

Remapping motion across modalities: tactile rotations influence visual motion judgments

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Abstract Multisensory interactions between haptics and vision remain poorly understood. Previous studies have shown that shapes, such as letters of the alphabet, when drawn on the skin, are differently perceived dependent upon which body part is stimulated and on how the stimulated body part, such as the hand, is positioned. Another line of research within this area has investigated multisensory interactions. Tactile perceptions, for example, have the potential to disambiguate visually perceived information. While the former studies focused on explicit reports about tactile perception, the latter studies relied on fully aligned multisensory stimulus dimensions. In this study, we investigated to what extent rotating tactile stimulations on the hand affect directional visual motion judgments implicitly and without any spatial stimulus alignment. We show that directional tactile cues and ambiguous visual motion cues are integrated, thus biasing the judgment of visually perceived motion. We further show that the direction of the tactile influence depends on the position and orientation of the stimulated part of the hand relative to a head-centered frame of reference. Finally, we also show

that the time course of the cue integration is very versatile. Overall, the results imply immediate directional cue integration within a head-centered frame of reference.

Keywords Multisensory · Cue integration · Crossmodal interaction · Motion perception · Haptics · Vision

Abbreviations

VMD Visual motion display
ms milliseconds

Introduction

At least since the 1970s, it has been known that tactile stimulations are phenomenally perceived in a dominantly head-centered frame of reference. Corcoran described this fact as “phenomena of the disembodied eye” (Corcoran 1977, p. 247). In his experiments, bilaterally asymmetrical figures were drawn on different body parts, such as the forehead, the back of the head, or on the palm while holding the hand in different positions. Participants reported “seeing” (Corcoran 1977, p. 247) the figures reversed on the forehead or when the surface of the palm faced away from the head. The results indicated that tactile stimulations were re-mapped into a head-centered frame of reference.

Likewise, Oldfield and Phillips (1983) had subjects who feel character-shaped objects with a finger from above or from below. Although the same pattern was felt on the skin, the letter was perceived mirror-reversed, when felt from below. The authors concluded that the letters were felt and seen within a common “spatial framework”

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(Oldfield and Phillips 1983, p. 626). Later, Sekiyama (1991) systematically varied hand position and orientation, as well as the tactile stimulus location, asking participants to report the perception of the letters ‘p’, ‘q’, ‘d’, and ‘b’. The results further supported the spatial-framework hypothesis, and the author proposed that tactile stimuli are perceived by “embodied head axes” (Sekiyama 1991, p. 491) in that the stimuli are processed relative to the head axis, but this axis can bend within the possible range of movement of the body.

While all these studies suggest that tactile stimulations are remapped into a head-centered frame of reference, they all relied on explicit reports of how the tactile stimulus was consciously perceived. It remains an open question if the head-centered remapping of tactile stimuli only occurs if participants are explicitly asked to report the tactile stimulation or if such a remapping also occurs more automatically in multimodal integration.

Investigations of multimodal integrations of tactile motion cues with other modalities are receiving increasing interest in recent years. For example, Blake et al. (2004) found that judgments of visually perceived motion direction could be disambiguated when participants actively and simultaneously touched a rotating globe while viewing a similar globe on a screen in a mirror setup. Additional brain imaging experiments further revealed that the middle temporal visual complex MT+ was differentially affected not only by visual information of motion but also by tactile information, albeit much weaker (Blake et al. 2004).

Interactions of moving stimuli have also been investigated in an aftereffect paradigm (Mather et al. 1998). In this case, horizontal or vertical motion patterns were displayed to invoke motion perception in a particular direction. Directional motion was shown to cause habituation, so that subsequent motion stimuli were perceived moving in the opposite direction more often. Recently, such motion aftereffects have also been confirmed in correlation with tactile dynamic stimuli (Carter et al. 2008) and have even been shown to interact between touch and vision (Konkle et al. 2009). These results show that motion cues may not only be integrated across modalities, but they may also lead to crossmodal inhibition.

Our experiments target motion cue integration between touch and vision. We addressed the following questions: (1) if circular tactile motion may interact with visually perceived rotating motion, (2) if this interaction is sensitive to the position and orientation of the stimulated body part, and (3) how this cue interaction unfolds in time. To this end, we conducted three experiments, in which a tactile rotation was administered on the right hand of participants, who had to judge the motion direction of concurrently presented, ambiguous visual motion displays (VMD; Lakatos and Shepard 1997).

Experiment 1

In each trial, a rotating tactile stimulus was administered on the right hand of the participant, and visual motion was displayed on a screen. Participants had to report first in which direction the presented visual motion was perceived rotating. To turn the participants’ attention to the tactile stimulation as well, we switched the rotation direction of the tactile stimulus in some trials (*switch trials*) but not in others (*non-switch trials*), and we asked participants to also report changes in the direction of tactile stimulation. To assess the time course of the influence of tactile stimulation on visual perception, the time of the direction change in switch trials was varied. Moreover, to assess the participants’ ability to accurately judge visual motion, we also included trials with non-ambiguous motion displays.

Method

Participants

Nineteen participants (13 women) with a mean age of 23.8a (SD = 2.91), who were mostly undergraduate psychology students of the University of Würzburg, were recruited for the experiment. They participated either to fulfill a course requirement or for the payment of 7 Euros.

Apparatus and stimuli

The experimental setup consisted of a 21-inch CRT monitor to display the VMD and a tactile stimulator, which was positioned in front of the monitor. A computer keyboard was placed to the left of the monitor to collect participants’ judgments about the visual and tactile stimulations.

The tactile stimulation was generated by a small metal wheel, which was mounted on a spring that was attached to a rotating disk, which was rotated by two motors either in clockwise or in counterclockwise direction. In consequence, the wheel circled either clockwise or counterclockwise on the participant’s right hand (Fig. 1a). The wheel had a flat surface with a thickness of 4 mm, and it was 12 mm in diameter. It moved along a circle with a diameter of 40 mm at a rate of 0.65 cycles per second. An integrated loudspeaker played white noise to mask the sound of the motors. In this way, any potential auditory clues about the tactile rotation direction or direction switches were masked. The tactile stimulator was fastened to the hand by means of elastic straps. It could be attached from both sides to either stimulate the palm or the back of the hand. In the remainder of this article, we refer to clockwise rotations when the wheel rotated clockwise from the perspective of the stimulation device toward the hand and to counterclockwise rotations otherwise.

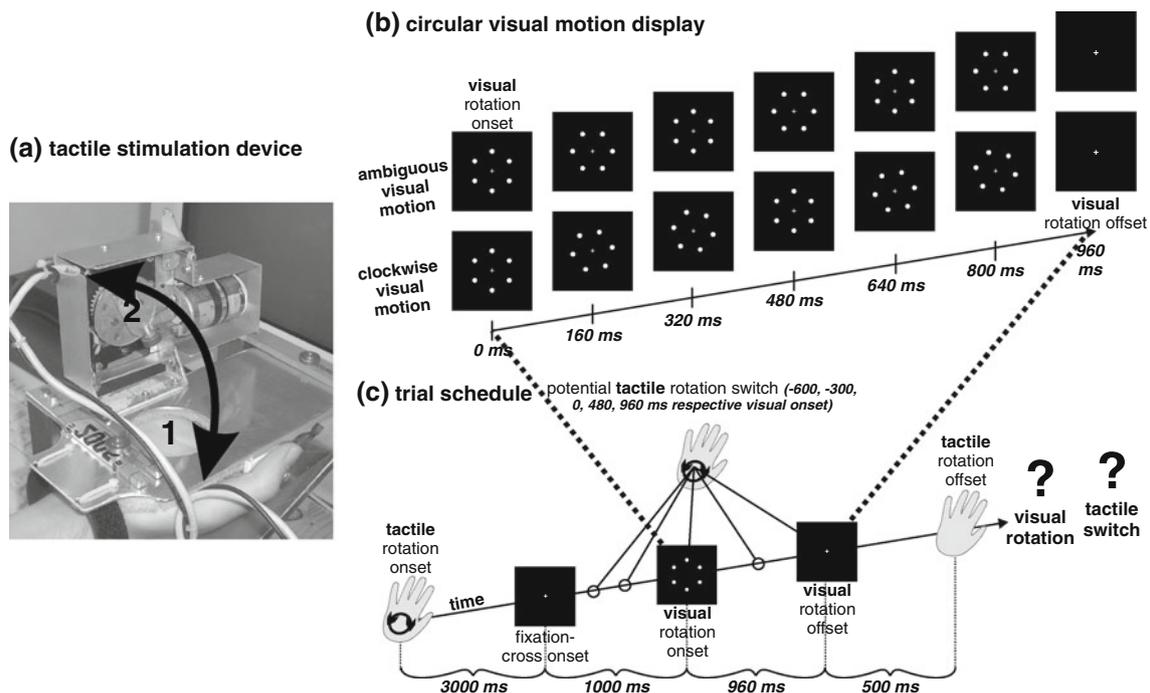


Fig. 1 **a** Tactile stimulation device: the participants' right hand was inserted, so that the to-be stimulated surface *I* faced the opening. During the experiment, the housing of the wheel 2 was flipped down to administer the stimulation. **b** Ambiguous and non-ambiguous

(in this case clockwise) sequences of dot arrangements that were displayed during one trial; **c** sequence of events within each trial of Experiments 1 and 2

The VMD was created by iteratively presenting patterns of dots that were arranged in a circle (Fig. 1b; Lakatos and Shepard 1997; Wohlschläger 2000). Six white dots were shown around a white fixation cross on an otherwise black screen. The dots had a diameter of 3 mm and were arranged with equal distances on an imaginary circle of 36 mm in diameter. To generate the impression of circular motion, sequences of patterns with six dots were presented, in which each newly presented pattern was a rotated version of the previous one (Fig. 1b). Each single pattern was presented for 160 ms. The first pattern in a sequence was always the pattern in which one dot was located at the 12 o'clock position. To generate ambiguous visual stimuli, the arrangement of dots was iteratively rotated by 30° . The resulting sequence of dot-displays created the impression of circular motion, but it was ambiguous with respect to the direction of the motion. Non-ambiguous visual stimuli were generated by rotating the arrangement by -20° or $+20^\circ$ every 160 ms, thus generating a nearly unambiguous counterclockwise or clockwise rotation impression, respectively.

Procedure

After giving informed consent, participants were seated in front of the CRT and the tactile stimulator and were asked to insert their right hand into the tactile stimulator, with the

finger tips of the hand facing to the left and the palm of the hand facing the participant (Fig. 2a). The tactile stimulation was administered block-wise either onto the volar (i.e. the palm) or onto the dorsal part (i.e. the back) of the hand.

Figure 1c shows the trial setup. A trial began with the stimulation of the hand in an either clockwise or counterclockwise direction. The CRT display was black at the beginning of a trial. After 3,000 ms, a white fixation cross (4 mm side length) appeared at the center of the screen, which was displayed until visual motion offset. After an additional 1,000 ms, the VMD was presented. The total presentation time of the VMD was 960 ms, effectively displaying six successive dot-displays for 160 ms each. The tactile stimulation stopped 500 ms after the offset of the VMD.

After tactile stimulation offset, participants were asked to report the perceived direction of the VMD, answering with their left hand with a left or right key press for counterclockwise or clockwise rotation, respectively. Finally, participants were asked whether a change in the tactile stimulation direction occurred, but not in which direction, answering again with their left hand with an up or down key press for a switch or non-switch detection, respectively. Immediately afterward, the next trial began.

We manipulated the position of the tactile stimulation, type of tactile stimulation, the switch time in switch trials, and the ambiguity of the VMD. In non-switch trials, the

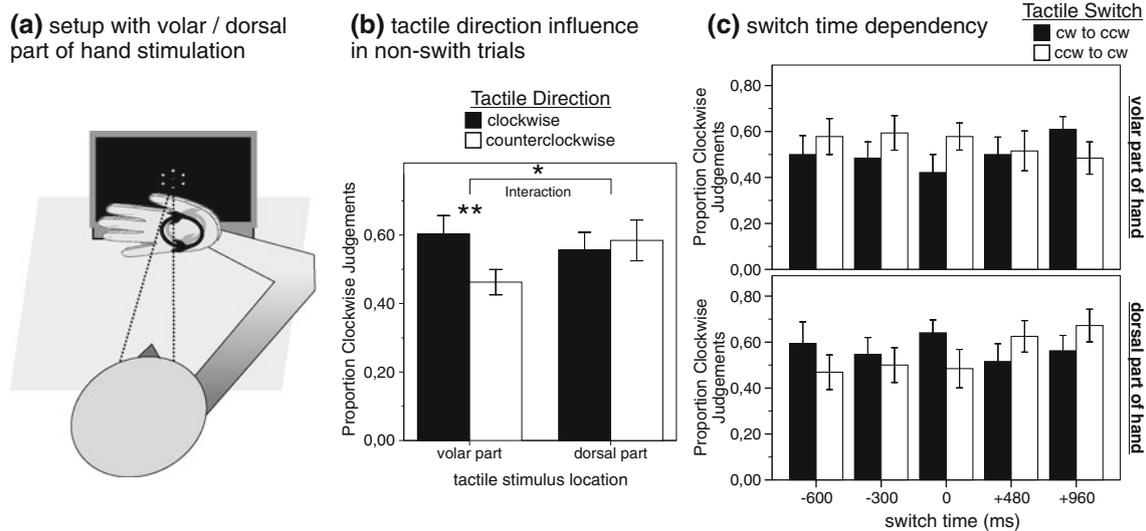


Fig. 2 **a** In Experiment 1, the hand was placed directly under the screen and was aligned with the screen, with the palm of the hand facing the participant. In one block, the palm (i.e. *volar part*) of the hand was stimulated, while the back (i.e. *dorsal part*) of the hand was stimulated in the other block. **b** Impact of tactile rotation direction and

tactile stimulation was either clockwise or counterclockwise. In switch trials, it could change from clockwise to counterclockwise or vice versa. Moreover, this switch occurred either 600 or 300 ms before, simultaneously with, or 480 or 960 ms after the onset of the VMD.

To measure the influence of tactile stimulation on visually perceived motion, ambiguous VMDs were presented in two-thirds of all trials. To assess the participants' ability to detect motion in the VMD, unambiguous VMDs were presented in the other one-third of all trials. Participants who failed to consistently judge unambiguous trials correctly were excluded from the analysis.

The experiment consisted of two blocks of 120 trials each, which were separated by a short break during which the stimulation device and the hand were readjusted. For one half of the participants, the palm of the hand was stimulated in the first block, and the back of the hand was stimulated in the second block. The block order was reversed for the other half of the participants.

Each block consisted of 60 non-switch trials (30 clockwise, 30 counterclockwise) and 60 switch trials (6 repetitions for each combination of switch time and initial rotation direction). For each kind of tactile stimulation, in two-thirds of trials an ambiguous VMD was displayed and in one-third of trials, a non-ambiguous VMD was presented (one-sixth clockwise, one-sixth counterclockwise).

The visually perceived motion was operationalized as the proportion of trials in which the VMD was categorized as rotating clockwise and computed for each trial type. Two participants classified visual motion direction correctly in only 53.75 and 72.50% of the non-ambiguous

stimulus position on the proportion of clockwise answers in non-switch trials; *asterisks* indicate significant differences or interactions ($*P < 0.05$, $**P < 0.01$); **c** impact of tactile rotation direction, stimulus position, and switch time on the proportion of clockwise answers in switch trials

trials. They were classified as outliers (box-plot method, Tukey 1977) and were excluded from further analysis. One additional participant was excluded, who always reported clockwise visual motion perception in the ambiguous visual trials throughout the experiment.

Results

In the analysis, we focused on the visually ambiguous trials because we expected these trials to be affected strongest by tactile stimulation. To evaluate the effect of the tactile stimulation, we analyzed the visually ambiguous non-switch trials. To evaluate the time course of tactile visual integration, we furthermore analyzed the visually ambiguous switch trials.

Figure 2b shows the proportion of “clockwise” answers for the visually ambiguous non-switch trials. A two-factor 2×2 within subject ANOVA with factors tactile direction (clockwise vs. counterclockwise) and stimulus position (volar or dorsal part of hand) revealed that the tactile direction alone marginally influenced the perceived motion direction, $F(1,15) = 4.39$, $P = 0.054$.¹ However, the tactile direction had a stronger influence on perceived motion if the palm of the hand was stimulated than if the back of the hand was stimulated, $F(1,15) = 5.22$, $P = 0.037$. When the palm of the hand was stimulated, the visually perceived motion was biased assimilative in the direction of the tactile rotation, $t(15) = 3.79$, $P = 0.002$. On the

¹ We report Greenhouse-Geisser-corrected P -values but uncorrected dfs.

other hand, if the back of the hand was stimulated, there was no influence of the tactile rotation on visually perceived motion, $t(15) = 0.53$, $P = 0.602$. Thus, tactile rotation significantly influenced visually perceived motion when the volar part of the hand was stimulated.

Figure 2c shows the visually perceived motion for visually ambiguous switch trials for both stimulus positions, both tactile directions, and the five switch times. The data suggest that the crucial switch in the visual bias lies at the time of or shortly after visual motion display onset. This interaction appears stronger when the palm of the hand is stimulated. A three-factor $5 \times 2 \times 2$ within subject ANOVA with the factors switch time (−600, −300, 0, 480, 960 ms respective visual onset), stimulus position (volar, dorsal), and tactile rotation switch (clockwise to counterclockwise or vice versa) revealed a marginal interaction between the three factors, $F(4,60) = 2.56$, $P = 0.072$. No other factor or interaction reached significance, all P s > 0.219.

Discussion

Given these results, we can conclude that tactile motion cues were integrated into the visual motion perception. The consequent influence on the visually perceived motion was assimilative with respect to the stimulation direction on the palm, given the palm of the hand was stimulated. When the back of the hand was stimulated, the tactile directional influence tended to be reversed, but this reversal did not reach significance. Since it is certainly more difficult to perceive a directional stimulation on the back of the hand than it is on the palm, we decided to focus on stimulating only the palm of the hand in the subsequent experiments.

Experiment 2

Experiment 1 hinted at the possibility that the cue integration took place in a head-centered frame of reference, but several interactions did not reach significance—most likely due to the lack of sensitivity on the dorsal part of the hand. Experiment 2 was conducted to further investigate this suspicion. Thus, we always stimulated the palm of the hand, but the palm could face toward or away from the participant's head (Fig. 3a).

Methods

Participants

Twenty-one participants (14 women) with a mean age of 22.6a (SD = 3.29), who were mostly undergraduate psychology students of the University of Würzburg, were

recruited for the experiment. As in Experiment 1, the participants either fulfilled a course requirement or they received a payment of 7 Euros.

Procedure

Apparatus and procedure were identical to Experiment 1, but the position and orientation of the hand-stimulator was changed. Participants were requested to insert their right hand into the stimulator, with the fingers pointing toward the screen and the stimulated palm either facing upwards or downwards. Note that when the palm faced upwards (toward the participant), a clockwise path of the tactile stimulation was also clockwise in a head-centered frame of reference; however, when the palm faced downwards and tactile stimulation was applied from below, the path of a clockwise tactile stimulation was counterclockwise in a head-centered frame of reference. Hence, it was possible to test whether identical tactile stimulations can induce a different bias on visual rotation judgment dependent on the position of the volar part of the hand relative to the participant.

Three participants who classified visual motion direction correctly in only 72.50, 75.00, and 79.75% of the non-ambiguous trials have been removed from further analysis (box-plot method). One additional participant was excluded, who judged all ambiguous visual rotations to be clockwise.

Results

Figure 3b shows that tactile rotations influenced visually perceived motion dependent on the orientation of the stimulated palm of the hand in non-switch trials. A two-factor 2×2 ANOVA with within-subject factors tactile direction (clockwise vs. counterclockwise) and hand orientation (palm up vs. palm down) revealed a strong interaction, $F(1,16) = 15.95$, $P = 0.001$. There was also a marginally significant main effect of tactile direction, $F(1,16) = 3.31$, $P = 0.088$. Individual t tests showed an assimilative visual judgment bias when the palm faced upwards, $t(16) = 3.39$, $P = 0.004$. A contrastive visual judgment bias (in the direction opposite of the tactile stimulation) was observed when the palm faced downwards, $t(16) = 2.31$, $P = 0.035$.

Figure 3c illustrates the visually perceived motion as a function of switch time, tactile direction, and hand orientation for the switch trials. In all cases, except at +480 ms for stimulation from below, visual judgment was assimilative with respect to the rotation direction that took place upon visual onset when the stimulation was applied from above and contrastive when the stimulation was applied from below. A $5 \times 2 \times 2$ ANOVA with the factors switch

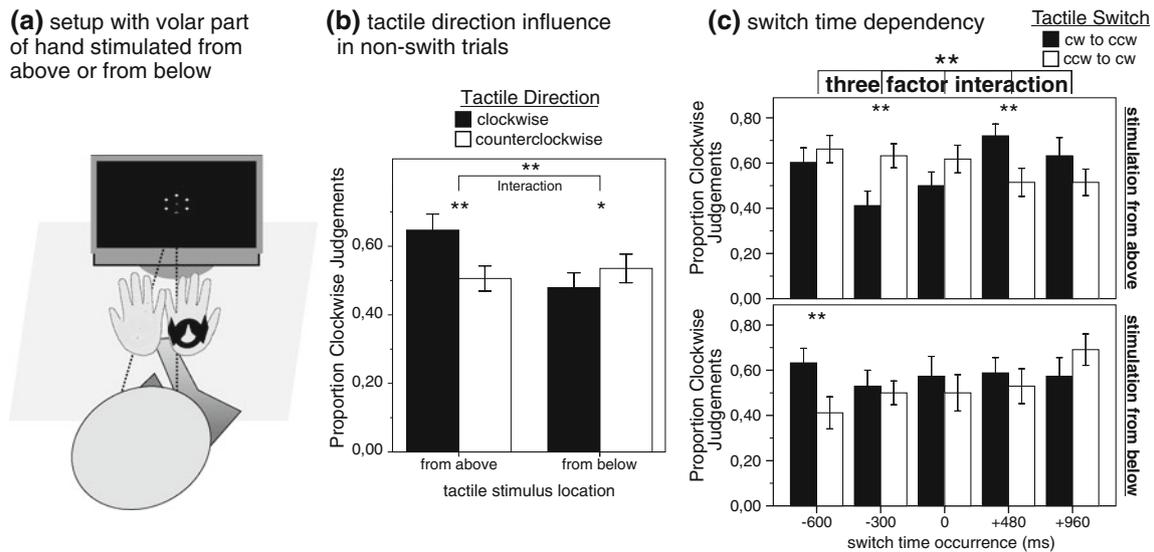


Fig. 3 **a** In Experiment 2, the hand was placed on the table in front of the screen with the fingertips toward the screen and the hand's palm facing upwards (while horizontally aligned with the table) in one block and facing downwards in the other block. **b** Impact of tactile rotation direction and stimulus position on the proportion of

time (−600, −300, 0, 480, 960 ms respective visual onset), stimulus position (volar, dorsal), and tactile rotation direction (clockwise to counterclockwise or vice versa) revealed that all three factors interacted, $F(4,64) = 4.74$, $P = 0.005$. Also, the interaction between switch time and rotation direction alone reached significance, $F(4,64) = 3.02$, $P = 0.040$. Thus, stimulations from both sides influenced visual judgments dependent on the timing of the tactile rotation switch.

Discussion

Experiment 2 revealed two major findings. First, the influence of the tactile stimulation was modulated by the orientation of the stimulated body surface with respect to a head-centered frame of reference. Identical tactile stimulations on the skin resulted in different biases on visually perceived motion if the hand faced either upward or downward.

Second, as in Experiment 1, the tactile stimulation at the onset of the VMD determined visually perceived motion. Even if the tactile motion switched direction during a trial, the tactile motion direction that took place upon visual onset biased the visual motion perception. Only if the tactile switch occurred during the VMD observation, neither the previous tactile direction nor the new direction had a significant visual bias.

Since the hand-orientation-dependent tactile modulation was also observable in the switch trials, cue integration occurred very instantly with respect to the tactile direction

clockwise answers in non-switch trials; *asterisks* indicate significant differences or interactions ($*P < 0.05$, $**P < 0.01$); **c** impact of tactile rotation direction, stimulus position, and switch time on the proportion of clockwise answers in switch trials

that was applied upon VMD onset and with respect to a head-centered frame of reference.

Experiment 3

Although the dependence on the timing of the tactile switches already suggests a fast cue integration mechanism, it is unclear whether this is due to a particular stimulus property of the switch or whether it is due to the tactile rotation alone. Thus, we conducted Experiment 3, in which the onset of the tactile stimulation was varied around the onset of the VMD, whereas potential switches were always applied after visual offset. Thus, Experiment 3 further investigated the plasticity of the observed cue integration.

Methods

Participants

Twenty-four undergraduate psychology students of the University of Würzburg (21 women) with a mean age of 20.4a (SD = 3.39) were recruited for the experiment. They participated in order to fulfill a course requirement.

Apparatus and Stimuli

The VMD was exchanged with a more continuous stimulus arrangement, which consisted of 16 color gradients from

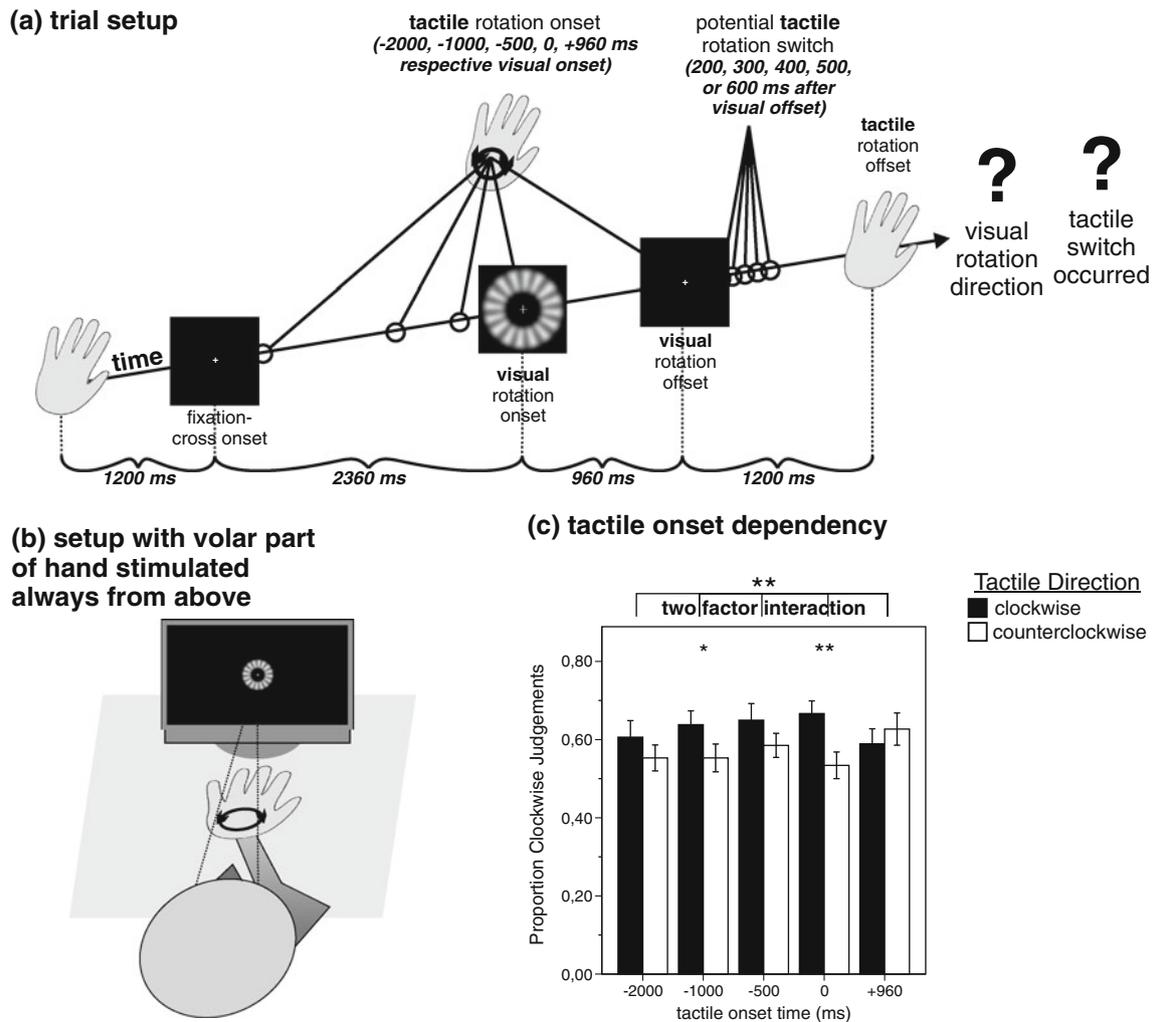


Fig. 4 **a** The sequence of events in each trial of Experiment 3 illustrates that the tactile motion onset varied around the VMD onset. **b** The hand was placed in front of the screen on the table with the

dark to light gray, which were arranged on a ring (Fig. 4a, b; inner diameter: 4 cm, outer diameter: 9.5 cm). To generate the impression of circular motion, as before, this circular display was iteratively rotated every 160 ms. For ambiguous visual stimuli, the display was iteratively rotated by 11.25° , while for non-ambiguous visual motion, the display was rotated by -7.5° or $+7.5^\circ$, generating a counterclockwise or clockwise rotation impression, respectively.

Procedure

As in Experiment 2, only the palm of the hand was stimulated, but it was always facing upwards with the fingers pointing toward the screen. Each trial began with a pause of 1,200 ms, after which the fixation cross appeared (Fig. 4a). The VMD appeared 2,360 ms afterward (visual onset) and remained visible for 960 ms (visual offset). Tactile stimulation began $-2,000$, $-1,000$, -500 , $+0$, or

$+960$ ms relative to the VMD onset. Tactile stimulation stopped 1,200 ms after visual offset. In addition, a tactile rotation switch could occur either 200, 300, 400, 500, or 600 ms after visual offset. As in experiments 1 and 2, participants were asked to report the visually perceived motion direction and the presence or absence of tactile direction switches with key presses.

The experiment consisted of 240 trials in total. One hundred and twenty trials were non-switch trials (60 clockwise, 60 counterclockwise), and 120 trials were switch trials (12 repetitions of each combination of switch time and initial rotation direction). For each kind of tactile stimulation, in two-thirds of trials an ambiguous VMD was displayed and in one-third of trials, a non-ambiguous VMD was presented (one-sixth clockwise, one-sixth counterclockwise). If a tactile switch occurred, it occurred equally likely at any one of the five specified points in time after visual offset.

Two participants classified visual motion direction correctly in only 95.00 and 95.83% of the non-ambiguous trials. Due to the overall higher accuracy of participants in non-ambiguous trials with the new VMD ($M = 0.9868$, $SD = 0.0128$), they were classified as outliers (box-plot method) and were thus removed from further analysis.

Results

Figure 4c shows that the bias due to the tactile rotation direction again influenced visually perceived motion, and this influence depended on the timing of the tactile stimulation onset. A two-factor 2×5 ANOVA with within-subject factors tactile direction (clockwise, counterclockwise) and tactile onset time ($-2,000$, $-1,000$, -500 ms, $+0$, or $+960$ ms relative to visual onset) revealed an interaction, $F(4,84) = 3.89$, $P = 0.015$. Also, the main effect of tactile direction was significant, $F(1,21) = 8.74$, $P = 0.008$. The main effect of tactile onset time, however, was not significant, $F(4,84) = 0.87$, $P = 0.471$. Individual t tests showed an assimilative visual judgment bias when the tactile onset happened before ($1,000$ ms) or at the same time of visual onset (0 ms), $t(21) = 2.51$, $P = 0.020$; $t(21) = 5.88$, $P < 0.001$, respectively. However, for $2,000$ and 500 ms, the difference did not reach significance, $t(21) = 1.53$, $P = 0.141$; $t(21) = 1.48$, $P = 0.153$, respectively. There was no influence of tactile direction on the visual judgment with a tactile onset at the time of visual offset (onset time $+960$ ms), $t(21) = -1.06$, $P = 0.300$.

A three-factor $2 \times 5 \times 2$ ANOVA with within-subject factors tactile direction (clockwise vs. counterclockwise), tactile onset ($-2,000$, $-1,000$, -500 , $+0$, or $+960$ relative to visual onset), and switch (switch occurred vs. no switch occurred) revealed no additional significant interactions (all P s > 0.553). This verifies that the switches in tactile rotation direction, which only occurred after visual offset, had no influence on the results.

Discussion

Overall, the results confirmed the cue integration mechanisms observed in Experiments 1 and 2 with a different VMD. But the results also shed further light on the timing of this mechanism, thus corroborating evidence that the process is generally very immediate.

Interestingly, the results showed that the influence of tactile direction on visual motion judgment was highest when the tactile stimulus started simultaneously with the VMD onset. This suggests that motion cue integration was even stronger, when the motion cues were correlated in their respective onset times.

General discussion

Summary of results

The aim of the experiments was to investigate (1) whether tactile circular motion can influence visual motion judgments, (2) whether this transfer depends on the position and orientation of the stimulated part of the hand and (3) how immediate and adaptive this interaction unfolds in time. The experiments showed that cue integration took place, consequently biasing visual judgment toward the direction of tactile stimulation. This cue integration took place in a head-centered frame of reference, since the integration was assimilative when the hand faced the participant, but reversed when the stimulated part of the hand faced away from the participant's head. Moreover, the timing of this cue integration mechanism was fast, seeing that a tactile switch upon visual motion onset instantly biased the visual motion judgment in the novel rotation direction. Thus, the tactile rotation direction that was applied at the time of visual onset was the crucial determinant for the directional bias in visual judgment. Finally, the third experiment showed that the cue integration mechanism applied nearly instantly. Even if the tactile stimulation was initiated concurrently with the activation of the VMD, cue integration was observable. However, if the tactile onset occurred at the same time as the offset of the VMD, no effect was observable. Thus, directional cue integration is a very fast mechanism that does not only appear in explicit reports of tactile perceptions but also directly influences current visual motion perception.

Relation to previous studies

Our results generally confirm that tactile stimulation can help to disambiguate visually ambiguous cues about motion (Blake et al. 2004; James and Blake 2004) but also about object perception (Newell et al. 2001; Wijntjes et al. 2009). In difference to these studies, however, we observed cue integration even without spatially well aligning the presented tactile and visual cues. Moreover, the somatosensory information was passively perceived, generated by a stimulation device, rather than actively generated by touching an object. Also, our experiments investigated switch-time and onset-time dependencies, showing that the visual bias depended on the tactile rotation direction upon visual onset, regardless of whether the tactile direction just switched or even whether it was just initiated.

Also, the intermodal aftereffect experiments by Konkle et al. (2009) are related to our results. Konkle et al. (2009) showed intermodal, contrastive aftereffects from touch to vision, while we observed assimilative effects. The most important difference between the experiments was that in

our experiments tactile stimulation continued until after VMD offset, whereas in Konkle et al. (2009)'s experiment stimulation stopped 1 s before visual onset. In consequence, we did not observe contrastive aftereffects between touch and vision, but rather integrative, assimilative effects. Also in contrast with Konkle et al. (2009), our results showed that tactile and visual stimulations did not need to be spatially well aligned to observe crossmodal cue interactions. The recorded cue integration may have been fostered by the additional dual task paradigm. This paradigm enforced the encoding of both rotating stimuli, but refrained from suggesting a particular form of encoding. The results suggest that the tactile rotation directions were co-encoded in a head-centered frame of reference, although only tactile directional switches had to be monitored.

These differences to the related previous studies suggest that the observed cue integration in our experiments was neither due to an aftereffect nor due to location-dependent multimodal cue integration mechanisms. Rather, directional tactile information was integrated into directional visual information without immediate location dependence.

In the literature, there is growing evidence that the focus of attention can modulate crossmodal binding (Oruc et al. 2008). Moreover, timing and spatial location are relevant for crossmodal interactions to occur (Hartcher-O'Brien et al. 2008; Sanabria et al. 2005). Zmigrod et al. (2009) proposed the term "temporal event files" for such binding mechanisms. Their results suggest that binding generally occurs given sufficient spatial and temporal coincidence, while only those aspects can be retrieved and bound together that are relevant for the specific task at hand. In our experiments, this task relevancy was ensured due to the dual task paradigm.

Stimulus orientation dependency

Besides multisensory interactions of moving stimuli, studies with point-like location stimuli showed that tactile perception can be influenced by visual stimuli dependent on posture or even on current tool use (Holmes and Spence 2004; Maravita et al. 2003). In particular, it was shown that the presentation of visual distractors in the form of light flashes did not depend on the visual hemisphere in which somatosensory information of the hand was processed, but rather on the location of the hand in a head-centered frame of reference. The location of the visual stimulus had to be close to the current location of the hand in space, irrespective of visual hemispheric or retinal perception. Most of these experiments were conducted on location-based discrimination tasks. However, speeded discrimination tasks with multiple vibrotactile targets at the same location could also be disrupted by incongruent visual distractor stimuli (Holmes et al. 2006). Moreover, it was shown that

sequential auditory and tactile stimuli interfere in directional movement judgment tasks, where again the relative hand position had a strong effect on the type and degree of interference, as did the synchronicity in the presentation of the bi-modal stimuli (Craig 2006; Sanabria et al. 2005; Soto-Faraco et al. 2003). These studies suggest that visual and tactile perceptions interact when the visual stimulation is sufficiently well aligned with the location of the tactile stimulation, where the alignment depends on the positioning of the limbs in space.

Our results also confirmed tactile stimulus interactions with visual stimulations. However, in our case the stimuli were dynamically rotating. Moreover, the transfer did not depend on the spatial proximity of the tactile and visual stimuli, but rather on the orientation of the stimulated skin surface with respect to a head-centered frame of reference. This result is in accordance with the aforementioned work on the perception of letters and other symbols that are drawn on different parts of the body (Corcoran 1977; Oldfield and Phillips 1983; Sekiyama 1991). Our results are in line with the proposition of "embodied head axes" (Sekiyama 1991, p. 491), which determine the explicit perception of tactile stimuli. However, in our experiments we studied implicit cue integration and did not rely on explicit reports about tactile perceptions. Moreover, the variations in tactile onset and switch times revealed that the time course of this integration was very immediate and adaptive.

Neuroscience accounts

Neuroscience studies suggest some candidate areas, which may be involved in realizing the observed transfer from tactile stimulation to visual judgment. Single-cell recordings in monkeys suggest that the peripersonal space of the body surface—and especially hand, arm, and face—is encoded by multisensory neurons in posterior parietal cortical areas (Andersen et al. 1997; Cohen and Andersen 2004; Leinonen 1980; Leinonen et al. 1979) and in the premotor cortex (area F4) (Rizzolatti et al. 1997). These neurons integrate at least re-afferent motor, proprioceptive, tactile, auditory, and visual information sources and encode the space around the body in various frames of reference (Cohen and Andersen 2004; Lådavas and Farnè 2004). Furthermore, among these populations are neurons that strongly correlate with particular circular movements (area 7a) (Sakata et al. 1986). These neurons were shown to have large receptive fields, suggesting the integration of circular motion information across large spatial areas. Similar neurons were also identified in the neighboring dorsal part of the medial superior temporal area (MSTd), which appears to be responsible for the decoding and the stabilization of self-motion (Andersen et al. 1997).

It remains unclear to what extent these two neural populations are distinct. However, there is evidence that a neural pathway exists between MST and visual motion perception area MT (V5) (Sakata et al. 1986). Moreover, it was shown that neurons in area 7 of the macaque monkey respond in a direction-sensitive manner to moving somatosensory stimulation, visual stimulation, or both (Leinonen 1980). Duhamel et al. (1998) suggest that the ventral intraparietal area (VIP) in the macaque is responsible for integrating visual and somatosensory information in a head-centered frame of reference. Thus, body posture information has already been integrated at this point between vision and somatosensation.

Increasing evidence suggests that similar movement integration areas exist in humans (Soto-Faraco et al. 2003). It was shown that the deep areas in the intraparietal sulcus have equivalent properties to VIP in monkeys (Bremmer et al. 2001; Macaluso and Driver 2001). Moreover, it was shown that spatial attention to one sensory modality shows corresponding activity in the spatially corresponding parts of the unimodal cortical areas of other sensory modalities (Macaluso and Driver 2001). For example, attention to one somatosensory location on one arm yielded increased activity of the corresponding visual location areas in the contralateral occipital gyrus. Also, tactile stimulations yielded modulations in the contralateral side during visual perception tasks, in that irrelevant but congruent, concurrent tactile stimulation yielded increased activity in the contralateral occipital gyrus (Macaluso and Driver 2001). Comprehensive reviews of multisensory integration studies from neuroimaging data can be found elsewhere (Calvert and Thesen 2004; Thesen et al. 2004).

With respect to motion perception, it has been shown that visual motion perception in area MT (V5) is also modulated by tactile motion stimuli (Beauchamp 2005; Blake et al. 2004; Sathian et al. 2004). Similar motion cue modulations can be expected to have produced the results in our experiments. However, the observed nearly instant influence of tactile stimulations on visual motion perception furthermore suggests that this tactile motion cue modulation occurs very fast given tactile motion onsets and is highly adaptive considering sudden switches in tactile direction.

Conclusions

We have shown that tactile circular stimulations on the palm of the hand can influence visual judgments due to rotational cue integration in a head-centered spatial representation. Moreover, the tactile bias on visual motion judgments was very versatile since a tactile directional switch immediately transferred into a switch in the

direction of the visual judgment bias. Also, a tactile rotational onset upon visual onset yielded the assimilative cue integration effect. Thus, the cue integration effect was immediate and adaptive, suggesting a very fast mechanism.

From a broader perspective of multisensory interactions in various embodied frames of reference, the results essentially show that moving tactile stimuli on the skin are quickly and adaptively mapped into a head-centered frame of reference, dependent on the orientation of the stimulated skin surface. Although spatial re-mappings are also considered crucial for the effective, intentional control of behavior (Andersen and Buneo 2002), our experiments focused on the multimodal sensory side. Thus, it remains a future research challenge to enhance these investigations to potential sensory-motor cue integration mechanisms.

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