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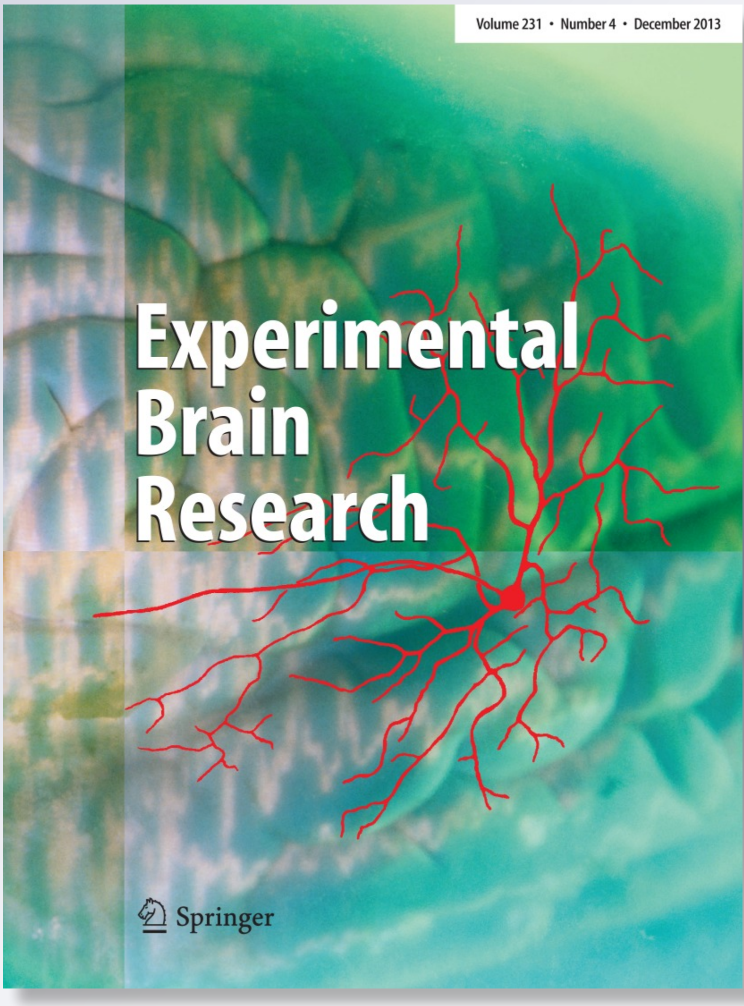

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RESEARCH ARTICLE

Intra- and intermodal integration of discrepant visual and proprioceptive action effects

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Abstract Integration of discrepant visual and proprioceptive action effects puts high demands on the human information processing system. The present study aimed to examine the integration mechanisms for the motor (Exp. 1) and visual modality (Exp. 2). According to theories of common coding, we assumed that visual as well as proprioceptive information is represented within the same cognitive domain and is therefore likely to affect each other (multisensory cross talk). Thus, apart from the often-confirmed visual dominance in multisensory integration, we asked about intra- and intermodal recall of either proprioceptive or visual information and whether there were any differences between the motor and visual modality. In a replication paradigm, we perturbed the relation between hand movements and cursor movements. The task required the (intra- vs. intermodal) replication of an initially performed (seen) hand (cursor) movement in a subsequent motor (visual) replication phase. First, mechanisms of integration were found to be dependent on the output modality. Visual action effects interfered the motor modality, but proprioceptive action effects did not have any effects on the visual modality. Second, however, intermodal integration was more susceptible to interference, and this was found to be independent from the output modality. Third, for the motor modality, the locus of perturbation (perturbation of cursor amplitude or perturbation of hand amplitude) was irrelevant, but for the visual modality, perturbation of hand amplitudes reduced the cross talk. Tool use is one field of application of these kinds of results, since the optimized integration of conflicting action effects is a precondition for using tools successfully.

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Introduction

Tool use in modern technical environments is often characterized by spatial separation and distortion between visual and motor action effects. High demands are put on the human processing system to integrate this discrepant information from the sensory system, often without actors being aware of it. The ideomotor principle (James 1890; Greenwald 1970) represents the idea of action representation with regard to the action's effects. The authors state that each intended action needs a (pre)defined goal. As a consequence, planning of goal attainment is modulated by anticipatory representations of the intended action effect. According to Greenwald (1970) the activation of anticipatory codes moderate the selection, initiation and execution of an intended movement. The theory of event coding (TEC, Hommel et al. 2001) furthers this approach. Information from the sensory system concerning an action is coded and represented within the same domain. As a result of this, action effects and movement planning are nondistinct entities. In this vain, in the early 1990s, Prinz already proposed that, by means of the common representation, movement production is controlled by codes specifying the action goal in extracorporeal space (common coding approach; Prinz 1997). TEC further proposes that when perceptual stimuli share some features with planned actions (e.g., size or motion direction), these stimuli can either foster those actions or interfere with them depending on their similarity, i.e., their amount of feature overlap (for an overview see also Hommel et al. 2001). A computational approach on this interaction between extracorporeal events and cognitive factors dealing with action planning is the idea of a statistically optimal visual–haptic integration, similar to maximum-likelihood estimation (MLE) (Ernst and Banks 2002). For each modality, the nervous system estimates the perceptual stimulus features. The estimates are corrupted by noise inducing variance to the signal (e.g., decreasing visual contrast makes detection of a visual stimulus difficult, and variance in responses increases). Multisensory integration follows the principle of minimum variance in the combined percept, which means each unified estimate contributes with its reciprocal variance to it. Consequently, the total variance of the combined percept is lower than that for each unified percept. In this line, visual dominance occurs when lower variance is associated with the visual estimations (i.e., high reliability of the visual information) than that for the haptic estimations (e.g., Ernst and Banks 2002; Knoblich and Kircher 2004; Kunde et al. 2007; Massen and Prinz 2007; Reuschel et al. 2010; Rieger et al. 2005; Sülzenbrück and Heuer 2009; Takahashi et al. 2009) and the other way round for haptic dominance (e.g., Ernst and Banks 2002; Sutter and Ladwig 2012; Sutter et al. 2013). Although multisensory integration is very flexible and adaptive, actions become slow and inaccurate when motor and visual information does not correspond (e.g., Müsseler and Sutter 2009; Proctor et al. 2004; Sutter et al. 2011).

A recent study by Ladwig et al. (2012) focused on the accuracy of visual–proprioceptive integration and whether the interaction between visual and proprioceptive action effects depended on their amount of feature overlap. The setting basically involved trials consisting of two phases (Fig. 1, intra-modal conditions only): In phase 1, participants moved a pen on a covert digitizer tablet in order to move a cursor on a display from a start to a target bar (genuine closed-loop task). Subsequently, they inverted the movement direction on the digitizer tablet in order to reproduce the initially performed hand amplitudes (of phase 1) without receiving any visual feedback. Additionally, either the cursor amplitude or the hand amplitude was perturbed. That is, in the condition with perturbed cursor amplitude (Fig. 1a), the initial cursor movement was shorter, equal to or longer than the constant hand motion on the tablet. In the condition with perturbed hand amplitude (Fig. 1b), the initial hand movement was shorter, equal to or longer than the constant cursor motion on the display. The dependent variable was the mean deviation between initial and replicated hand amplitudes. If visual and proprioceptive action effects were independent from each other, then replicated hand amplitudes should be very precise, irrespective of the task in phase 1. Cognitive and computational approaches (e.g., Ernst and Banks 2002; Hommel et al. 2001), however, propose a cognitive representation of the action integrating information from both senses. If information from both senses was integrated in an event code, retrieval of information from one sense might be affected from the other sense, which means visual information from phase 1 could bias motor replications in phase 2 (= aftereffects). These aftereffects represent the interaction between modalities (= cross talk). Cross talk could be the same across conditions with perturbed hand or cursor amplitudes (same amount of aftereffects in both conditions = symmetric) or it could differ, being in one condition larger than in the other (asymmetric).

Results confirmed the latter. In control trials, in which initial cursor and hand amplitudes corresponded, replicated hand amplitudes were very precise. However, in trials in which they did not correspond, replicated hand amplitudes were shorter than required when the initially seen cursor amplitude was shorter than the initially performed hand amplitude, and it was longer than required when the initially seen cursor amplitude was longer than the initially performed hand amplitude. A 90° rotation of cursor amplitudes reduced these aftereffects. This kind of cross talk between visual and proprioceptive action effects can be ascribed to the amount of overlap of feature codes from both modalities being processed within the same cognitive domain (Hommel et al. 2001). Higher feature overlap leads to increased cross talk. Furthermore, the cross talk was asymmetric with larger aftereffects in the condition with perturbed hand amplitudes compared to the condition with perturbed cursor amplitudes. The authors argued—in line with the model of multisensory integration by Ernst and Banks (2002)—that the perturbation of hand amplitudes increased variance in the motor system substantially, so that motor information became less reliable. Consequently, visual action effects contributed stronger to the percept than in the other condition.

As outlined in the above section, former studies examined the influence of perturbed cursor amplitude or perturbed hand amplitude on the motor system and were able to show that the manual reproduction of former actions was notably susceptible to gain changes. The purpose of the present study is to extend these findings by contrasting the susceptibility of the proprioceptive as well as the visual modality in two experiments. In Experiment 1, we use the same motor replication task as Ladwig et al. (2012) did. In one block, we ask participants to replicate the initially performed hand amplitude with the pen on the digitizer tablet (intra-modal condition). In another block, participants replicate the initially seen cursor amplitude with the pen on the digitizer tablet (intermodal condition). In Experiment 2, we introduce a visual replication task. To replicate the initially seen cursor amplitude (intra-modal condition) or the initially performed hand amplitude (intermodal condition),

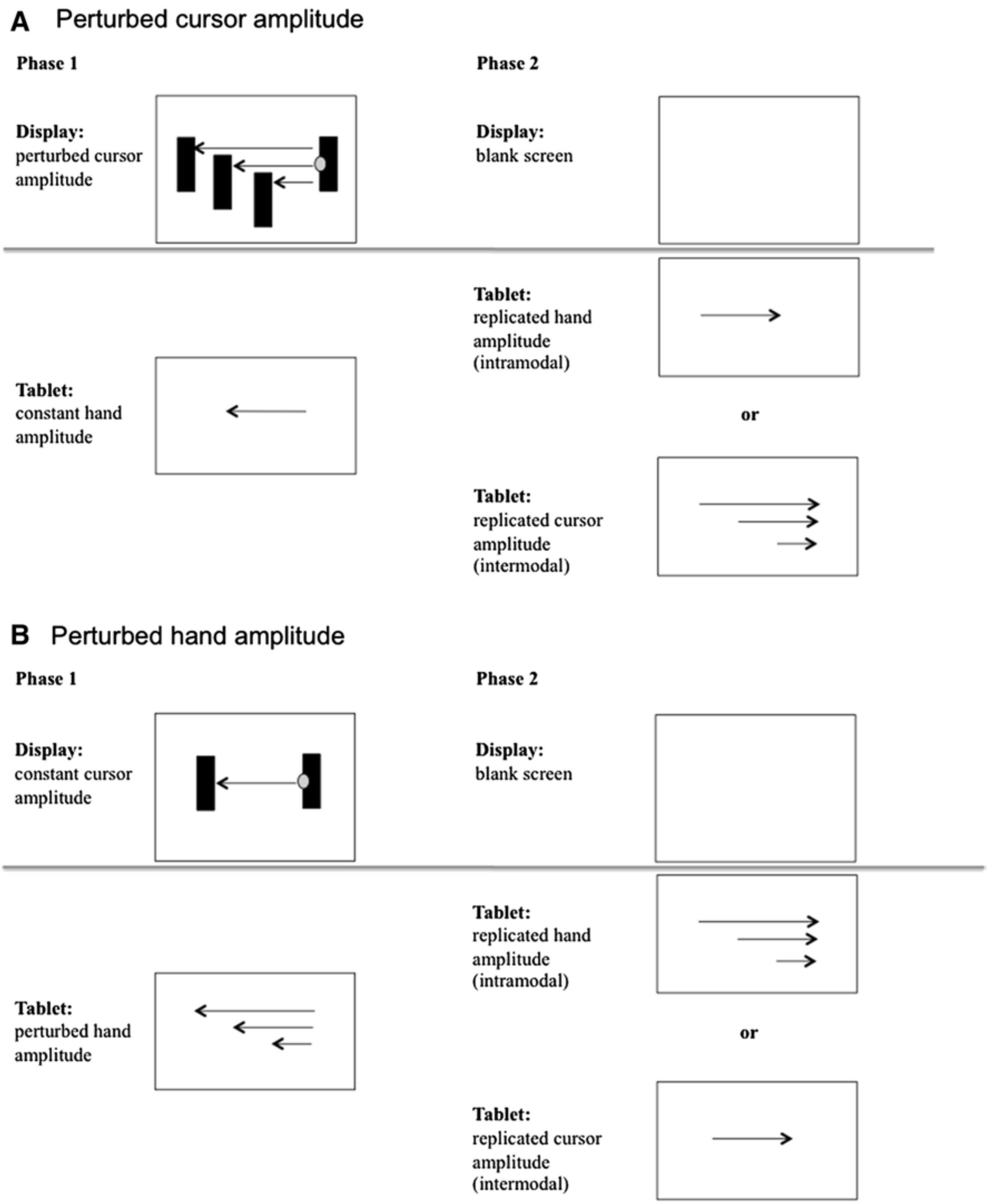

Fig. 1 **a** Perturbed cursor amplitude (*top*): In phase 1, the cursor amplitude varied by three different gains while the hand amplitude remained constant across trials. The subsequent phase 2 required reproducing the initially performed hand amplitude or the initially seen perturbed cursor amplitude without any visual feedback. **b** Perturbed hand amplitude (*bottom*): In phase 1, the cursor amplitude remained constant across trials, while the hand amplitude varied by three different gains. The subsequent phase 2 required reproducing the initially perturbed hand amplitude or the initially constant cursor amplitude without any visual feedback

participants press a key to control a horizontally moving cursor on the display. The intra- and intermodal comparisons aim to demonstrate the mechanisms of cross talk in visual–proprioceptive integration for the motor (Exp. 1) and visual (Exp. 2) modalities.

Experiment 1

Based on Ladwig et al. (2012), we set up a replication task in which participants perform constant (perturbed) hand movements with a pen on a digitizer tablet receiving perturbed (constant) visual online-feedback on a screen. Subsequently, participants are asked to replicate either the initially performed hand amplitude (intra-modal condition) or the initially seen cursor amplitude (intermodal condition) without receiving any visual feedback (blockwise variation). By contrasting these conditions, the present study aims at distinguishing between intra- and intermodal integration of discrepant visual and proprioceptive action effects. In Exp. 1, the intra-modal condition requires participants to retrieve proprioceptive information from phase 1 to manually replicate the initially performed hand amplitude. In the intermodal condition, retrieval of visual information from phase 1 enables the participants to manually replicate the initially seen cursor amplitude.

The first hypothesis (H1) generally predicts larger aftereffects in the intermodal condition than in intra-modal condition. In other words, the retrieval of proprioceptive information for the subsequent replication of hand amplitudes is expected to be more precise because the required information for detection, estimation and recall is assumed to be immediately available. On the contrary, information to detect, estimate and replicate visual action effects has to be accumulated by comparing internally predicted and observed visual effects (see also Rieger et al. 2005).

Furthermore, when Ladwig et al. (2012) asked the participants to replicate initially performed hand movements, the authors observed stronger aftereffects with perturbed hand amplitudes (while cursor amplitudes were constant) than with perturbed cursor amplitudes (while hand amplitudes remained constant). This asymmetric cross talk might have resulted from motor information becoming less reliable in this condition (cf. Ernst and Banks 2002). Thus, the second hypothesis (H2) predicts for intra-modal replications stronger aftereffects for perturbed hand amplitudes than for perturbed cursor amplitudes (= replication of asymmetric cross talk found by Ladwig et al. 2012). For intermodal replications, this asymmetry should occur inversely: Aftereffects should be more pronounced for intermodal replications that require the reproduction of perturbed cursor amplitudes while hand amplitudes remain constant. That is, on the one hand, visual information has to be accumulated by comparing internally predicted and observed visual effects. On the other hand, perturbed visual information leads to higher variance in visual information, so that visual information contributes less and proprioceptive information contributes more to the percept.

Methods

Apparatus, task and stimuli

The experiment was carried out in a dimly lit room and controlled by an Apple Macintosh computer running Matlab software with the Psychophysics Toolbox extension (Kleiner et al. 2007). Figure 2 depicts the experimental setup. Participants were positioned in front of a DIN-A3 digitizer tablet (WACOM Intuos2, 100 Hz sampling rate) holding a pen in their dominant right hand while the non-dominant left hand rested on their lap. A fiberboard with a cutout groove was mounted onto the digitizer tablet (width and length of the groove 4 and 500 mm). To perform horizontal strokes on the tablet, participants moved the tip of the pen (WACOM Intuos2 Grip Pen) in the groove. An occluder with a curtain prevented direct vision of the digitizer tablet and the participant's right hand. The experimental tasks and visual feedback of the hand movements were presented on a 22″ color CRT display, with a distance of approximately 600 mm between the participant and display (Fig. 2, Display A: Iiyama HM204DT, Vision Master

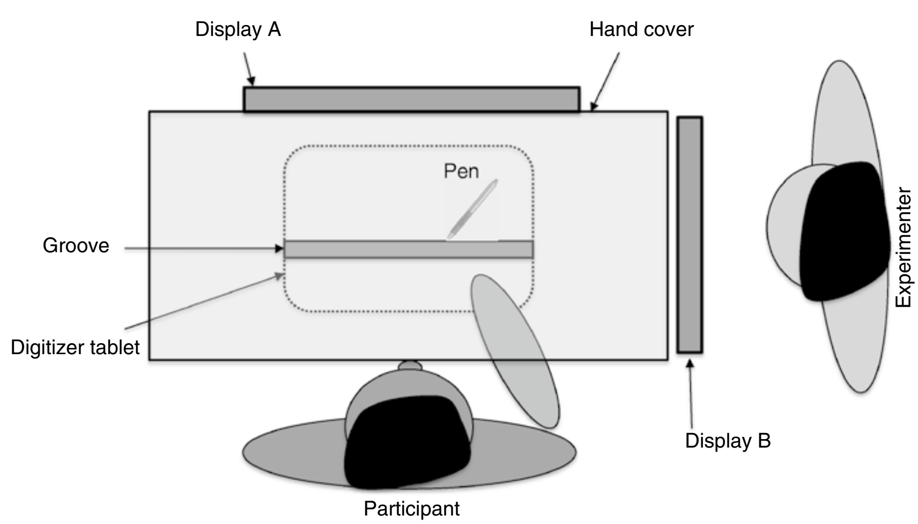

Fig. 2 Sketch of the experimental setup

Pr514, 100 Hz refresh rate, 1,024 × 768 pixel). The experimenter sat next to the participants and monitored the log file providing information about participant's performance on a separate display (Fig. 2, Display B).

In phase 1 of each trial, two black bars (rectangles of 2 × 8 mm each) and a gray circular cursor (diameter 4 mm) appeared on the white screen (Fig. 1, left). The cursor was positioned onto the right bar, and the task in phase 1 required moving it to the bar on the far side as accurately as possible by moving the pen leftward along the groove on the digitizer tablet. When the cursor had reached the left bar, phase 2 started: The screen turned blank, and participants had to move the pen back—rightward—without any visual feedback (Fig. 1, right). In one block, the task in phase 2 required reproducing the initially performed hand amplitude as accurately as possible. In another block, the task in phase 2 required reproducing the initially seen cursor amplitude as accurately as possible. The start position of the cursor on the left side inverted the movement directions.

In phase 1, the relation between cursor amplitude and hand amplitude was perturbed by three different gain factors. Figure 1a (top) depicts the task for perturbed cursor amplitudes while the hand amplitude remained constant at 120 mm across trials. The applied gain factors (1:1.5, 1:1.0, 1:0.5) resulted in cursor amplitudes of 180, 120 or 60 mm, so that the cursor amplitude was longer, equal to or shorter than the hand amplitude. In phase 2, when participants were instructed to replicate the initially performed hand amplitude, the reproduction required moving the pen by 120 mm. Thus, the motor reproduction in phase 2 required the recall of the motor information from phase 1 (intra-modal), while the visual information from phase 1 was irrelevant for solving the task and had to be ignored. And the other way round in phase 2, when participants were instructed to replicate the initially seen cursor amplitude, the recall required moving the pen by 180, 120 or 60 mm. Motor recall in phase 2 required the reproduction of visual information from phase 1 (intermodal), while the motor information from phase 1 was irrelevant and had to be ignored.

Figure 1b (bottom) depicts the task for perturbed hand amplitudes while the cursor amplitude remained constant at 120 mm across trials. The applied gain factors (1:1.5, 1:1.0, 1:0.5) resulted in hand amplitudes of 180, 120 or 60 mm, so that the hand amplitude was longer, equal to or shorter than the cursor amplitude. In phase 2, when participants were instructed to replicate the initially performed hand amplitude (intra-modal), the reproduction required moving the pen by 180, 120 or 60 mm. In the intermodal condition, when participants were instructed to reproduce the initially seen cursor amplitude, the reproduction required to move the pen by 120 mm.

Procedure and design

Participants ($N = 18$) were randomly assigned to the perturbation conditions: Nine participants ran through the condition of perturbed cursor amplitudes (Fig. 1a, top), and the other nine participants ran through the condition of perturbed hand amplitudes (Fig. 1b, bottom).

For each group, the experiment consisted of four blocks: Blocks 1 and 2 involved reproducing the hand amplitude (intra-modal). In block 1, the movement direction in phase 1 was from right to left and in phase 2 from left to right. In block 2, the movement directions were reversed (not depicted). The order of movement direction blocks was counterbalanced across participants. Blocks 3 and 4 involved reproducing the cursor amplitude (intermodal). In block 3, the movement direction in phase 1 was from right to left and in phase 2 from left to right. In block 4, reversed movement directions were required (not depicted). The order of movement direction blocks was counterbalanced again across the participants. Half of the participants within each group started with cursor amplitude replications and the other half with hand amplitude replications.

Each block consisted of 45 trials (three gain factors with 15 repetitions each, randomly presented), and another nine trials presented in advance of each block in order to familiarize subjects with the task (the same three gain factors as used in the experimental trials with three repetitions each, randomly assigned). The experiment lasted about 45 min.

Before a block started, participants were instructed to move as accurately as possible and to produce continuous and smooth forth and back movements with the pen without interrupting. In the blocks of hand amplitude replications, they were further instructed to reproduce the initially performed hand amplitude in phase 2 as accurately as possible and to monitor their hand motion in phase 1 carefully. In the blocks of cursor amplitude replications, they were instructed to reproduce the initially seen cursor amplitude in phase 2 as accurately as possible and to monitor the cursor motion in phase 1 carefully. At the beginning of each trial, the cursor as well as the start and target bar was presented on the screen. Participants were instructed to move the cursor from the start to the target bar by moving the pen on the tablet. A first click of the pen's button unlocked the cursor, and participants moved it to the opposite target bar while receiving continuous visual feedback. When the cursor was positioned on the target bar, participants pressed the pen's button a second time. Then, both bars as well as the cursor disappeared, and participants started the replication of the hand or the cursor amplitude—depending on the condition—by reversing the movement direction with the pen. When they thought to have reproduced the required amplitude, they finally pressed the pen's button to terminate the trial. Subsequently, a new trial was presented.

The experiment was based on a 2 × 2 × 3 mixed design with the between-subject factor perturbed amplitude (cursor vs. hand amplitude), and the within-subject factors replicated amplitude (cursor vs. hand amplitude replications) and gain (to-be-replicated movement shorter vs. equal vs. longer compared to the irrelevant amplitude). Trials were considered as erroneous and omitted from analyses when the initial movement trajectory was noncontinuous (with $v = 0$ within the initial hand movement) and/or its direction changed, when the initial movement overshot the target area, when the second or third button click occurred while the cursor was outside the target area and when the observed replicated amplitude was shorter than or equal to 10 mm.

Participants

A total of 18 students (17 female) of the RWTH Aachen University, aged from 18 to 29 years ($M = 23.3$; SD = 3.1), volunteered for the experiment. All participants were right handed, had normal or corrected-to-normal vision and were naïve with respect to the purpose of the experiment.

Results

Mean deviations (in mm) between to-be-replicated amplitudes and observed replicated amplitudes were calculated for error-free trials (error rate at 4.6 %).

Figure 3 depicts the results for blocks with perturbed cursor amplitudes (left) and perturbed hand amplitudes (left). The ANOVA revealed a significant main effect for the factor gain [$F(2,32) = 220.30$; $p < 0.01$, $\eta^2 = 0.93$] and a significant interaction with the factor replicated amplitude [$F(2,32) = 38.34$; $p < 0.01$, $\eta^2 = 0.71$]. A trend was observed for the interaction between the factors replicated amplitude and perturbed amplitude [$F(1, 16) = 3.19$; $p < 0.10$, $\eta^2 = 0.17$]. Other main effects or interactions did not reach significance ($p > 0.33$).

For replicated hand amplitudes (Fig. 3, black and gray triangles), performance was quite accurate when in phase 1 the relation between hand and cursor amplitude was 1:1 [$M = 3$ mm; $t(17) = 1.77$; $p < 0.1$]. When in phase 1 the hand amplitude was shorter than the cursor amplitude, replications of hand amplitudes significantly overshot [$M = 12$ mm; $t(17) = 5.18$; $p < 0.001$]. When in phase 1 the hand amplitude was longer than the cursor amplitude, replications of hand amplitudes significantly undershot [$M = -9$ mm; $t(17) = -5.67$; $p < 0.001$]. For replicated cursor amplitudes (Fig. 3, black and gray squares), performance was also quite accurate when in phase 1 the relation between hand and cursor amplitude was 1:1 [$M = 0.5$ mm; n.s.]. When in phase 1 the cursor amplitude was shorter than the hand amplitude, replications of cursor amplitudes significantly overshot [$M = 29$ mm; $t(17) = 10.48$; $p < 0.001$]. When in phase 1 the cursor amplitude was longer than the hand amplitude, replications of cursor amplitudes significantly undershot [M = −31 mm; $t(17) = -7.29$; $p < 0.001$].

Discussion

In Exp. 1, we observed significant deviations in phase 2 when visual and motor information in phase 1 did not correspond. We interpret these as short-term aftereffects induced by cross talk between visual and proprioceptive action effects. In line with H1, these aftereffects were more pronounced in cursor amplitude replications (intermodal recall), when visual information from phase 1 had

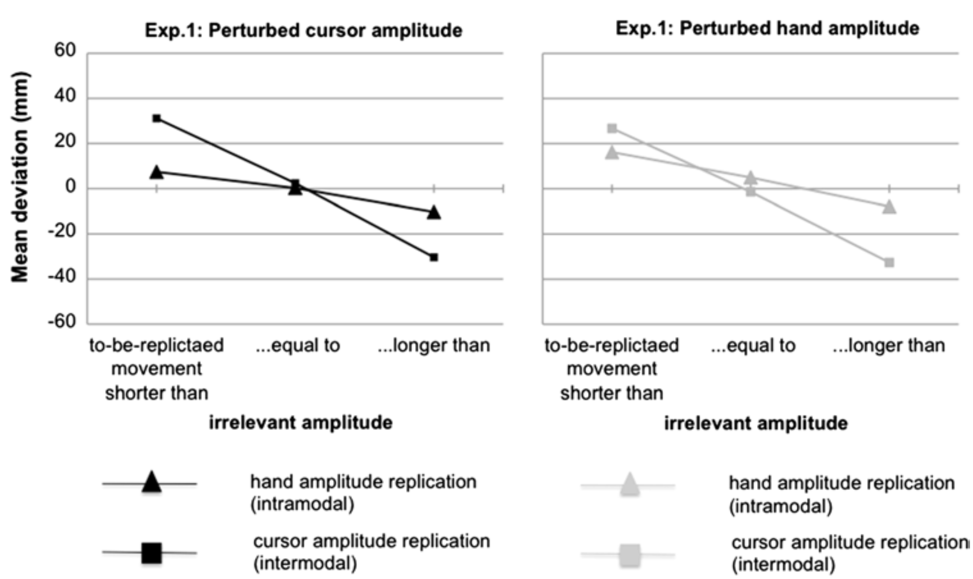

Fig. 3 Experiment 1. Mean deviation (mm) of hand amplitude replications (*triangles*) and cursor amplitude replications (*squares*) as a function of gain. The *zero line* indicates optimal replications. *Left* Deviations of blocks with perturbed cursor amplitudes. *Right* Deviations of blocks with perturbed hand amplitudes

to be recalled to program a motor response in phase 2, than in hand amplitude replications (intra-modal recall). The results seem to confirm that intra-modal replications are fostered by anticipatory representations of the intended action effect. These match the initially performed hand amplitude, so that proprioceptive information to estimate and replicate the hand action is immediately available (Rieger et al. 2005). When visual information from phase 1 has to be recalled and translated into a motor program (intermodal replication), it seems absolutely reasonable (cf. Hommel et al. 2001) that this translation makes visual recall very susceptible to interference from proprioceptive feedback.

H2 could not be confirmed. The main effect of the factor perturbed amplitude and the interactions with the factors replicated amplitude and gain did not reach significance. In intra-modal conditions, hand amplitude perturbations did not cause larger aftereffects than did cursor amplitude perturbations, and this effect did not invert in intermodal conditions. Remember that we assumed that performing varying hand amplitudes in the intra-modal condition increased variance in the motor system (in contrast to performing constant hand amplitudes), so that motor information would contribute less and visual information would contribute more to the percept in hand amplitude perturbations than in cursor amplitude perturbations and the other way round for intermodal replications. In contrast to the former study by Ladwig et al. (2012), visual information has to be recalled in the present study as well when the participants are asked to replicate the cursor amplitude in one block. It could be that visual feedback plays a more prominent role and cancels out the formerly found asymmetric cross talk.

Experiment 2

Experiment 2 will clarify whether the intra- and intermodal recall in a visual replication task will produce the same pattern of aftereffects as observed for the motor replication task. The task in phase 1 remains the same, but in phase 2 the motor replication task is replaced by a visual replication task. Participants are now asked to move the cursor on the display by pressing the space bar instead of moving the pen on the digitizer tablet. In Exp. 2, intra-modal (intermodal) recall describes the task of recalling visual (proprioceptive) information to visually reproduce the initially seen cursor amplitude (performed hand amplitude).

Concerning intra- versus intermodal aftereffects, two alternative hypotheses are likely: (a) Comparable to Exp. 1, we predict more prominent aftereffects in intermodal replications than in intra-modal replications (H3a). Analogous to Exp. 1, but now for the visual sense, the recall of visual information for reproducing initially seen cursor amplitudes is expected to be most precise because required information for detection, estimation and recall is assumed to be immediately available. On the other hand, information to detect, estimate and replicate proprioceptive action effects has to be accumulated by comparing internally predicted and observed proprioceptive effects (Rieger et al. 2005). (b) Considering the dominance of the visual sense, it could also be that we will not find any aftereffects of proprioception in intra-modal visual replications, but only visual aftereffects in intermodal visual replications (H3b).

Furthermore, in Exp. 1, the amount of aftereffects did not differ between conditions with perturbed hand amplitudes and perturbed cursor amplitudes. For Exp. 2, two outcomes are likely: In line with Exp. 1, we expect no differences between aftereffects of perturbed cursor amplitudes and perturbed hand amplitudes (H4a). On the other hand, if vision predominates action control and if there are no aftereffects in intra-modal replications, then increased (decreased) visual variance in perturbed cursor (hand) amplitudes should lead to prominent (less prominent) aftereffects in intermodal replication (H4b).

Methods

Stimuli, design and procedure

These were the same as in Exp. 1 except for the replication task. In Exp. 1, participants were instructed to reproduce initially seen or performed amplitudes of phase 1 by moving the pen on the digitizer tablet in phase 2. This motor task in phase 2 was replaced by a visual replication task. For that, a keyboard was placed on top of the occluder. In phase 1, participants operated the pen with their dominant right hand, and in phase 2, they controlled the keyboard's space bar with the index finger of their nondominant left hand. Figure 4 depicts the task setting for perturbed cursor amplitudes (Fig. 4a, top) and perturbed hand amplitudes (Fig. 4b, bottom). As in Exp. 1, participants unlocked the cursor by pressing the pen's button, moved the cursor from the start position to the opposite target bar and pressed the pen's button again (phase 1). After that, the two bars disappeared from the screen, and the cursor remained visible at its final position. Pressing the space key of the keyboard controlled the cursor on the screen and produced a linear cursor motion in the opposite direction (back to the initial start position). In advance of each block, participants were instructed to reproduce the initially seen cursor amplitude or the initially performed hand amplitude. Thus, participants pressed the space key until they thought the reproduced cursor amplitude matched the initially seen or performed amplitude.

Visual replications of cursor amplitudes in phase 2 now required recall of visual information from phase 1

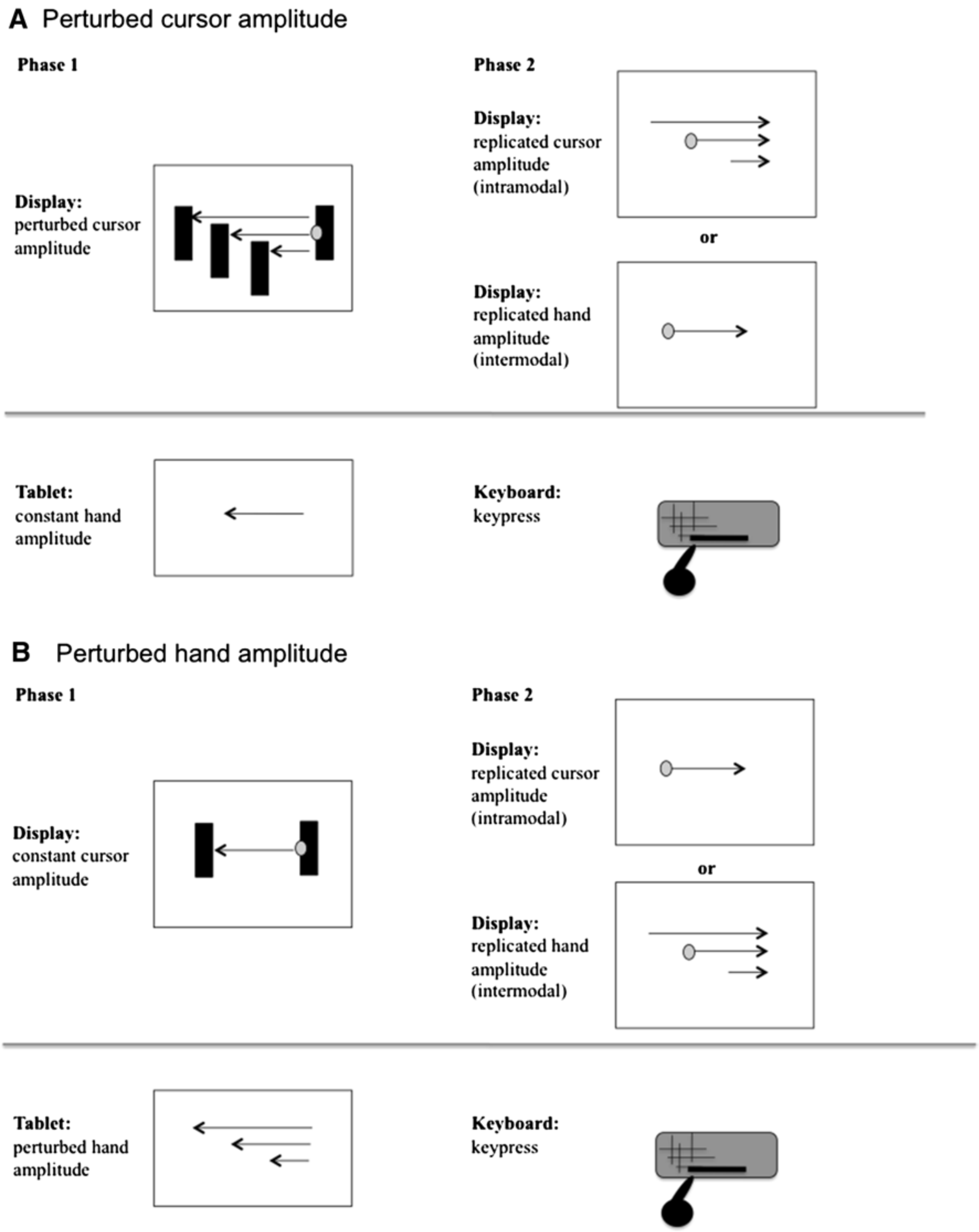

Fig. 4 **a** Perturbed cursor amplitude (*top*): In phase 1, the cursor amplitude varied by three different gains while the hand amplitude remained constant across trials. The subsequent phase 2 required reproducing the initially perturbed cursor amplitude or the initially constant hand amplitude by moving a cursor on the screen via keypress. **b** Perturbed hand amplitude (*bottom*): In phase 1, the hand amplitude varied by three different gains while the cursor amplitude remained constant across trials. The subsequent phase 2 required reproducing the initially constant cursor amplitude or the initially perturbed hand amplitude by moving a cursor on the screen via keypress

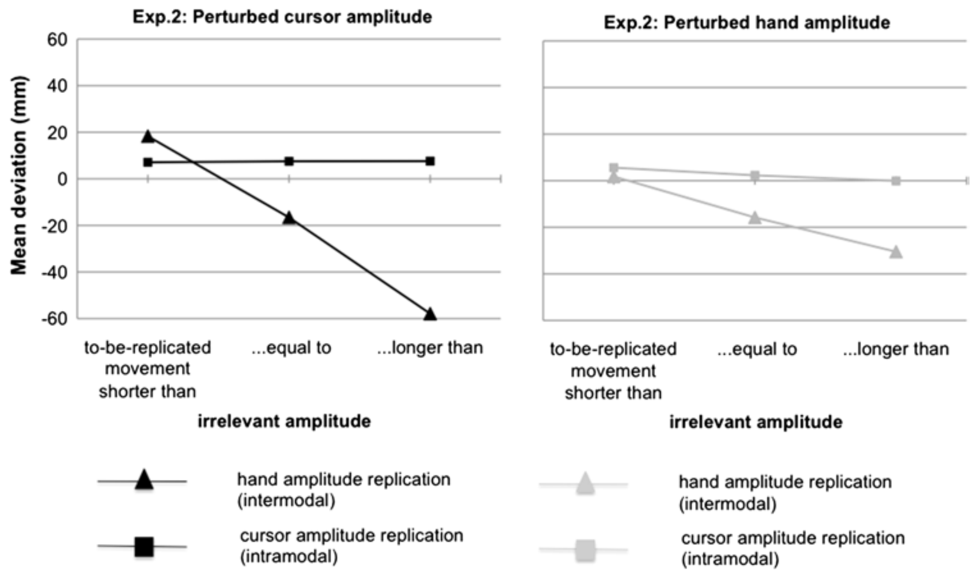

Fig. 5 Experiment 2. Mean deviation (mm) of cursor amplitude replications (*squares*) and hand amplitude replications (*triangles*) as a function of gain. The *zero line* indicates optimal replications. *Left* Deviations of blocks with perturbed cursor amplitudes. *Right* Deviations of blocks with perturbed hand amplitudes

(intra-modal). Visual replications of hand amplitudes in phase 2 now required recall of motor information from phase 1 (intermodal).

Participants

Another 16 students (11 female) of the RWTH Aachen University, aged from 20 to 38 years ($M = 24.13$; $SD = 4.9$), volunteered for the experiment. All participants were right handed, had normal or corrected-to-normal vision and were naïve with respect to the purpose of the experiment.

Results

Again, mean deviations (in mm) between to-be-replicated amplitudes and observed replicated amplitudes were calculated for error-free trials (error rate at 3.9 %). Deviations were analyzed using a 2 × 2 × 3 mixed ANOVA.

Figure 5 depicts the results for blocks with perturbed cursor amplitudes (left) and perturbed hand amplitudes (right). The ANOVA revealed significant main effects for the factors gain [$F(2, 28) = 107.24$; $p < 0.001$, $\eta^2 = 0.89$] and replicated amplitude [$F(1, 14) = 13.61$; $p < 0.01$, $\eta^2 = 0.5$]. The interaction between gain and replicated amplitude was also significant [$F(2, 28) = 91.33$; $p < 0.001$, $\eta^2 = 0.87$]. The factor gain also interacted significantly with the factor perturbed amplitude [$F(2, 28) = 11.89$; $p < 0.001$, $\eta^2 = 0.46$]. The three-way interaction between the factors replicated amplitude, perturbed amplitude and gain [$F(2, 28) = 21.71$; $p < 0.001$, $\eta^2 = 0.61$] also reached significance. Other effects or interactions did not reach significance (p's > 0.47).

The three-way interaction can be ascribed to differently pronounced aftereffects in the intermodal condition: In blocks with perturbed cursor amplitude (Fig. 5, black triangles 18.3, −16.6, −57.9 mm), aftereffects were more pronounced than in blocks with perturbed hand amplitudes (Fig. 5, gray triangles 1.8, −15.8, −30.5 mm). On the other hand, in intra-modal conditions (Fig. 5, black squares 7.1, 7.5, 7.6 mm and gray squares 5.6, 2.3, −0.1 mm), there were no aftereffects at all, except a slight inaccuracy across all conditions.

Post hoc tests showed significant overshoots for intramodal replications with perturbed cursor amplitudes [$M = 7.1$ mm, $t(7) = 4.33$, $p < 0.01$; $M = 7.5$, $t(7) = 4.29$, $p < 0.01$; $M = 7.6$ mm, $t(7) = 3.95$, $p < 0.01$]. Intra-modal replications with perturbed hand amplitude overshot only significantly when in phase 1 the cursor amplitude was shorter than the hand amplitude [$M = 5.6$ mm, $t(7) = 2.86$, $p < 0.05$; $M = 2.3$ mm and $M = -0.1$ mm, n.s.].

Intermodal replications with perturbed cursor amplitudes were quite accurate when in phase 1 the relation between hand and cursor amplitude was 1:1 [$M = -16.6$ mm, $t(7) = -2.13$, $p < 0.10$], but significantly overshot/undershot when in phase 1 the hand amplitude was shorter/longer than the cursor amplitude [$M = 18.3$ mm, $t(7) = 2.77$, $p < 0.05$ and $M = -57.9$ mm, $t(7) = -7.02$, $p < 0.01$]. For perturbed hand amplitudes, intermodal replications were quite accurate when in phase 1 hand amplitudes were shorter than or equal to cursor amplitudes [$M = 1.8$ mm, n.s. and $M = -15.8$ mm, $t(7) = 2.17$, $p < 0.10$], and significantly undershot when in phase 1 hand amplitudes were longer than cursor amplitudes [$M = -30.5$ mm, $t(7) = -4.90$; $p < 0.01$].

Discussion

In Exp. 2, we found severe aftereffects in intermodal replications, which means when proprioceptive information from phase 1 had to be recalled for the visual reproduction of the hand amplitude in phase 2, visual information from phase 1 interfered replications considerably. The recall of intra-modal visual information, however, was totally unaffected by proprioceptive information from phase 1, so that we did not find any aftereffects in intra-modal replications. The results confirmed hypothesis H3b and demonstrated that visual action effects not only predominate but also solely controlled visual actions.

Furthermore, for intermodal replications, we found reduced aftereffects for perturbed hand amplitudes than for perturbed cursor amplitudes. This result confirmed hypothesis H4b. However, intermodal replications were quite inaccurate with a general bias to undershoot in phase 2. One reason for this could be an inefficient spatial representation and translation of the proprioceptive information from phase 1. Another more apparent reason could be the design of the visual replication task. Pressing and holding the space bar set the cursor into motion. Cursor acceleration and velocity were constant, and participants had no control concerning the ballistics. Thus, cursor ballistics in phase 2 differed considerably from the manual/visual temporal–spatial patterns of phase 1, and participants reported the cursor motion in phase 2 of being less fast. The shortened cursor amplitude in phase 2 indicates that participants concentrated more on reproducing the temporal pattern of phase 1 than the spatial ones. A more direct approach to control for this in future experiments would be by using eye gaze for the visual replication task. Nevertheless, present findings demonstrated reduced aftereffects for intermodal replications with perturbed hand amplitudes.

General discussion

Recent studies (Ladwig et al. 2012; Rieger et al. 2005; Sülzenbrück and Heuer 2009) found short-term and long-term aftereffects in manual actions resulting from discrepancies between proprioceptive feedback and visual feedback. The aim of the present study was to further examine short-term aftereffects in the motor (Exp. 1) and visual modality (Exp. 2). Additionally, the direction of cross talk between proprioceptive and visual action effects was investigated. In line with TEC (Hommel et al. 2001), we assumed that information from both senses is represented in the same domain and is therefore likely to affect each other. Thus, apart from the often-confirmed visual dominance in multisensory integration, we asked about intra- and intermodal recall of either proprioceptive information or visual information and whether there was a difference between the motor and visual modality.

First, in Exp. 1, we observed a general interference from discrepant proprioceptive and visual information in terms of aftereffects in motor replications. When the to-be-replicated amplitude was shorter (longer) than the irrelevant amplitude, participants undershot (overshot), while replications were quite accurate for equal action effects. This pattern successfully replicates findings by Ladwig et al. (2012). The aftereffects can be interpreted in line with cognitive approaches (Hommel et al. 2001; Prinz 1997) as multisensory cross talk within the event code.

Second, focusing on which information had to be recalled in the replication phase, intra-modal replications showed fewer aftereffects than intermodal replications (Fig. 3). A reason for this could be that in intermodal replications visual information has to be translated into a motor action. This translation process could make the whole action more susceptible to irrelevant proprioceptive information, while in intra-modal replications, proprioceptive information is immediately available for the replication and irrelevant visual information can be totally ignored (Berkenblit et al. 1995; Adamovich et al. 1998).

In Exp. 2, we asked whether this cross talk would also apply for a visual replication task. Phase 1 was identical to Exp. 1. In phase 2, participants now received visual feedback and were asked to replicate the initially performed cursor amplitude on the display by moving the cursor via key-press (visual modality, intra-modal replication). Discrepant feedback in phase 1—i.e., proprioceptive interference from the initially performed hand amplitude—might (or due to visual dominance might not) cause aftereffects in phase 2. For intermodal replications, however, visual interference from the initially seen cursor amplitude should cause large(r) aftereffects when participants were asked to replicate the initially performed hand amplitude. Contrary to Exp. 1, we did not find any aftereffects in intra-modal replications. It seems that the visual sense completely overrules proprioceptive information. This means in comparison with Exp. 1 that visual information interferes the intra-modal recall of proprioceptive information in motor replications, but not the opposite. This finding once more supports the visual dominance in action control and shows that the visual sense does not only attenuate the impact of proprioceptive information (Knoblich and Kircher 2004; Müsseler and Sutter 2009; Wang et al. 2012), but in some conditions, vision seems to be completely immune to discrepant proprioceptive feedback (cf. Mechsner et al. 2001). For intermodal replications in the visual domain, aftereffects were as large as for intermodal replications in the motor domain, despite the general inaccuracy in the visual domain. Apart from methodological constraints discussed in Exp. 2, it could be that those intermodal visual replications ended up without passing the former starting point of the initially seen cursor movement. However, in order to replicate the initial hand amplitude accurately, passing the initially seen starting point would have been necessary. A reason for this bias might be that participants evolved strategies to perform the replication, which might involve visual markers on the screen in the form of an after image of the start bar. This after image may serve as a kind of virtual anchor or borderline. Furthermore, the visual starting point of the cursor almost matched the starting point of the hand movement. This might consolidate the virtual anchor and hence a certain inhibition to pass it. Future experiments should control for that by spatially uncoupling the cursor start position in phase 2 from the cursor end position in phase 1.

We further investigated the impact of the locus of perturbation in phase 1 on aftereffects in phase 2. Ladwig et al. (2012) found larger aftereffects for perturbed hand amplitudes (with constant cursor amplitudes) than for perturbed cursor amplitudes (with constant hand amplitude) in their intra-modal manual replication task. They argued that perturbed hand amplitudes increased variance in proprioception and that this made motor replications more susceptible to visual action effects. However, this was not replicated in the present study. The asymmetry of aftereffects only occurred within the visual domain (intermodal replications), but not in the other conditions. We assume that in our setting manual replications of hand and cursor amplitude increased variance in both sensory systems and that this cancelled the asymmetry effect out in Exp. 1. However, in the visual modality (Exp. 2) constant cursor amplitudes in phase 1 reduced aftereffects in intermodal replications. This makes perfect sense, since if vision predominates action control and if there are no aftereffects in intra-modal replications, then the interference of (predominant) visual information should be larger for variable cursor amplitudes than for constant ones.

Finally, we want to discuss some methodological aspects concerning the second trial phase that should be taken into account for future studies. In Exp. 1, the motor replication task involved a motor action of the dominant hand, with the tablet and hand obscured from sight. In Exp. 2, the key-press of the visual replication task was done with the nondominant hand on the keyboard located on top of the occluder (above the tablet), and with the keyboard and nondominant hand visible. We established this task design to make the manual action involved in the visual replication task most distinctive from that in phase 1. As we discussed above, we believe that the most direct approach on visual replication would be by eye gaze measured with an eye-tracking system. This would also control for possible confounds from manual motor action in phase 2.

To sum up, the present findings demonstrated the interaction between visual and proprioceptive action effects represented within the same cognitive domain (Ernst and Banks 2002; Hommel et al. 2001). Mechanisms of integration were found to be dependent on the output modality. Visual action effects interfered the motor modality, but proprioceptive action effects did not have any effects on the visual modality. However, intermodal integration was more susceptible to interference, and this was found to be independent from the output modality. Tool use is one field of application of these kinds of results, since the optimized integration of conflicting action effects is a precondition for using tools successfully.

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