Supporting information

Drift and sensory modality

The basis of our sensory mismatch hypothesis is that senses have systematic errors. If the target for a movement is presented differently (e.g in a different modality), the bias in target localisation will be different. Therefore, the drift in endpoints of repeated movements will be in a different direction if the target is the location of the unseen left hand than if the target is presented visually. In order to investigate whether this is the case, we reanalysed two conditions of an earlier experiment performed with another purpose [1].

Methods

Five subjects each indicated four target positions on a horizontal plane with their unseen hand. We reanalysed the indicated positions for condition P and those of one control condition CR [1]. In condition P, subjects were brought into a normally lit room, and sat down behind a table before being blindfolded. They were asked to move their left hand under the table to find a tactile target. Subsequently, subjects indicated the position of their left hand (which was under the table) with their right hand by pointing at the corresponding position on the tabletop. In the control condition CR, a visual target was visible through a mirror, so that the hand was invisible. Subjects had to indicate its position with their right hand on the tabletop. In both conditions, the indicating right hand started at a position just in front of the waist. The subjects were allowed to correct their initial movement if they felt that they had made an error. Experiments were performed in series of 40 trials, consisting of 10 trials towards each of the four target positions. Each series was repeated three or four times.

Because there were only 10 trials per target in this experiment, we did not use our non-linear model (equation (4) of the main paper), but a linear fit. The same linear fit to the sets of 10 data-points was subtracted in the original analysis in order to obtain a reliable measure of the variance (as explained in the analysis section of [1]). The drift vector was the difference in the fitted values for the x and y co-ordinates between the last and first trial of a block, averaged over the three or four repetitions. We averaged the drift over subjects for each of the four locations.

Results

The results are presented in figure 5 of the main paper. The average drift in condition P (blue circles) is systematically different from that CR (red disks), following the prediction. The drift when moving to the proprioceptive targets is more or less fronto-parallel, whereas the drift for the visual targets (CR condition) varies with target position (viewing direction). These results suggest that the drift to visual targets is partly caused by visual errors that are absent for the proprioceptive targets.

Discussion

The difference in drift between the two experimental conditions is consistent with the sensory mismatch hypothesis. Other aspects of the observed drift are also in line with the sensory mismatch hypothesis. This hypothesis proposes that the drift in the two conditions with vision is caused by visual and proprioceptive mislocalisation. As the visual mislocalisation is primarily in the viewing direction [2], we expect a visual component of drift in the viewing direction. This is clearly the case: the drift in the CR condition varies with target position in accordance with the viewing direction. Corresponding to the assumptions of our model, the drift in condition P is in the same direction as the bias in this condition (figure 1 of [1]).

The effect of movement precision on drift speed.

We showed in the main experiment a remarkable correspondence between the observed speed of drift and the one predicted on the basis of the measured variability. In order to test whether this correspondence was accidental, we reanalysed the data from an experiment for which we knew that the execution errors are much smaller. In that experiment, subjects made planar movements between a limited set of targets in a normally lit room [3].

Methods

The methods and equipment are described in more detail in the original paper [3]. Thirteen right-handed colleagues volunteered to take part in the study after being informed about what they would be required to do. Subjects sat in a normally lit room, behind a graphics tablet. A black Brentano figure on a white background was projected directly onto the tablet in the hand visible condition. For the hand invisible condition, a box was placed on the tablet; the

Brentano figure was projected onto the transparent upper surface of the box; mirror ensured that subjects saw the stimulus at the level of the tablet without being able to see their hand.

The centre of the Brentano figure was about 40 cm below eye-height, and about 20 cm in front of the subject. The two vertical shafts each had a length of 8 cm. A red target dot (diameter 0.2 cm) could appear either 8cm to the right of the figure or on one of the three arrowheads of the Brentano illusion. Subjects were asked to bring the tip of a pen to the red target dot. After they finished their movement, a new target dot appeared. The endpoint of one movement was the starting position of the pointing movement to the next target. No instructions were given about the speed of the movement. Positions were sampled at 200 Hz with an accuracy of about 0.25 mm.

The conditions with and without feedback of the hand were performed in different sessions. A session contained two blocks of 400 trials, one for each configuration of the Brentano figure. The order of the blocks within a session and the order of conditions between sessions were counterbalanced across subjects. As subjects could take a short break in between the blocks, but did not have to, we only analysed the data of the first block.

The errors in this experiment are not only caused by variability and the mismatch between vision and proprioception, but also contain the effect of the illusion. This effect is systematic for the primary error for each subject-target combination. By averaging across subjects and target position, the effect of the illusion on the primary error is averaged out. The (unsigned) secondary error, however, is contaminated by this effect of the illusion, and we will therefore not analyse this error. We have neither an independent measure of the sensory mismatch, nor a prediction for the direction of the drift. We therefore estimated the direction of the sensory mismatch by the direction of the bias averaged over the last 100 trials. The primary error in a trial is defined as the component of the error in that direction. Due to the lack of an independent measure of the amplitude of the sensory mismatch, we cannot make a complete prediction for the drift. We will only be able to predict the time-course from the ratio between the perceptual variance ($\sigma_v^2 + \sigma_p^2$) and the execution variance (σ_{ex}^2). These are determined on the basis of the measured variances in the hand visible condition and the last 100 trials of the hand visible condition respectively. We will compare the fit of the model (equation (4)) to the data using the ratio obtained in this way with one using the ratio obtained in the main experiment.

Results

As expected, the subjects were very accurate in the hand visible condition: we found a standard deviation of 0.113 cm, which we consider as our measure for the execution error σ_{ex}.

The standard deviation in the positions of the last 100 trials of the hand in visible condition was 1.192cm, which we consider to be caused by variability in both perception and execution ($\sqrt{\sigma_p^2 + \sigma_v^2 + \sigma_{ex}^2}$). By subtracting the execution variance, our estimate for the perceptual precision is 1.187cm. This leads to a ratio between variance in perception and execution of $\left(\sigma_p^{\ 2} + \sigma_v^{\ 2}\right)/\sigma_{ex}^{\ 2} = 110$. Unfortunately, we cannot determine the mismatch between vision and proprioception directly, because light scattered from the projection surface made it impossible to perform the experiment in total darkness. Instead of predicting the drift completely (as in figure 4), we therefore fitted equation (4) to the data using the sensory mismatch as single fit-parameter. The model fitted the data very well using the measured ratio of variances (blue curve), with a systematic sensory mismatch of 3.6cm. If we assumed the same speed of drift as in figure 4, the model did not fit the data well (dashed red curve). The speed of drift depends thus on the variability in task performance in the way the model predicts.

Discussion

We showed by reanalysing the data from a previous experiment [3] that the speed of drift depends in the same way on the precision of perceptual localisation and motor execution as in our own experiment. This adds further support to our claim that vision and proprioception are not mutually calibrated, but only combined based on their respective reliabilities.

References

1. van Beers RJ, Sittig AC, Denier van der Gon JJ (1996) How humans combine simultaneous proprioceptive and visual position information. Experimental Brain Research 111: 253-261.
2. van Beers RJ, Sittig AC, Denier van der Gon JJ (1999) Integration of proprioceptive and visual position-information: An experimentally supported model. Journal of Neurophysiology 81: 1355-1364.
3. de Grave DDJ, Brenner E, Smeets JBJ (2004) Illusions as a tool to study the coding of pointing movements. Experimental Brain Research 155: 56-62.