tag{2}$$

According to this equation, the optimal weights (visual weight w_v) are composed of their reliability (visual reliability r_v; proprioceptive reliability r_p), standardized at the total reliability (analogously for the proprioceptive weight w_p). Thus, less reliable estimates have lower weights and a more modest contribution to the bimodal percept. The reliability (r) is defined by the inverse of the variance (σ^2):

$$r = \frac{1}{\sigma^2} \tag{3}$$

The variance determined as the parameter of the psychometric function corresponded to the standard deviation σ. Hence, we entered this parameter in Eq. 3 to compute the reliability for each modality.

Moreover, the MLE assumes that the noise of different unimodal estimates is Gaussian distributed and that these distributions are mutually independent from each other. On this basis, the reliability of the bimodal percept is the sum of the unimodal reliabilities:

$$r_{vp} = r_v + r_p \tag{4}$$

Accordingly, the bimodal percept (${\sigma^2}_{vp}$) will be less variable compared with the single modalities:

$$\sigma^2_{vp} = \frac{\sigma^2_v\sigma^2_p}{\sigma^2_v + \sigma^2_p} \tag{5}$$

Thus, the second prediction of the MLE consists of a bimodal reduction in variance, compared with the unimodal estimates. A maximal reliability of the combined percept, i.e., a minimal variance, indicates an optimal integration of both percepts.

To test the MLE model, we performed regression analyses and determined the fit between individual predicted bimodal and observed bimodal values. Furthermore, we tested whether the regression line resulting from these analyses was comparable to the identity line (with a slope of one and an intercept of zero), i.e., whether predicted and observed values were identical.

Results

The aim of this study was to investigate whether optimal integration of movement information occurs within different workspaces and for different judgment types. First, we tested for optimal integration of angular movements in the ipsilateral and contralateral workspaces, which required a relative judgment. Second, we examined whether optimal integration also holds for a one-segmented straight movement path that required an absolute judgment. Therefore, we assessed the bias and the variance as measures of accuracy and precision, respectively, for each condition (Table 1).

Optimal integration across the workspace

We investigated whether humans are able to integrate visual and proprioceptive trajectory information in an optimal manner, irrespective of the side of workspace (ipsi- vs. contralateral). Therefore, we used an angular path trajectory for which we already demonstrated an optimal integration in our previous study in the center workspace (Reuschel et al. 2010). In contrast, here, the path trajectories started in the ipsi- or contralateral workspace. We did not induce an artificial conflict between both sensory percepts, i.e., we did not add any noise to one of the two modalities. Thus, we first tested for a natural discrepancy between the visual and the proprioceptive bias, i.e., whether participants' bias was more acute for proprioception than for vision, as shown previously (Appelle 1971; Lakatos and Marks 1998; Reuschel et al. 2010). For both sides of workspace (Fig. 3a), participants perceived the path trajectory as more acute in proprioception (red bars) than in vision (blue bars) (ipsilateral: $t_{(40)} = -4.33$; $P < 0.01$; contralateral: $t_{(43)} = -1.93$; $P < 0.05$). Moreover, we found that the bimodal biases (black bars) laid between both unimodal estimates and differed significantly from the visual (ipsilateral: $t_{(41)} = 2.06$; $P < 0.05$; contralateral: $t_{(43)} = 1.89$; $P < 0.05$) and proprioceptive biases (ipsilateral: $t_{(42)} = -2.94$; $P < 0.01$; contralateral: $t_{(43)} = -1.93$; $P < 0.05$). Hence, we used this natural discrepancy to test the first prediction of the MLE for both workspaces separately, i.e., we examined whether the bimodal percept resulted as a weighted average of the visual and proprioceptive biases (cf. Eq. 1).

The observed bimodal bias (black bars) and the weighted average of the unimodal biases (gray bars) did not differ from each other in both the contralateral ($t_{(40)} = -0.11$; $P = 0.91$) and the ipsilateral workspaces ($t_{(38)} = 0.78$; $P = 0.44$). Moreover, we used regression analyses to test whether the participants' predicted bias could reliably describe the observed bimodal bias, i.e., if both are nearly identical (circles and solid lines in Fig. 3b). Indeed, the

Table 1 Measures and predictions of perceived path trajectory within all conditions

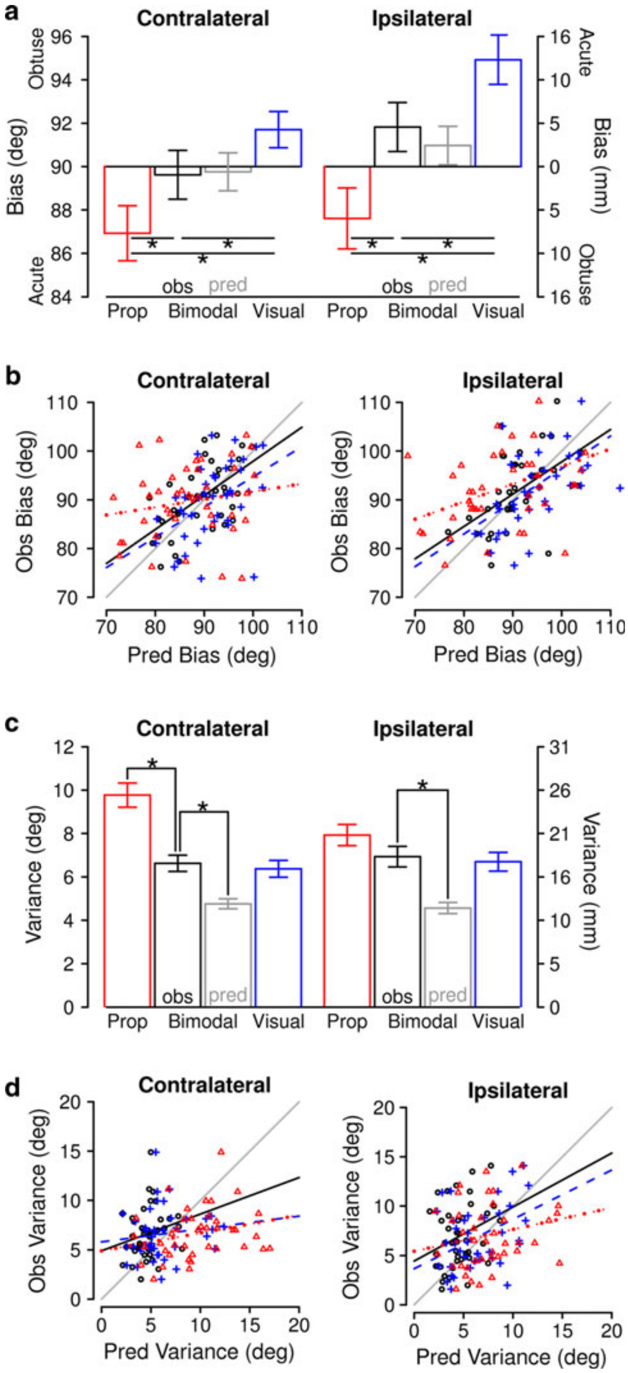
	Relative judgment ipsi		Relative judgment contra		Absolute judgment	
	Mean ± SD (°)	Displ. (mm)	Mean ± SD (°)	Displ. (mm)	Mean ± SD (°)	Displ. (mm)
Bias						
Proprioceptive	87.61 ± 9.52	−6.25	86.93 ± 8.61	−8.04	−0.77 ± 6.96	−0.61
Visual	94.93 ± 7.72	12.89	91.71 ± 5.66	4.47	0.22 ± 3.44	0.57
Obs. Bimodal	92.96 ± 9.38	7.75	90.17 ± 7.70	0.44	−0.69 ± 4.65	−0.81
Pred. Bimodal	90.97 ± 6.00		89.76 ± 5.92		−0.02 ± 3.80	
Variance						
Proprioceptive	7.93 ± 3.33	20.74	9.77 ± 3.79	25.55	7.29 ± 3.64	19.06
Visual	6.73 ± 2.90	17.62	6.37 ± 2.61	16.68	3.77 ± 2.28	9.87
Obs. Bimodal	7.22 ± 3.52	18.89	6.69 ± 2.50	17.51	4.37 ± 2.33	11.44
Pred. Bimodal	4.67 ± 1.80		4.76 ± 1.55		3.03 ± 1.61	
Weights						
Proprioceptive	0.42 ± 0.20		0.34 ± 0.23		0.26 ± 0.19	
Visual	0.58 ± 0.20		0.66 ± 0.23		0.74 ± 0.19	

The angular biases, variances (in degrees), and the weights, averaged across subjects, with the corresponding standard deviations (SD) and the hand displacement (Displ.) (in millimeters) for the absolute and relative judgment task in the right (ipsi) and left (contra) workspaces. The results are listed separately for the proprioceptive, visual, and for the observed (Obs.) as well as for the predicted (Pred.) bimodal percept

observed bimodal estimates are similar to those predicted for the contralateral workspace ($R^2 = 0.33$; $F_{(1,37)} = 18.54$; $P < 0.01$) and ipsilateral workspace ($R^2 = 0.27$; $F_{(1,37)} = 13.75$; $P < 0.01$). Furthermore, the slope of the bimodal bias for both workspaces differed significantly from zero (contralateral: Slope = 0.70; $t_{(37)} = 4.32$; $P < 0.01$; ipsilateral: Slope = 0.66; $t_{(37)} = 3.71$; $P < 0.01$), but was rather comparable to one (contralateral: $t_{(37)} = -1.86$; $P = 0.07$; ipsilateral: $t_{(37)} = -1.88$; $P = 0.07$) with an intercept not statistically different from zero (contralateral: $t_{(37)} = 1.93$; $P = 0.06$; ipsilateral: $t_{(37)} = 1.93$; $P = 0.06$), i.e., the fit to all participants' bimodal biases (solid lines in Fig. 2b) within both workspaces approached unity (gray lines in Fig. 3b).

When we compared the weights for vision and proprioception, we found that the weights for vision were higher than for proprioception in the ipsilateral ($t_{(41)} = -2.50$; $P < 0.05$) as well as in the contralateral ($t_{(42)} = -4.35$; $P < 0.01$) workspace, i.e., vision influenced the predicted bimodal percept more than proprioception. Moreover, visual (ipsilateral: $t_{(41)} = 2.50$; $P < 0.05$; contralateral: $t_{(42)} = 1.55$; $P < 0.01$) and proprioceptive weights (ipsilateral: $t_{(41)} = -2.50$; $P < 0.05$; contralateral: $t_{(42)} = -1.55$; $P < 0.01$) differed significantly from 0.5 in both workspaces. This means that we could predict the bimodal bias reliably by individually weighting the unimodal estimates according to their relative reliability and not only by averaging them, i.e., equally weighting both modalities' biases.

The second prediction of the MLE implies a less variable (more reliable) percept in the bimodal, compared with the unimodal condition due to Eq. 5. To test the second prediction of the MLE, we compared the unimodal variances with the bimodal variance in each workspace (Fig. 3c). For the contralateral workspace, we indeed found a less variable percept in the bimodal (black bar) compared with the proprioceptive condition (red bar) ($t_{(40)} = 5.09$; $P < 0.01$), but revealed a comparable variance for the bimodal and the visual (right bar) condition ($t_{(39)} = -0.85$; $P = 0.40$). However, in the ipsilateral workspace, the bimodal percept was as precise as the proprioceptive ($t_{(41)} = 0.94$; $P = 0.35$) and the visual one ($t_{(41)} = -0.68$; $P = 0.50$). This implies that the precision of the (observed) bimodal percept did not increase, as predicted by the MLE, i.e., that unimodal variances have not been integrated in an optimal manner. Nevertheless, we calculated the bimodal variance predicted by the MLE (Eq. 5) and compared both the predicted and the observed bimodal variance. We found that in both workspaces the predicted bimodal percept (gray bars) was less variable than the observed bimodal percept (black bars) (contralateral: $t_{(39)} = 4.65$; $P < 0.01$; ipsilateral: $t_{(39)} = 4.70$; $P < 0.01$), i.e., the MLE underestimated the bimodal variance. Furthermore, we found that the predicted bimodal variances could not describe the observed bimodal percepts (solid lines in Fig. 3d), such that correlation coefficients for both workspaces were not significant ($P > 0.05$), and thus the regression lines differed significantly from the identity (gray lines in Fig. 3d) ($P > 0.05$). This means that the observed bimodal variances of each participant did not resemble those predicted by the MLE model for both ipsilateral and contralateral workspaces. As a consequence, the data are inconsistent with the second prediction of the MLE. However, participants linearly combined and weighted the unimodal



◀ **Fig. 3** Results of the relative judgment task in the contralateral (left panels) and ipsilateral (right panels) workspaces. **a** and **c** Mean biases (**a**) and variances (**c**) of the unimodal percepts (*red bars* prop: proprioceptive and *blue bars* visual) and the observed (*black bars* obs) and predicted bimodal percepts (*gray bars* pred) with standard errors of the mean. Significant mean differences are marked with an asterisk. **b** Observed (obs) bimodal biases of each participant are plotted as a function of predicted bimodal biases (*black circles* and *solid lines*), visual biases (*blue crosses* and *dashed lines*), or proprioceptive biases (*red triangles* and *dotted lines*) as predictor (pred). **d** Observed (obs) bimodal variance of each participant is plotted as a function of the predicted bimodal variance (*black circles* and *solid line*), the visual variance (*blue crosses* and *dashed lines*), or the proprioceptive variance (*red triangles* and *dotted lines*) as predictor (pred). *Gray lines* in b and d represent the identity slope

percepts by their relative reliabilities within both the ipsilateral and the contralateral workspaces, which is consistent with the first prediction of the MLE.

Unimodal capture for lateral workspace?

Since the results do not perfectly adhere to the predictions of the MLE model, we next tested whether one of the unimodal percepts could better predict the bimodal estimates in the contralateral and ipsilateral workspaces. With regard to the relationship between the accuracy of the bimodal and the unimodal estimates, we found that the visual bias was a reliable predictor for the bimodal bias in the contralateral ($R^2 = 0.21$; $F_{(1,42)} = 11.37$; $P < 0.01$) and ipsilateral workspaces ($R^2 = 0.39$; $F_{(1,40)} = 25.33$; $P < 0.01$). However, the regression lines (dashed lines in Fig. 3b) look very similar to the identity (gray lines), but were not quite aligned with it (contralateral: Slope = 0.62; $t_{(42)} = -2.04$; $P < 0.05$; *Intercept* = 32.71; $t_{(42)} = 1.93$; $P = 0.06$; ipsilateral: Slope = 0.67; $t_{(40)} = -2.52$; $P < 0.05$; *Intercept* = 29.39; $t_{(40)} = 2.34$; $P < 0.05$). The proprioceptive bias could only moderately predict the bimodal bias in the ipsilateral workspace ($R^2 = 0.15$; $F_{(1,41)} = 7.31$; $P < 0.01$) and not at all in the contralateral workspace ($R^2 = 0.03$; $F_{(1,42)} = 1.49$ $P = 0.23$). Moreover, the regression lines (dotted lines in Fig. 3b) were not comparable to the identity (gray lines) in both parts of the workspace, i.e., the slope differed from one (contralateral: Slope = 0.16; $t_{(42)} = -6.19$; $P < 0.01$; ipsilateral: Slope = 0.36; $t_{(41)} = -4.87$; $P < 0.01$) and the intercept from zero (contralateral: *Intercept* = 75.68; $t_{(42)} = 6.43$; $P < 0.01$; ipsilateral: *Intercept* = 60.83; $t_{(41)} = 5.22$; $P < 0.01$).

To explain the variance in bimodal estimate, visual variance could account for bimodal variance only in the ipsilateral ($R^2 = 0.18$; $F_{(1,40)} = 8.64$; $P < 0.01$), but not in the contralateral workspace ($R^2 = 0.02$; $F_{(1,38)} = 0.71$; $P = 0.41$). Nonetheless, both regression lines (dashed lines in Fig. 3d) differed significantly from the identity (gray lines) (contralateral: Slope = 0.13; $t_{(38)} = -5.45$; $P < 0.01$; *Intercept* = 5.80; $t_{(38)} = 5.48$; $P < 0.01$; ipsilateral: Slope = 0.5; $t_{(40)} = -2.88$; $P < 0.01$; *Intercept* = 3.66; $t_{(40)} = 2.93$; $P < 0.01$). The proprioceptive variance could not account for bimodal variance in neither the contralateral ($R^2 = 0.07$; $F_{(1,39)} = 2.74$; $P = 0.11$) nor the ipsilateral workspace ($R^2 = 0.05$; $F_{(1,40)} = 1.99$; $P = 0.17$); these regression lines (dotted lines in Fig. 3d) deviate completely from the unit slope (contralateral: Slope = 0.18; $t_{(38)} = -7.36$; $P < 0.01$; ipsilateral: Slope = 0.22; $t_{(40)} = -4.99$; $P < 0.01$) and the intercept

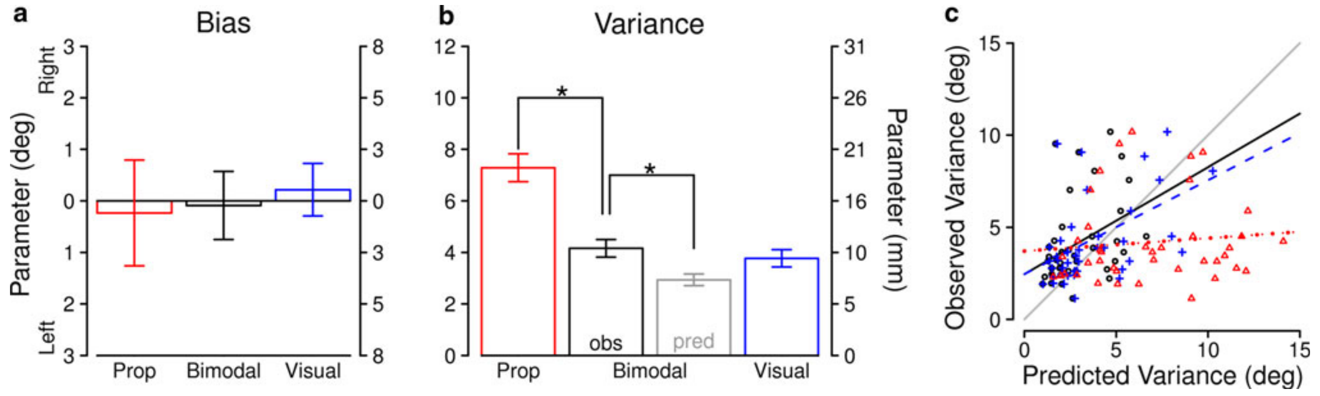


Fig. 4 Results of the absolute judgment task. **a** Mean biases of the proprioceptive (*red bar* prop), bimodal (*black bar*), and visual (*blue bar*) percepts with standard errors of the mean. **b** Mean variances of the unimodal percepts (*red* and *blue bars*) and the observed (*black bar* obs) and predicted (*gray bar* pred) bimodal percepts with standard errors of the mean. Significant mean differences are marked with an asterisk. **c** Observed (obs) bimodal variance of each participant is plotted as a function of the predicted bimodal variance (*circles* and *solid line*), the visual variance (*blue crosses* and *dashed lines*), or the proprioceptive variance (*red triangles* and *dotted lines*) as predictor (pred). The *gray line* represents the identity slope

(contralateral: $Intercept = 4.90$; $t_{(38)} = 4.31$; $P < 0.01$; ipsilateral: $Intercept = 5.43$; $t_{(40)} = 4.90$; $P < 0.01$) of the identity (gray lines). To conclude, the visual modality was sometimes a better predictor for the bimodal estimate than the proprioceptive one. However, neither modality alone provided a substantial better prediction than the MLE did.

Optimal integration of direction judgement

In the second task, participants had to detect the direction (left- or right-directed) of a straight trajectory moving away from their body. We first examined whether the visual and the proprioceptive biases show a natural discrepancy as observed in the first task. However, we found that the biases for both the proprioceptive and the visual percepts (red and blue bars) were very accurate, within a couple degrees (Fig. 4a), and all three estimates were not significantly different from zero (proprioception: $t_{(43)} = -0.22$; $P = 0.82$; vision: $t_{(44)} = 0.42$; $P = 0.68$; bimodal perception: $t_{(43)} = -0.45$; $P = 0.66$). Consequently, both unimodal biases were comparable ($t_{(43)} = -0.48$; $P = 0.63$) and did not differ from the bimodal bias (black bar) (vision: $t_{(42)} = 0.73$; $P = 0.47$, proprioception: $t_{(41)} = -0.16$; $P = 0.88$). Due to the fact that all three estimates did not differ from each other, i.e., that there is no natural discrepancy between the two unimodal percepts, we were unable to test the first prediction of the MLE, i.e., to test whether the bimodal percept resulted as a weighted average of the visual and proprioceptive biases.

We then tested the second prediction of the MLE which implies that the bimodal percept should be less variable (more reliable) than the unimodal percepts. Indeed, we found that the bimodal percept (gray bar in Fig. 3b) was less variable than the proprioceptive one (red bar) ($t_{(40)} = 4.48$; $P < 0.01$), but nearly similar to the visual one (blue bar) ($t_{(42)} = -1.81$; $P = 0.08$). However, the observed percept (black bar) was more variable than the predicted bimodal one (gray bar) ($t_{(39)} = 3.48$; $P < 0.01$), which is inconsistent with the prediction of the MLE. Nonetheless, the observed bimodal variability was moderately related to those predicted (circles and solid line in Fig. 4c), with an R^2 of 0.15 ($F_{(1,38)} = 6.67$; $P < 0.05$) and a slope of 0.58 (not significantly different from one: $t_{(38)} = -1.86$; $P = 0.07$). However, the intercept differed significantly from zero ($t_{(38)} = 3.30$; $P < 0.01$), so that the regression line was not aligned with the identity (gray line in Fig. 4c), i.e., the predicted bimodal variance systematically underestimated the observed bimodal variance.

To summarize, the highly accurate percepts for the absolute judgment task with straight paths prevented us from testing for linear combination of the unimodal percepts. Moreover, the variance of the bimodal percept for judging movement direction did not improve compared with the unimodel estimates, as would be predicted by the MLE model.

Unimodal capture for direction judgement?

Since we did not find that the bimodal variance was reduced accordingly to the MLE model, we next tested whether this variance could be better accounted by those of the unimodal percepts. As consistent with our finding that bimodal variance did not differ from the visual one but was smaller than the proprioceptive one, we found that bimodal variance correlated with visual variance ($R^2 = 0.23$; $F_{(1,40)} = 11.88$; $P < 0.01$) but not with proprioceptive variance ($R^2 = 0.01$; $F_{(1,39)} = 0.46$; $P = 0.50$). Indeed, the regression line for vision (dashed line in Fig. 4c) looks similar to the identity (gray line), but the slope (0.51) differed significantly from a slope of one ($t_{(40)} = -3.27$; $P < 0.01$) and an intercept of zero ($t_{(40)} = 3.84$; $P < 0.01$). Not surprisingly, the proprioceptive regression line (dotted line) deviates obviously from the identity (Slope = 0.07; $t_{(39)} = -9.22$; $P < 0.01$; *Intercept* = 3.71; $t_{(39)} = 4.66$; $P < 0.01$). Thus, neither the visual nor the proprioceptive modality alone serves as a reliable predictor for the bimodal percept, and neither percept could describe the bimodal variance substantially better than the MLE.

Discussion

In our previous study, we found that humans integrate path trajectory information of vision and proprioception in an optimal way (Reuschel et al. 2010). Here, we aim to test whether optimal integration would generalize across different workspaces and judgment types. Our findings indicate that information of both modalities is linearly integrated within different workspaces (ipsi- and contralateral), i.e., bimodal accuracy fell between both unimodal biases. However, we found that multisensory information was not combined in an optimal way, since participants' bimodal precision did not improve compared with both unimodal conditions. Thus, our results are only partly consistent with MLE model for outer parts of the workspace. Yet the estimates from the single modalities alone did not fair better in predicting those for the bimodal. Furthermore, we found very accurate percepts for the absolute judgment task, i.e., a one-segmented straight path. On this account, we were unable to test for an optimal linear combination of visual and proprioceptive accuracy. Like the relative judgment, absolute judgments of bimodal stimulus did not lead to optimally greater precision. Hence, the present results do not suggest that multisensory information is optimally integrated while judging the absolute direction of a one-segmented path. And while participants tended to use mainly visual information for bimodal estimates, this sensory information alone did not provide a better prediction of precision than the MLE.

Accuracy of path trajectory discrimination

When participants judged the angle of the two-segmented path trajectories (in the ipsi- as well as in the contralateral workspace), they were very accurate in the bimodal visual–proprioceptive condition, while visual- and proprioceptive-based estimates deviated from a right angle of 90° in opposite directions by about 3°. This was comparable to our previous study (Reuschel et al. 2010) and to the results of Lakatos and Marks (1998). All three modalities revealed highly accurate estimates based on absolute judgments, with biases deviating less than 1° from straight ahead. This fits well with the results of other studies where participants used vision or proprioception (Darling and Williams 1997; Gentaz and Hatwell 1996; Gentaz et al. 2001; Henriques and Soechting 2003) or both modalities simultaneously (Hermens and Gielen 2003) to judge directions of one-segmented stimuli. The particularly high degree of accuracy for judging the direction of motion of a proprioceptive stimulus is also consistent with our previous findings (Fiehler et al. 2009).

Precision of path trajectory discrimination

The side of workspace determined the precision for relative judgments as a function of modality. Visual precision was similar across the ipsilateral (variance = 6.73°) and contralateral workspaces (variance = 6.37°). Other studies, however, revealed more reliable visual percepts than those found in the present study (Chen and Levi 1996; Gray and Regan 1996; Onley and Volkmann 1958; Regan et al. 1996), possibly because of differences in stimulus presentation (all-at-once vs. sequential). Estimates of the felt angular path trajectories were more precise in the ipsilateral (variance = 7.39°) than in the contralateral workspace (variance = 9.77°). Hence, proprioceptive estimates were more variable than visual and bimodal estimates in the space contralateral to the moving arm, whereas all three modalities were similarly precise within the ipsilateral workspace. The higher precision of proprioception in the ipsilateral workspace is consistent with other studies on angle discrimination at the ipsilateral side (Alary et al. 2008; Levy et al. 2007; Voisin et al. 2002a, b) and with the angular discrimination we found in the center workspace (Reuschel et al. 2010). The reduced proprioceptive precision in the contralateral workspace is probably due to anatomical constraints. Rossetti et al. (1994) found decreased pointing precision for extreme joint postures, which was furthermore proportional to the increase in subjective discomfort. Moreover, there are kinematic advantages (e.g., faster reaction times) for reaching movements that are performed in the ipsilateral compared with the contralateral workspace (Carey et al. 1996; Fisk and Goodale 1985; Ishihara and Imanaka 2007).

The precision in the absolute judgment task varied with modality. Estimates of the direction of the visual trajectory were somewhat variable (variance = 3.77°); however, they are consistent with other studies presenting visual movement stimuli (Darling and Pizzimenti 2001; Krukowski et al. 2003).

Taken together, precision of path trajectory discrimination depends on the sensory information provided by the target. Furthermore, it seems to be important to notice in which mode visual stimuli are presented (all-at-once or sequential) or whether proprioceptive stimulus presentation restricts anatomical capabilities (e.g., too faraway from the shoulder).

Limits of optimal integration of path trajectories

Indeed, we found in both workspaces that unimodal estimates of angles are linearly combined and weighted by their relative reliabilities, as consistent with the first prediction of the MLE (Eq. 1). Thus, this result fits nicely with a wide range of previous studies which found that information is linearly integrated across different modalities (Alais and Burr 2004b; Ernst and Banks 2002; Helbig and Ernst 2007, 2008; Reuschel et al. 2010; van Beers et al. 1996, 1999).

However, the highly accurate estimates of direction that we found for the absolute judgment task prevent us from testing the first prediction of the MLE. Moreover, the lack of improved precision for the bimodal estimates of the absolute and relative judgment task, independent of workspaces, contradicts the aforementioned studies.

There are some recent results that demonstrate situations where the MLE model does not apply, especially with respect to the second prediction of increased bimodal precision (Serwe et al. 2009; Winges et al. 2010). Since these studies used absolute judgments based on one-segmented path structures, they confirm our results of the absolute judgment task.

Winges et al. (2010) suggested that the lack of optimal integration could be due to correlated noise of both modalities. Since the MLE assumes that the unimodal noise distributions are independent, optimal integration could fail when the noise distributions are correlated. Possibly, the unimodal noise distributions within the outer workspaces are more correlated than those for angular path structures presented in the center workspace. In addition, due to the highly accurate and comparable biases for the absolute judgment task, noise distributions are more likely to be correlated. Furthermore, Green and Angelaki (2010) pointed out that additional noise could also result from transformation processes between different reference frames used by the involved modalities. Maybe transformation processes between visual and proprioceptive coordinates are nosier in the lateral workspace resulting in more variable bimodal estimates at the ipsilateral and contralateral sides. Since we asked participants to decide between two alternatives after perceiving the path trajectory, we could rule out any effect of motor noise given in pointing studies (e.g., van Beers et al. 1996, 1999). However, our judgment task could induce some indeterminable decision noise, e.g., because of interferences between side of workspace and side of required key press. To sum up, different sources of noise could explain the variable bimodal percept found in the outer workspaces.

Rosas et al. (2005) and Oruc et al. (2003) argued that *optimal combination is one possibility but not the combination rule under all conditions* (Rosas et al. 2005, p 809) and suggested alternative combination rules like suboptimal weighting of cues or reliance on only one of both cues. Our additional analyses showed that participants mostly rely on visual information. Nevertheless, vision alone did not provide a substantially better explanation of the bimodal performance than the MLE did. Thus, we could rule out a reliance on only one of both senses. A recent study (Serwe et al. 2009) also failed to find optimal integration and proposed the probabilistic cue switching model (PCS), which provided the best fit for their data. Also, Drewing and Jovanovic (2010) found that experimental variables (like the conflict between sensory information channels) could determine which integration strategy is used. In addition, interindividual differences in integration strategies due to individual learning history play an important role. The learning history, and likewise the priors, might change from trial to trial and could induce switching between strategies within the individual participant's behavior. For future research, it seems to be important to take into account trial-by-trial changes of individual variables and the associated behavior. Prior information plays a crucial role in Bayesian theories of integration (Körding and Wolpert 2006; MacNeilage et al. 2008) and improves bimodal prediction (Brenner et al. 2006; Oruc et al. 2003; Scheidt et al. 2005). Thus, combining MLE and Bayesian models like in Kalman or particle filters (Körding and Wolpert 2006; MacNeilage et al. 2008) seem to be a fruitful future direction that might provide a better explanation of results which are inconsistent with the MLE.

Conclusion

The present results confirmed optimal integration according to the MLE only under some conditions. We found that sensory information about angular visual and proprioceptive path trajectories during relative judgments is linearly combined in the ipsi- and contralateral workspace. Detecting direction (absolute judgment) of one-segmented path trajectories was highly accurate across all modalities and so prevented us from testing for optimal integration across the two single modalities. For both the absolute and the relative judgment tasks in the ipsi- and contralateral workspaces, bimodal estimates were not as precise as predicted by optimal integration. This suggests that optimal integration may be one, but not the only, way to explain how the brain combines multisensory information for estimating movement paths. To understand how the brain deals with multisensory information, it is important to consider a broad range of factors that could determine humans' integration ability and to explore how neural populations represent and implement these factors.

Acknowledgments This research was supported by grant Fi 1567 from the German Research Foundation (DFG) assigned to Katja Fiehler and Frank Rösler, the research unit DFG/FOR 560 'Perception and Action', and the TransCoop-Program from the Alexander von Humboldt Foundation assigned to Katja Fiehler and Denise Y.P. Henriques. Denise Y.P. Henriques is an Alfred P. Sloan fellow. We thank Stefan Westermann and Christian Friedel for programming the experiment, Patricia Franke for acquiring data, and Knut Drewing and Iseult Beets for helpful comments on the manuscript.

References

Alais D, Burr D (2004a) No direction-specific bimodal facilitation for audiovisual motion detection. Brain Res Cogn Brain Res 19:185–194

Alais D, Burr D (2004b) The ventriloquist effect results from near-optimal bimodal integration. Curr Biol 14:257–262

Alary F, Goldstein R, Duquette M, Chapman CE, Voss P, Lepore F (2008) Tactile acuity in the blind: a psychophysical study using a two-dimensional angle discrimination task. Exp Brain Res 187:587–594

Appelle S (1971) Visual and haptic angle perception in the matching task. Am J Psychol 84:487–499

Brenner E, van Beers RJ, Rotman G, Smeets JB (2006) The role of uncertainty in the systematic spatial mislocalization of moving objects. J Exp Psychol Hum Percept Perform 32:811–825

Carey DP, Hargreaves EL, Goodale MA (1996) Reaching to ipsilateral or contralateral targets: within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. Exp Brain Res 112:496–504

Chen S, Levi DM (1996) Angle judgement: is the whole the sum of its parts? Vision Res 36:1721–1735

Darling WG, Pizzimenti MA (2001) A coordinate system for visual motion perception. Exp Brain Res 141:174–183

Darling WG, Williams TE (1997) Kinesthetic perceptions of intrinsic anterior-posterior axes. Exp Brain Res 117:465–471

Drewing K, Jovanovic B (2010) Visuo-haptic length judgment in children and adults. In: Kappers AML (ed) EuroHaptics 2010, LNCS 6192. Part II. Springer, Berlin Heidelberg, pp 438–444

Driver J, Noesselt T (2008) Multisensory interplay reveals crossmodal influences on 'sensory-specific' brain regions, neural responses, and judgments. Neuron 57:11–23

Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415:429–433

Ernst MO, Bülthoff HH (2004) Merging the senses into a robust percept. Trends Cogn Sci 8:162–169

Fiehler K, Reuschel J, Rösler F (2009) Early non-visual experience influences proprioceptive-spatial discrimination acuity in adulthood. Neuropsychologia 47:897–906

Fisk JD, Goodale MA (1985) The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. Exp Brain Res 60:159–178

Flanagan JR, Rao AK (1995) Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. J Neurophysiol 74:2174–2178

Gentaz E, Hatwell Y (1996) Role of gravitational cues in the haptic perception of orientation. Percept Psychophys 58:1278–1292

Gentaz E, Luyat M, Cian C, Hatwell Y, Barraud PA, Raphel C (2001) The reproduction of vertical and oblique orientations in the visual, haptic, and somato-vestibular systems. Q J Exp Psychol A 54:513–526

Gepshtein S, Burge J, Ernst MO, Banks MS (2005) The combination of vision and touch depends on spatial proximity. J Vis 5:1013–1023

Ghilardi MF, Gordon J, Ghez C (1995) Learning a visuomotor transformation in a local area of work space produces directional biases in other areas. J Neurophysiol 73:2535–2539

Goble DJ, Brown SH (2009) Dynamic proprioceptive target matching behavior in the upper limb: effects of speed, task difficulty and arm/hemisphere asymmetries. Behav Brain Res 200:7–14

Goodbody SJ, Wolpert DM (1999) The effect of visuomotor displacements on arm movement paths. Exp Brain Res 127:213–223

Gray R, Regan D (1996) Accuracy of reproducing angles: is a right angle special? Perception 25:531–542

Green AM, Angelaki DE (2010) Multisensory integration: resolving sensory ambiguities to build novel representations. Curr Opin Neurobiol 20:353–360

Helbig HB, Ernst MO (2007) Optimal integration of shape information from vision and touch. Exp Brain Res 179:595–606

Helbig HB, Ernst MO (2008) Visual-haptic cue weighting is independent of modality-specific attention. J Vis 8:21.1–2116

Henriques DY, Soechting JF (2003) Bias and sensitivity in the haptic perception of geometry. Exp Brain Res 150:95–108

Hermens F, Gielen S (2003) Visual and haptic matching of perceived orientations of lines. Perception 32:235–248

Ishihara M, Imanaka K (2007) Motor preparation of manual aiming at a visual target manipulated in size, luminance contrast, and location. Perception 36:1375–1390

Jones SA, Henriques DYP (2010) Memory for proprioceptive and multisensory targets is partially coded relative to gaze. Neuropsychologia 48:3782–3792

Körding KP, Wolpert DM (2006) Bayesian decision theory in sensorimotor control. Trends Cogn Sci 10:319–326

Krukowski AE, Pirog KA, Beutter BR, Brooks KR, Stone LS (2003) Human discrimination of visual direction of motion with and without smooth pursuit eye movements. J Vis 3:831–840

Lakatos S, Marks LE (1998) Haptic underestimation of angular extent. Perception 27:737–754

Landy MS, Maloney LT, Johnston EB, Young M (1995) Measurement and modeling of depth cue combination: in defense of weak fusion. Vision Res 35:389–412

Levy M, Bourgeon S, Chapman CE (2007) Haptic discrimination of two-dimensional angles: influence of exploratory strategy. Exp Brain Res 178:240–251

MacNeilage PR, Ganesan N, Angelaki DE (2008) Computational approaches to spatial orientation: from transfer functions to dynamic Bayesian inference. J Neurophysiol 100:2981–2996

Meyer GF, Wuerger SM, Röhrbein F, Zetzsche C (2005) Low-level integration of auditory and visual motion signals requires spatial co-localisation. Exp Brain Res 166:538–547

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113

Onley JW, Volkmann J (1958) The visual perception of perpendicularity. Am J Psychol 71:504–516

Oruc I, Maloney LT, Landy MS (2003) Weighted linear cue combination with possibly correlated error. Vision Res 43:2451–2468

Proske U, Gandevia SC (2009) The kinaesthetic senses. J Physiol 587:4139–4146

Regan D, Gray R, Hamstra SJ (1996) Evidence for a neural mechanism that encodes angles. Vision Res 36:323–330

Reuschel J, Drewing K, Henriques DY, Rösler F, Fiehler K (2010) Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry. Exp Brain Res 201:853–862

Rosas P, Wagemans J, Ernst MO, Wichmann FA (2005) Texture and haptic cues in slant discrimination: reliability-based cue weighting without statistically optimal cue combination. J Opt Soc Am A Opt Image Sci Vis 22:801–809

Rossetti Y, Meckler C, Prablanc C (1994) Is there an optimal arm posture? Deterioration of finger localization precision and comfort sensation in extreme arm-joint postures. Exp Brain Res 99:131–136

Scheidt RA, Conditt MA, Secco EL, Mussa-Ivaldi FA (2005) Interaction of visual and proprioceptive feedback during adaptation of human reaching movements. J Neurophysiol 93:3200–3213

Sergio LE, Scott SH (1998) Hand and joint paths during reaching movements with and without vision. Exp Brain Res 122:157–164

Serwe S, Drewing K, Trommershauser J (2009) Combination of noisy directional visual and proprioceptive information. J Vis 9:28.1–2814

Sittig AC, Denier van der Gon JJ, Gielen CC (1985) Separate control of arm position and velocity demonstrated by vibration of muscle tendon in man. Exp Brain Res 60:445–453

Smeets JB, Brenner E (1995) Perception and action are based on the same visual information: distinction between position and velocity. J Exp Psychol Hum Percept Perform 21:19–31

Sober SJ, Sabes PN (2003) Multisensory integration during motor planning. J Neurosci 23:6982–6992

Sober SJ, Sabes PN (2005) Flexible strategies for sensory integration during motor planning. Nat Neurosci 8:490–497

Treutwein B (1995) Adaptive psychophysical procedures. Vision Res 35:2503–2522

van Beers RJ, Sittig AC, Denier van der Gon JJ (1996) How humans combine simultaneous proprioceptive and visual position information. Exp Brain Res 111:253–261

van Beers RJ, Sittig AC, Denier van der Gon JJ (1999) Integration of proprioceptive and visual position-information: an experimentally supported model. J Neurophysiol 81:1355–1364

Voisin J, Benoit G, Chapman CE (2002a) Haptic discrimination of object shape in humans: two-dimensional angle discrimination. Exp Brain Res 145:239–250

Voisin J, Lamarre I, Chapman CE (2002b) Haptic discrimination of object shape in humans: contribution of cutanous and proprioceptive inputs. Exp Brain Res 145:251–260

Wichmann FA, Hill NJ (2001) The psychometric function: I. Fitting, sampling, and goodness of fit. Percept Psychophys 63:1293–1313

Winges SA, Eonta SE, Soechting JF (2010) Does temporal asynchrony affect multimodal curvature detection? Exp Brain Res 203:1–9

World Medical Association Declaration of Helsinki (2000) Ethical principles for medical researches involving human subjects. http://www.wma.net/en/30publications/10policies/b3/

Wuerger SM, Hofbauer M, Meyer GF (2003) The integration of auditory and visual motion signals at threshold. Percept Psychophys 65:1188–1196

Yuille AL, Bülthoff HH (1996) Bayesian theory and psychophysics. In: Knill D, Richards W (eds) Perception as Bayesian inference. Cambridge University Press, Cambridge