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Kinematic cross-correlation induces sensory integration across separate objects

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Abstract

In a basic cursor-control task, the perceived positions of the hand and the cursor are biased towards each other. We recently found that this phenomenon conforms to the reliability-based weighting mechanism of optimal multisensory integration. This indicates that optimal integration is not restricted to sensory signals originating from a single source, as is the prevailing view, but that it also applies to separate objects that are connected by a kinematic relation (i.e. hand and cursor). In the current study, we examined which aspects of the kinematic relation are crucial for eliciting the sensory integration: (i) the cross-correlation between kinematic variables of the hand and cursor trajectories, and/or (ii) an internal model of the hand-cursor kinematic transformation. Participants made out-and-back movements from the centre of a semicircular workspace to its boundary, after which they judged the position where either their hand or the cursor hit the boundary. We analysed the position biases and found that the integration was strong in a condition with high kinematic correlations (a straight hand trajectory was mapped to a straight cursor trajectory), that it was significantly reduced for reduced kinematic correlations (a straight hand trajectory was transformed into a curved cursor trajectory) and that it was not affected by the inability to acquire an internal model of the kinematic transformation (i.e. by the trial-to-trial variability of the cursor curvature). These findings support the idea that correlations play a crucial role in multisensory integration irrespective of the number of sensory sources involved.

Introduction

When working with a computer, one commonly uses a mouse or track pad to steer the cursor on the monitor. Although one clearly perceives the cursor and the hand as separate 'objects', a number of studies indicate an intriguing perceptual interaction between them that acts across the spatial reference frames. That is, the perceived position of the hand (in the horizontal plane) is biased to where the cursor (in the frontal plane) would be if mapped onto the same plane of motion, and vice versa. This effect is observed both when there is a slight discrepancy in the hand and cursor movement directions (Rand & Heuer, 2013, 2016; Debats *et al.*, 2017) and in the movement amplitudes (Ladwig *et al.*, 2012, 2013; Kirsch *et al.*, 2016). In a recent study, we found that the relative strength of these perceptual attraction biases varies with the relative reliability of unimodal hand and cursor position estimates, consistent with optimal-integration model predictions (Debats *et al.*, 2017). As these two objects – the hand being part of the body, and the cursor as a part of the outside world – are bound by their kinematic relation only, it must be some aspect of this relation that elicits the integration. In our aim to further understand integration across separate objects, we here assessed which aspects of the kinematic relation are crucial for the hand-cursor sensory integration to occur.

It may not seem surprising that we found evidence of optimal sensory integration in a cursor-control task, because over the past several years optimal integration has been shown in a wide variety of tasks both within and across the visual, auditory, haptic and proprioceptive modalities (for reviews, see, e.g., Ernst, 2006; Cheng *et al.*, 2007; van Dam *et al.*, 2014). The neural process of optimal sensory integration produces a weighted average of unisensory estimates, whereby the weights reflect the relative reliabilities (i.e. inverse variances) of these estimates (e.g. Ernst & Banks, 2002). In this process, the variance of the integrated perceptual estimate is minimized if all boundary conditions, such as stochastic independence of the individual estimates, are met (Ernst, 2012). Sensory integration does, obviously, not occur for any given set of sensory signals. The integration is preceded by a process of causal inference,

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that is, the assessment of whether sensory signals originate from a single sensory source (for reviews, see, e.g., Shams & Beierholm, 2010; Spence, 2011; Ernst, 2012; van Dam *et al.*, 2014). In particular, integration has been found to depend on temporal synchrony (Bresciani *et al.*, 2005), temporal correlations (Parise *et al.*, 2012), and on the spatial separation between the sensory sources (Gepshtein *et al.*, 2005). The effect of spatial separation can be overcome by providing explicit evidence that the separated sources of information refer to a single object, as indicated by previous studies on integration in tool use (Helbig & Ernst, 2007; Takahashi *et al.*, 2009; Takahashi & Watt, 2014). Such evidence is not provided in a cursor-control task, because there the spatially separated signals originate from the hand and from the cursor, two clearly distinct objects. The finding of sensory integration in a cursor-control task is therefore not trivial (Debats *et al.*, 2017).

It is important here that different strengths of sensory integration are possible. Sensory integration can be complete, in which case it results in a single combined percept. This best-known case of integration is referred to as sensory fusion. Weaker forms of integration are also possible, in which case separate percepts related to each unisensory signal persist yet with a bias towards each other (e.g. Hillis *et al.*, 2002). This is what we refer to as sensory coupling. To capture these weaker forms of integration, the standard model for optimal multisensory integration (e.g. Ernst & Banks, 2002) can be expanded with a so-called coupling prior (for reviews, see, e.g., Shams & Beierholm, 2010; Ernst & Di Luca, 2011). In its simplest form, the coupling prior can be formalized as a two-dimensional Gaussian probability distribution, as proposed by Ernst (2006, 2012). The first principal axis of this distribution (i.e. the long axis) specifies the *a priori* belief regarding the relation between two individual sensory estimates. The orthogonal axis, reflecting the coupling prior variance, indicates the strength of this belief and determines the integration strength (a zero variance corresponds to sensory fusion, and any value larger than one corresponds to sensory coupling). The coupling prior can be taken as a representation of the causality judgement, reflecting the strength of the belief that separate signals originate from the same source (Körding *et al.*, 2007). Optimal integration models that include a coupling prior have adequately captured behaviour in, for example, audio-visual and visual-tactile numerosity judgements (e.g. Shams *et al.*, 2005; Bresciani *et al.*, 2006; Adams, 2016) and audio-visual spatial judgements (Körding *et al.*, 2007). Optimal sensory coupling also predicts the main characteristics of the perceptual attraction biases seen in cursor-control tasks (Debats *et al.*, 2017).

As indicated above, sensory integration is not expected for sensory signals that come from spatially separated sources, unless explicit evidence of object unity is provided. Our previous findings of sensory integration in a cursor-control task suggest that object unity is not required if the separate objects are bound by a kinematic relation (Debats *et al.*, 2017). In other words, a kinematic relation seems to affect the causality judgements, thus influencing the strength of sensory integration. In the current study, we manipulated two core characteristics of the hand-cursor kinematic relation to assess their role in this process.

First, the normal kinematic relation in a cursor-control task is characterized by strict cross-correlations between the hand trajectory in the horizontal plane and the cursor trajectory in the frontoparallel plane. Cross-correlations here are measures of the correspondence of time series of kinematic characteristics of the hand and cursor trajectories (e.g. the instantaneous directions and velocities). We hypothesize that such kinematic cross-correlations influence the causality judgement and thus the coupling strength. Such an effect of correlations in the spatial domain would be in line with the previously established role of temporal correlations on the strength of audio-visual integration (Parise *et al.*, 2012). As per our knowledge, the influence of spatial correlations has not been studied before, but it is plausible that sensory correlations in general affect multisensory processing along a common mechanism (Parise & Ernst, 2016). If kinematic cross-correlations are critical for sensory integration across separate objects, the coupling strength should decline when the cross-correlations between kinematic signals are reduced by a complex nonlinear kinematic transformation.

Second, in a cursor-control task the systematic relation between hand movements and cursor motion (i.e. the kinematic transformation) can be learned. The acquired internal representation of this relation is generally designated as internal model (cf. Wolpert & Kawato, 1998). We hypothesize that the precision of the internal model determines the causality judgement and thus the coupling strength. Acquisition of an internal model is strongly impaired when the kinematic transformation varies across successive movements. Even for two variable kinematic transformations, learning is not consistently found (e.g. Hegele & Heuer, 2010). In contrast, internal model acquisition is not directly affected by the complexity of the kinematic transformation as even complex nonlinear transformations can be learned (e.g. Heuer & Sülzenbrück, 2013). Note that internal models can be acquired for relations between other variables than kinematic ones (e.g. Koh & Meyer, 1991; Bott & Heit, 2004), although the outcome of such function learning is generally not termed 'internal model'. Internal model acquisition (or more generally, learning the relation between variables) is thus not specific to the active aspect of our task (i.e. that hand-object movement causes the motion of the cursor object). If indeed the acquisition of an internal model of the hand-cursor transformation is critical for eliciting sensory integration, the coupling strength should decline when the kinematic transformation is made variable across trials.

In short, in the current study we assessed the role of kinematic cross-correlations and internal model acquisition on the strength of sensory integration by manipulating the complexity and trial-to-trial variability of the hand-cursor kinematic transformation. We used our previous experimental procedure (Debats *et al.*, 2017; cf. Rand & Heuer, 2013, 2016) in which participants made out-and-back movements with their right hand between the centre of a semicircular workspace and its boundary. The outward hand movement on the horizontal plane was accompanied by the corresponding motion of a cursor – a little dot – on the frontoparallel monitor. Participants' task was to judge where either their hand or the cursor had hit the boundary. We tested three transformation conditions: a baseline condition with a simple transformation (straight hand movement leads to straight cursor movement), a condition in which the transformation was complex (straight hand movement leads to curved cursor movement) and constant across trials, and a condition in which the transformation was complex and variable across trials.

Materials and methods

Participants

The experiment was conducted in accordance with the declaration of Helsinki and approved by Bielefeld University's local ethics committee. Thirteen right-handed participants (aged 19–31 years; eight female) volunteered to participate in the experiment, after giving written informed consent. They were compensated with a payment of 6.- € per hour.

Apparatus

As illustrated in Fig. 1A, participants were seated at a table with a digitizer tablet on top of it (Wacom Intuos4 XL; 48.8 by 30.5 cm) and faced a computer monitor at 60-cm viewing distance (Samsung MD230; 23 inch; 50.9 by 28.6 cm). With their right hand, they moved a stylus on the tablet (holding it as in writing), and when required they pressed a small button on the stylus with their thumb or index finger. The tablet was partially covered by a 5-mm-thick pvc template to create a semicircular workspace of 15 cm radius. The workspace's border served as a mechanical stop for the hand movements and is referred to as the 'stopper ring'. A horizontal opaque board occluded the hand and stylus from view. The position of the stylus was recorded and mapped online to the position of a cursor on the monitor (17-ms delay), using MATLAB with the Psychophysics Toolbox extensions (Kleiner *et al.*, 2007). A chinrest was provided for convenience. During the experiment, the room was dark such that only the images on the monitor were visible. All images were presented in light grey on a black background.

Task

Participants were instructed to perform out-and-back movements from the centre of the semicircular workspace to its boundary (i.e. the stopper ring). During the outward hand movement, the corresponding motion of a cursor (a 6-mm-diameter white dot) was shown on the frontoparallel monitor. After each out-and-back movement, the word 'HAND' or 'CURSOR' appeared on the monitor to instruct participants to report the memorized final position (i.e. the position when hitting the stopper ring) of either the hand or the cursor, respectively. A visual marker then appeared at the far left or far right side of an invisible semicircular track (that corresponded to the stopper ring). Participants moved the marker along the track by making small movements to the left or right (< 1 cm amplitude) with the stylus on the tablet. Once satisfied with the marker's position, they confirmed their judgement by pressing the stylus button. There were no time constraints in making these position judgements.

Participants were instructed to move comfortably fast and to return upon hitting the stopper ring. This resulted in a 1.05 ± 0.04 s average duration of the outward hand movements (i.e. the time for covering 3 to 97% of the 15 cm movement distance) and 0.51 ± 0.03 s average resting time at the endpoint (i.e. the time for the hand being beyond 97% of the movement distance). To prevent stereotyped directions of the outward movements – and hence stereotyped position judgements – we instructed participants to move approximately in one of eight movement directions in each trial ($-56°$ to $56°$ relative to straight ahead, in steps of $16°$). These approximate directions were instructed by means of a little WIFI-like symbol being displayed before movement onset and presented in semirandomized order (see Design). Specific details on, for example, the size and relative timing of all displayed items can be found in Debats *et al.* (2017), Experiment 2.

Visuomotor transformations

The mapping from hand movement to cursor movement was manipulated according to three transformation conditions (see Fig. 1B). In the baseline condition termed *Simple*, there was a small visuomotor rotation of the cursor motion relative to the direction of the hand movement to cause a discrepancy between the final hand position and the final cursor position. We used eight levels of visuomotor rotation: $-17.5°$ to $17.5°$ in steps of $5°$. Once back in the centre position, participants were instructed to judge either the final hand or the final cursor position. The discrepancy between the physical hand and cursor endpoints allowed us to assess the perceptual attraction, that is, how much the judged hand and cursor positions were

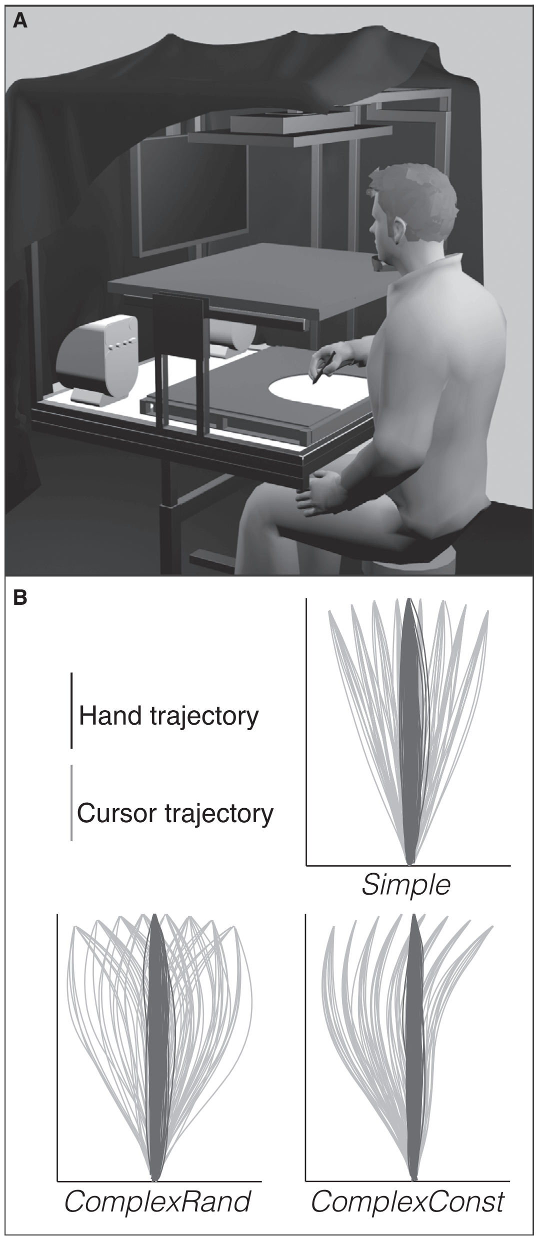

FIG. 1. Set-up and conditions. (Panel A) the experimental set-up with the digitizer tablet in the horizontal plane and the monitor in the frontoparallel plane. The workspace of the hand movements in the horizontal plane were restricted by the semicircular stopper ring (grey surface). (Panel B) The hand (dark grey) and cursor (light grey) trajectories as recorded for a single subject in the *BiHand* trials. For illustration purposes, the trajectories were aligned at a 90° trajectory endpoint; the actual trajectories' endpoints were spread over the stopper ring due to the instructed eight approximate movement directions. The three transformation conditions all contained discrepancies between the hand and cursor endpoints (i.e. the visuomotor rotation). In condition *ComplexConst*, the cursor trajectories additionally had a curvature, which was constant over all trials (left and right curvature was counterbalanced over participants). In condition *ComplexRand*, the magnitude and direction of the additional curvature varied randomly over trials.

biased towards each other. Participants were not informed about the presence of the visuomotor rotation (they were told that the experiment was about the effect of attention on remembered sensations) and only three out of the 13 participants reported noticing it in a structured post-experimental interview.

In the other two transformation conditions, we applied complex, nonlinear visuomotor transformations to the cursor trajectories in addition to the visuomotor rotations. In one complex condition, termed *ComplexConst*, the transformation was a distance-dependent visuomotor rotation such that for a straight hand path between start position and end position the path of the cursor was curved. More precisely, in a polar coordinate system with its origin in the start position, the cursor position was rotated relative to the hand position by an angle that was a sinusoidal function of the distance of the hand from the start position (in addition to the constant visuomotor rotation angle). The amplitude of the modulating sine function was fixed at either −11.25° or +11.25°, balanced across participants. In the other complex condition, termed *ComplexRand*, the complex transformation was made variable across trials by way of randomizing the amplitude of the modulating sine function. On each trial, the amplitude was randomly chosen from between −7.5° and −15° or between +7.5° and +15°. Whereas the visuomotor rotation generally went unnoticed, the complex visuomotor transformations were conspicuous.

Position judgements

We tested two bimodal and two unimodal trial types. In the bimodal trial types, the outward hand movement was accompanied by the cursor movement. After participants had returned their hand to the centre position they judged either the final hand position (*BiHand* trials) or the final cursor position (*BiCursor* trials), according to the instruction on the monitor (see Task). In one unimodal trial type, participants made the outward hand movement without accompanying cursor motion after which they were instructed to judge the final hand position (*UniHand* trials). In the other unimodal trial type, an outward cursor movement was shown while participants kept their hand static at the centre position (*UniCursor* trials). The shown cursor trajectory was a replay of a cursor trajectory recorded in a preceding BiCursor trial. Participants were instructed to judge the final cursor position after a delay that was equal to the average duration of the return movements in the preceding trials. The bimodal trials served to assess the strength of the perceptual attraction. From the unimodal trials, we obtained parameters that were needed for model predictions.

Design

The experimental trials differed with respect to three transformation conditions, four trial types and eight visuomotor rotations. The transformation conditions were performed in separate experimental sessions. Each of the 32 combinations of four trial types and eight visuomotor rotations was repeated 10 times, making a total of 320 trials per session. The three experimental sessions were performed on separate days, and the order of the three transformation conditions was balanced across participants (for one of the six different orders, there were three instead of two participants). Per repetition set, the order of the 32 trials was semirandomized such that each UniCursor trial occurred later in the trial sequence than the corresponding BiCursor trial (because the cursor trajectory presented in the UniCursor trials was recorded in the corresponding BiCursor trial). For the trials of each repetition set, we randomly allocated one of the eight visuomotor rotations to one of the eight approximate movement directions, thus preventing a systematic relation between movement direction and rotation. Each experimental session was preceded by a familiarization phase during which the experimenter gave verbal instructions on the required task execution. The familiarization ended when participants were able to correctly execute the task. We organized the total number of 320 trials per session (without familiarization) into six blocks with short breaks in-between. Each session took about 2.5 h to complete.

Data collection and outlier analysis

For each trial, we saved the Cartesian coordinates of the physical positions of cursor and/or hand at the end of the outward movement (defined as positions when the outward movement had covered 97% of the distance to the stopper ring) and the judged position of cursor or hand (defined as positions when the participants pressed the stylus button). These positions were converted into angles of a polar coordinate system with the origin in the movements' start position (i.e. the centre position of the semicircular workspace). The angular positions fully described the physical and judged end positions as their distance relative to the workspace's centre position was constant (i.e. fixed by the radius of the stopper ring and the corresponding semicircular track for the responses).

Before computing the dependent variables, we screened the data for outliers and hysteresis. First, a trial was classified as an outlier when (i) the direction of movement deviated more than 35° from the instructed direction, or (ii) the angular deviation between the physical and judged position was larger than 35°, which is twice the maximal visuomotor rotation. For each participant, there were 80 trials (8 rotations × 10 repetitions) per trial type (UniHand, UniCursor, BiHand, BiCursor) and transformation condition (Simple, ComplexConst, ComplexRand). Of these 80 trials, between 0 and 9 were excluded (mean criterion 1: 0.85 trials or 1.0%; mean criterion 2: 0.17 trials or 0.2%). Second, the start side of the response marker (i.e. randomly at either the far left or far right of the semicircular track) could systematically affect the position judgements due to hysteresis. To assess this, we computed for each experimental session (i.e. 320 trials), the regression of the judged positions on the physical positions with the constraint of a single slope, but two different intercepts for responses starting on the left or right side. The systematic differences in the responses starting right vs. left ranged from −4.6° to 2.3°. We corrected the position judgements by adding or subtracting half the intercept difference.

Dependent variables

We assessed the perceptual attraction between hand and cursor position estimates in terms of the overall coupling strength, the biases and the variability of the position judgements, and the asymmetry of the perceptual attraction. In addition, we derived model predictions for the biases, the variability and the asymmetry using a theoretical model for optimal multisensory integration.

To derive the magnitude of the biases in the position judgements, we computed for each of the bimodal trial types the angular deviation between the judged and the physical hand or cursor positions (for BiHand and BiCursor trials, respectively). We then regressed, for each trial type and transformation condition separately, the angular deviations on the visuomotor rotations. The slope of this regression indicates the biases (i.e. the attraction of the judgements towards the other modality) expressed as a weight (cf. Debats *et al.*, 2017). The slope in BiHand trials quantifies the weight w_{C_obs} given to the cursor's end position, with $w_{C\_obs} = 0$ indicating that the judged hand positions match the physical hand positions and $w_{C\_obs} = 1$ indicating that they match the physical cursor positions. The slope in BiCursor trials quantifies the weight w_{H_obs} given to the hand's end position, with $w_{H\_obs} = 0$ indicating that the judged cursor positions match the physical cursor positions and $w_{H\_obs} = 1$ indicating that they match the physical hand positions. We computed the same slopes for the unimodal trial types (UniHand and UniCursor), with the visuomotor rotation as a dummy variable in the regression. As these conditions contain just a single modality, these slopes should indicate no attraction (i.e. $w_{C\_obs} = 0$ and $w_{H\_obs} = 0$). To enable a direct statistical comparison between all transformation conditions and trial types, we quantified the judgement biases as the cursor weights (i.e. w_{C_obs} and $1-w_{H\_obs}$), indicating the bias towards the cursor position.

The variability of the position judgements was determined from the same regression analysis as the weight parameters. In particular, we computed the variance of the residuals for each trial type: UniHand ($\sigma^2_{H\_obs}$), UniCursor ($\sigma^2_{C\_obs}$), BiHand ($\sigma^2_{H.C\_obs}$) and BiCursor ($\sigma^2_{C.H\_obs}$). As dependent measure for the variability of the position judgements, we used the standard deviations (σ) rather than the variances because their units (degrees of arc) can be more easily interpreted than the units of variances (squared degrees of arc).

The coupling strength λ_{obs} was computed as the sum of the observed weights in the bimodal position judgements:

$$\lambda_{obs} = w_{H\_obs} + w_{C\_obs}. \quad (1)$$

A coupling strength of 1 indicates sensory fusion – hand and cursor are judged to be in the same position. A coupling strength of 0 indicates independence – judgements of cursor and hand positions are not attracted towards each other. Any strength between 0 and 1 indicates sensory coupling whereby the estimates of cursor and hand position are mutually attracted. It should be noted that numerically the coupling strength was not constrained to range between 0 and 1 because we determined w_{H_obs} and w_{C_obs} independently. It could exceed 1 if, for example, the hand position judgements were closer to the physical position of the cursor than the cursor position judgments themselves are (i.e. $w_{C\_obs} > 1-w_{H\_obs}$), and it could be less than 0 if, for example, hand position judgements would be biased away from the physical position of the cursor to a larger extent than the cursor position judgements would be biased towards the physical position of the hand. Such coupling strengths would indicate integration stronger than fusion and repulsion instead of attraction, respectively. Both phenomena are both empirically and theoretically (requiring, e.g., a negative coupling prior variance) unlikely.

The coupling asymmetry was defined from the observed weights in the bimodal position judgements as the coupling angle α_{obs}:

$$\alpha_{obs} = \mathrm{atan}(w_{H\_obs}/w_{C\_obs}). \quad (2)$$

This coupling angle increases with the bias towards the hand position, whereby an angle of 45° indicates symmetric coupling (i.e. $w_{H\_obs} = w_{C\_obs}$). An angle below 45° indicates that cursor position judgements are biased less towards the hand position than hand position judgements are biased towards the cursor position (i.e. $w_{H\_obs} < w_{C\_obs}$), and vice versa for a coupling angle larger than 45° (i.e. $w_{H\_obs} > w_{C\_obs}$). The coupling angle is independent of the coupling strength and thus enables an assessment of the relative magnitude of the attraction biases across transformation conditions with differing coupling strengths.

Last, we derived predictions for the judgement biases, variability and coupling asymmetry according to the coupling model proposed by Ernst (2006, 2012), for which the equations were derived by Debats *et al.* (2017). The predicted bimodal weights were accordingly computed as:

$$w_{H\_pred} = \frac{\sigma^2_{C\_obs}}{\sigma^2_{C\_obs} + \sigma^2_{H\_obs} + \sigma^2_{prior}}, \text{ and} \qquad w_{C\_pred} = \frac{\sigma^2_{H\_obs}}{\sigma^2_{C\_obs} + \sigma^2_{H\_obs} + \sigma^2_{prior}}. \quad (3)$$

Like with the observed weights, these predicted weights were converted to cursor weights (i.e. w_{C_pred} and $1-w_{H\_pred}$) to allow statistical comparisons. The variance of the coupling prior (σ^2_{prior}) was computed from the observed coupling strength λ_{obs} and the observed variances in the unimodal position judgements as:

$$\sigma^2_{prior} = \frac{1-\lambda_{obs}}{\lambda_{obs}}\left(\sigma^2_{C\_obs} + \sigma^2_{H\_obs}\right). \quad (4)$$

The predicted optimal variances for the bimodal position judgements were computed as:

$$\sigma^2_{C.H\_pred} = \frac{\sigma^2_{C\_obs}\left(\sigma^2_{H\_obs} + \sigma^2_{prior}\right)}{\sigma^2_{C\_obs} + \sigma^2_{H\_obs} + \sigma^2_{prior}}, \text{ and} \qquad \sigma^2_{H.C\_pred} = \frac{\sigma^2_{H\_obs}\left(\sigma^2_{C\_obs} + \sigma^2_{prior}\right)}{\sigma^2_{C\_obs} + \sigma^2_{H\_obs} + \sigma^2_{prior}}. \quad (5)$$

Like with the observed variances, we used the standard deviation for statistical comparisons. The predicted coupling angle was computed from the observed unimodal variances as:

$$\alpha_{pred} = \arctan\left(\sigma^2_{C\_obs}/\sigma^2_{H\_obs}\right). \quad (6)$$

Statistical analysis

Statistical comparisons across the three transformation conditions were made using ANOVAS for repeated measures, with *post hoc* paired-samples *t*-tests. Comparisons between behavioural data and model predictions were made by means of paired-samples *t*-tests. In addition, we computed Pearson's correlation coefficients between predicted and observed measures of individual biases, variability and coupling asymmetry. All means are given together with their standard errors.

Results

Our primary aim was to assess how the three transformation conditions affected the strength of the hand-cursor sensory integration (i.e. coupling strength λ_{obs}). Additionally, we tested how the transformation conditions affected the biases (i.e. cursor weights) in the position judgements, the variability (i.e. standard deviation) of the position judgements and the coupling asymmetry (i.e. coupling angle α_{obs}). For these measures, we compared the observed values with the values as predicted for optimal multisensory integration. This allowed us to discriminate between theoretically predicted effects (e.g. consequences of different coupling strengths) and other variations.

Coupling strength

Figure 2A shows the mean coupling strength for the three transformation conditions together with the individual coupling strengths. There

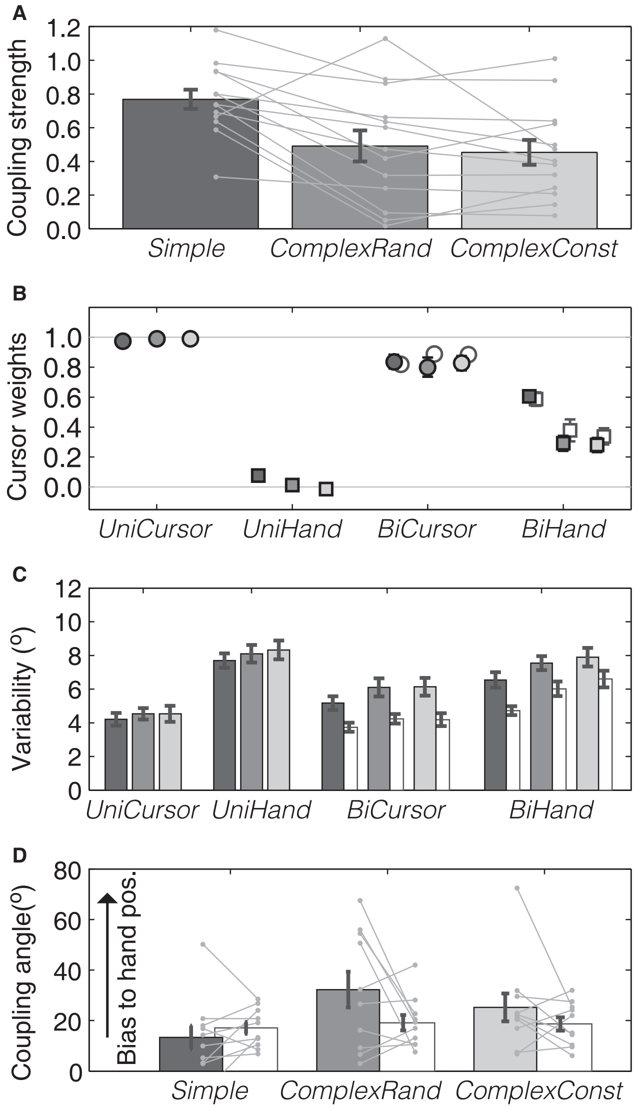

FIG. 2. Data and model results. In all panels, the filled dark, middle and light grey bars or symbols refer to the transformation conditions *Simple*, *ComplexRand* and *ComplexConst*, respectively. The open bars and symbols illustrate the model predictions. All error bars represent the standard error of the mean. (Panel A) The observed coupling strength in the three transformation conditions. The connected dots represent individual participants. (Panel B) The biases in the unimodal and bimodal position judgements as quantified by the cursor weights. (Panel C) The variability in the unimodal and bimodal position judgements, as quantified by the standard deviation. (Panel D) The coupling asymmetry for the three transformation conditions as quantified by the coupling angle. The connected dots represent individual participants.

was a clear effect of the transformation conditions on the coupling strength as confirmed by the ANOVA ($F_{2,24} = 13.340$, $P = 0.0001$). *Post hoc* pairwise comparisons indicated that the coupling strength was significantly reduced in the two conditions with a complex transformation, ComplexRand and ComplexConst, as compared to transformation condition Simple ($t_{12} = 3.345$, $P = 0.0058$, and $t_{12} = 6.256$, $P < 0.0001$, respectively), whereas there was no significant difference between conditions ComplexRand and ComplexConst ($t_{12} = 0.601$, $P = 0.5594$). Thus, the coupling strength was clearly affected by the complexity of the kinematic transformation, whereas is seemed unaffected by the transformation's trial-to-trial variability.

Unimodal biases and variability

The mean position judgement biases, as quantified by the cursor weights, are shown in Fig. 2B. For the UniCursor trials, the cursor weights were approximately 1, and for the UniHand trials, the cursor weights were approximately 0. This indicates that the unimodal cursor and hand position judgements were unbiased. The mean variabilities of the position judgements, as quantified by the standard deviations, are shown in Fig. 2C. Although the unimodal variabilities appeared slightly smaller in condition Simple than in the two complex transformation conditions, these variations were not significant, neither for UniCursor trials ($F_{2,24} = 0.784$, $P = 0.4680$) nor for UniHand trials ($F_{2,24} = 0.939$, $P = 0.4048$). The consistency of the unimodal variabilities across transformation conditions implies that the optimal coupling model predictions for the bimodal position judgements (which are based on the unimodal variabilities) predominantly reflect differences in coupling strength.

Bimodal judgement biases

For the two bimodal trial types, Fig. 2B illustrates the observed cursor weights (filled symbols) together with the weights predicted by the optimal coupling model (open symbols). For the BiCursor position judgements, the model predicts a slightly lower cursor weight for the condition with a higher coupling strength (i.e. Simple) than the two conditions with a lower coupling strength (i.e. ComplexRand and ComplexConst), but no difference between the latter two ($F_{2,24} = 7.562$, $P = 0.0028$; *post hoc* comparisons: $t_{12} = -2.783$, $P = 0.0166$; $t_{12} = -3.855$, $P = 0.0023$; and $t_{12} = 0.171$, $P = 0.8672$, respectively). This is because a stronger coupling implies a stronger attraction to the hand position and thus a lower cursor weight. This small decrease in cursor weights for condition Simple was, however, not seen in the observed cursor weights ($F_{2,24} = 0.281$, $P = 0.7573$). For the BiHand judgements, the model predicts a clearly higher cursor weight for condition Simple with the higher coupling strength than for conditions ComplexRand and ComplexConst with the lower coupling strength and no difference between the latter ($F_{2,24} = 12.667$, $P = 0.0002$; *post hoc* comparisons: $t_{12} = 3.172$, $P = 0.0080$; $t_{12} = 6.066$, $P = 0.0001$; and $t_{12} = 0.816$, $P = 0.4304$, respectively). The observed cursor weights were consistent with this predicted pattern ($F_{2,24} = 53.348$, $P < 0.0001$; *post hoc* comparisons: $t_{12} = 8.517$, $P < 0.0001$; $t_{12} = 8.685$, $P < 0.0001$; and $t_{12} = 0.344$, $P = 0.7368$, respectively).

Direct comparison between the predicted and observed cursor weights in Fig. 2B suggests that, for both the BiCursor and the BiHand position judgements, the observed cursor weights in the complex conditions tended to be smaller than the predicted weights. However, for none of the six comparisons of predicted and observed cursor weights the difference was actually significant, as indicated by paired-samples *t*-tests (all *P*-values > 0.10). Regression analysis between the individual observed and predicted cursor weights revealed correlations ranging from 0.72 to 0.84 across conditions, which supports the predictive value of the model.

Bimodal judgement variability

For the two bimodal trial types, Fig. 2C illustrates the mean standard deviations of the observed position judgements (filled bars) together with the mean standard deviations predicted by the optimal coupling model (open bars). Visual inspection of the unimodal and bimodal variabilities reveals a consistent pattern: the variability was smallest in UniCursor trials, largest in UniHand trials, and in the bimodal trials variability was in-between, being smaller in BiCursor trials than in BiHand trials. According to the model, the observed difference in coupling strength should lead to a lower variability in condition Simple than in the complex transformation conditions ComplexRand and ComplexConst for BiHand trials ($F_{2,24}$ = 11.935, P = 0.0007; *post hoc* comparisons: t_{12} = −3.042, P = 0.0102; t_{12} = −3.629, P = 0.0035; and t_{12} = −1.740, P = 0.1074, respectively), whereas for BiCursor trials this variation was not significant ($F_{2,24}$ = 2.095, P = 0.1450). A consistent pattern was present in the observed variabilities, where it was statistically significant for BiHand trials ($F_{2,24}$ = 4.865, P = 0.0168; *post hoc* comparisons: t_{12} = −2.306, P = 0.0397; t_{12} = −3.122, P = 0.0088; and t_{12} = −0.7271, P = 0.4811, respectively) and almost so for BiCursor trials ($F_{2,24}$ = 3.388, P = 0.0506).

Although the predicted variability varied across the three transformation conditions in the same way as the observed variability did, it was consistently smaller as confirmed by paired-samples *t*-tests (all P < 0.0333). This consistent difference between the observed and predicted variability is in line with our previous findings (Debats *et al.*, 2017), indicating that there is some unmodelled noise in this task. Pearson's correlation coefficients between observed and predicted standard deviations ranged from 0.66 to 0.97 except for two small correlations of 0.08 and 0.33.

Coupling asymmetry

For the analysis of the coupling asymmetry, as quantified by the coupling angle, the data of three participants were excluded because their coupling strength was less than 0.2 in at least one of the three experimental conditions. With such a weak coupling, estimates of the coupling angle become highly noisy because they are based on the ratio of small and noisy cursor weights. For the remaining 10 participants, the mean coupling angles are illustrated in Fig. 2D by the filled (i.e. observed values) and open (i.e. predicted values) bars. Individual participants are indicated by the connected little dots. The optimal coupling model predicts no difference in coupling angle between the three transformation conditions ($F_{2,18}$ = 0.256, P = 0.7771), which reflects the observation that these conditions had similar unimodal variances. The observed coupling angles, however, were lower for condition Simple than for the two complex transformation conditions ComplexRand and ComplexConst ($F_{2,18}$ = 6.434, P = 0.0078; *post hoc* comparisons: t_9 = −2.930, P = 0.0168; t_9 = −3.176, P = 0.0113; and t_9 = 1.322, P = 0.2187, respectively).

Direct comparisons between the individual observed and predicted angles did not reach statistical significance for any of the three conditions (all P > 0.11). Correlation coefficients between observed and predicted angles ranged from 0.21 to 0.58, whereby it should be noted that the coupling angle is a rather noisy measure in general.

Discussion

Recent studies have shown that, in a basic cursor-control task, the perceived position of the hand (cursor) is attracted to the position of the cursor (hand) as mapped onto the same plane of motion (Ladwig *et al.*, 2012, 2013; Rand & Heuer, 2013, 2016; Kirsch *et al.*, 2016). We previously found that this perceptual attraction between kinematically related hand and cursor 'objects' is consistent with optimal multisensory integration model predictions (Debats *et al.*, 2017). Here, we asked: which aspect of the hand-cursor kinematic relation is crucial for the brain to integrate the sensory information from these separate sources? We manipulated the hand-cursor transformation to assess whether sensory integration depends on kinematic cross-correlations and/or the ability to acquire an internal model of the transformation. We found a reduced coupling strength for a complex kinematic transformation (i.e. reduced kinematic correlations) as compared to a simple transformation (i.e. perfect kinematic correlations), and no effect of whether the complex transformation was constant over trials (thus allowing internal model acquisition) or randomly varying from trial to trial (and thus not allowing model acquisition). In the following, we discuss these findings and their implications.

Our current findings substantially extend those of our previous study (Debats *et al.*, 2017) in which we found that the neural process of optimal multisensory integration applies to sensory information from spatially distant separate objects, if those separate objects are bound by a kinematic relation. Our current findings provide clear evidence that the integration over separate objects is based on evidence of spatiotemporal sensory correlations. In contrast, we found that the ability to acquire an internal model of the transformation (i.e. to learn the hand-cursor mapping) was unrelated to the strength of the sensory integration. These findings suggest that sensory integration across separate objects is not achieved at the higher level of spatial representations, but rather in a bottom-up fashion, driven by correlated visual and proprioceptive signals.

Our current finding fits to recent studies that have shown that temporal cross-correlations have a profound influence on causal inference, and thereby on the strength of sensory integration (e.g. Shams & Beierholm, 2010; van Dam *et al.*, 2014). The role of temporal correlations was studied with sensory stimuli consisting of short series of events, such as beeps and flashes (e.g. Parise *et al.*, 2012). The current study is the first to manipulate kinematic cross-correlations, and our findings clearly indicate that spatiotemporal correlations can have equivalent effects as temporal correlations have. Our findings thus strengthen the claim that causal inference, and thereby multisensory integration, is based on sensory cross-correlations (Parise & Ernst, 2016), irrespective of the number of sensory sources involved.

In our data, we observed the hypothesized reduction in coupling strength for the complex transformation conditions as compared to the simple transformation condition. However, the coupling strength went not down to zero but to around 0.5. From our current data, we cannot conclude whether coupling strength would reduce further with a further reduction in kinematic correlations. Importantly, for the two levels of kinematic cross-correlations that we tested we did not specify the exact cross-correlations' magnitude. Such quantification is only possible when one knows which kinematic variables of the hand and cursor trajectories (e.g. instantaneous direction or velocity) are involved. We took the approach of using a simple linear transformation, for which there is a perfect correlation in all possible kinematic variables, and to robustly reduce this correlation by adding a curvature to the cursor trajectory. It is possible that a more subtle manipulation of specific kinematic variables would result in a more fine-grained modulation of integration strength. There are, however, reasons to doubt that a further reduction in coupling strength could occur. In a cursor-control task, reduced kinematic correlations exist only for the durations of experiments, whereas in daily life essentially all participants experience perfect kinematic correlations when they use computers. Thus, for cursor-control tasks, participants likely start any experiment with an established coupling prior that has been acquired during years of computer experience. All that one may expect from the limited experience of reduced kinematic correlations during an experiment is a certain short-term modulation of the established coupling prior.

We hypothesized that the strength of sensory integration might depend on whether or not the hand-cursor kinematic transformation is learned, that is whether or not an internal model of it has been acquired (cf. Wolpert & Kawato, 1998). Learning should be possible with the complex transformation that remained constant over trials, but not with the variable complex transformation (e.g. Hegele & Heuer, 2010). We implicitly assumed that the 28 pre-experimental practice trials were sufficient to learn the complex transformation at least to some degree, but possibly learning might have taken longer. To control for such slower learning, which would be indicated by a gradual increase in coupling strength for condition ComplexConst, we additionally compared the coupling strength between the first and second halves of the experimental trials. This revealed no differences both for condition ComplexConst (0.48 ± 0.08 and 0.43 ± 0.07, respectively) and for condition ComplexRand (0.49 ± 0.10 and 0.49 ± 0.09, respectively). This strengthens the conclusion that the strength of sensory integration is not mediated by the presence of an internal model of the complex visuomotor mapping. Furthermore, the lack of difference between the first and second halves of the complex transformation conditions suggests that the modulation of coupling strength by the reduced kinematic correlations is not cumulative. Instead, it seems that the modulation of integration strength depends on the immediate experience of higher or lower kinematic correlations in each single trial.

Overall the ideal-observer model predictions were rather well in line with the participants' behavioural data, confirming our previous findings (Debats *et al.*, 2017). Slightly equivocal findings were obtained for the bias of judged cursor position towards the position of the hand. In the two complex transformation conditions, the observed biases tended to be closer to the hand position (i.e. lower cursor weights) than predicted, and the coupling angles tended to be larger than predicted. Both these findings, if significant, would have indicated a perceptual bias to the hand position in addition to purely reliability-based weighting (i.e. independent of the hand and cursor unimodal reliabilities). In our previous study, we found that the cursor weights were affected by contextual cues, so it is not unlikely that a curved cursor trajectory urges the brain to rely more on the hand position information. Our current findings, however, are inconclusive in this respect. The only conspicuous deviations of the observed from the predicted values were seen in the variability of the bimodal position estimates. The observed variability was consistently larger than the model predictions for optimal sensory coupling, as derived from the variances of the unimodal hand and cursor position estimates and the coupling strength. This discrepancy between predictions and observations was also observed in our previous study (Debats *et al.*, 2017). It implies that there is some unmodelled noise in our task, which could, for example, be decisional noise or motor noise. Note that in spite of the differences in the means, the individual predicted variabilities are rather well correlated with the individual observed variabilities.

Finally, one may wonder why the brain integrates sensory information across separate objects with a high kinematic cross-correlation. This question is closely related to the question of whether our findings are limited to tool-use tasks or even cursor control, or whether they are generic to any type of systematic relation between two objects. On the one hand, optimal integration across objects might be a process that is dedicated to binding actions with their visual consequences (Reichenbach *et al.*, 2014; Kirsch *et al.*, 2016). Such a 'visuomotor binding' mechanism could serve to enable fast and flexible motor control in visually cluttered environments (Reichenbach *et al.*, 2014). According to this hypothesis, kinematic cross-correlations would lead to positive causality judgements and thus to sensory integration only if one of the two objects is a part of the body that, by actively moving, causes the motion of the external other object. (The notion of 'causality' might be confusing here: a positive causality judgement means that the sensory signals related to hand and cursor positions have the same 'cause' in the sense of the same source of the respective sensory signals, but this is different from a moving hand 'causing' movement of an external object.)

On the other hand, sensory integration across separate objects might be a by-product of a neural mechanism that has evolved to perform integration of redundant sensory signals from single sources. That is, spatiotemporal cross-correlations between sensory signals are, in most situations of everyday life, reliable evidence for them originating from a single physical source (i.e. object or event). According to this second explanation, sensory integration should occur for any two kinematically related objects, no matter whether or not active movement of the observer is involved. It would result in visuomotor binding as well as binding between external objects. In our view, it seems unlikely that the process of causal inference would differ for equally correlated sensory signals depending on how these signals are generated – involving active movements of the observer or not. Pending new evidence on the issue, we thus believe that our current findings hold regardless of whether one of the kinematically related objects is a part of the body or whether both of the kinematically related objects are parts of the external world.

To conclude, the present experiment reveals a clear reduction in the strength of sensory integration when the cross-correlations between kinematic variables of hand and cursor movements are reduced. This supports the claim that correlations play a crucial role in multisensory integration irrespective of the number of sensory sources involved.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

NBD and HH designed the experiment and analysed the data; NBD, MOE and HH wrote the manuscript.

Data accessibility

The raw data and supporting information are available at pub.uni-bielefeld.de/data/2914527, with https://doi.org/10.4119/unibi/2914527.

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