INVESTIGATING VISUAL, PROPRIOCEPTIVE AND TACTILE INTERACTION THROUGH SENSORIMOTOR ADAPTATION

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Abstract

Multisensory integration has classically been studied by looking at the relation of two senses, like visuo-tactile integration, visuo-proprioceptive adaptation or visuo-auditory interaction. But a coherent perception integrates mostly various senses at a time. Seldom studies tried to incorporate three senses and infer about their relative reliability in a given context. In the present study, which was inspired by a bimodal integration protocol, the adaptation and integration of three modalities vision, proprioception and touch in two directions, azimuth and depth were investigated. Subjects performed a reach and point task in a complete virtual environment. Results revealed first, that adaptation does not always follow the direction of the induced visual shift, but can be in the contrary direction in one dimension. Second, vision does not always dominate the integration process, but depending on the direction, other senses can be deemed as more reliable, showing a smaller adaptation effect than vision. Third, the individual relative reliabilities might reveal a flexible hierarchy where touch becomes the least reliable in azimuth but gains reliability in depth. We conclude that individual reliability, and through this the optimal integration process, can be influenced by many factors that could be characteristics of the sense itself, the interaction relationship between two or more senses and the task context.

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1 INTRODUCTION

In order to obtain a coherent perception of the external world and to potentially act upon it, humans must integrate information arriving from different sensory modalities. This integration enhances the perception of external stimuli as most of them are multisensory in nature and the combination leads to a reduction of noise or variance of the final sensory estimate (Ernst & Banks, 2002). This allows us, for example to correctly locate a potential target in space and execute movements towards it with high precision. It is hypothesised that this integration follows a statistically optimal strategy. In an optimal integration model (van Beers et al., 1999) the information of each sensory modality is weighted, taking into account the precision or reliability of each modality in the given context or task at stake. By integrating the weighted sources of sensory information, a single estimate is achieved, that can be used for instance to locate a stimuli or the position of the hand in space. In sighted people this process of locating body parts in external space has been thought to be dominated by vision (Burge, Girshick, & Banks, 2012), assigning it generally more weight than to other modalities such as proprioception or touch (Rock & Victor, 1964). This has been studied experimentally by bringing the feedback of different senses about an object's position into conflict (Ernst & Banks, 2002) or making people to wear optical prism glasses (Hay, Pick, & Ikeda, 1965). Prisms displace the visual field, creating a mismatch between visual and proprioceptive feedback about a target's position in space. The difference in the ability to locate a proprioceptive, visual or combined targets before and after the prism adaptation helped to determine the weight that is applied to each single modality (Redding & Wallace, 1996). Based on these experiments it was assumed that the system assigns higher weights to vision than to the other senses. These conclusions would support the popular assertion that humans are visually dominant animals (Posner, Nissen, & Klein, 1976).

However, newer evidence suggests that the weights are relative and depending on the circumstances or the given task (Burge et al., 2012). When visual feedback is reduced or not present, we seem to rely more on alternative sensory feedback like proprioceptive (Mon-Williams, Wann, Jenkinson, & Rushton, 1997) or auditory feedback (Alais & Burr, 2004), therefore increasing the weight for non-visual modalities and lowering the one of vision. The same can be observed when the hand is actively moved versus being moved passively by the experimenter, increasing or decreasing the relative weight of proprioception as compared to vision (Welch, Widawski, Harrington, & Warren, 1979). An interesting experiment by van Beers et al. has shown that the weights of vision and proprioception are modulated by direction in a localization task. In their study the pointing behaviour to visual, proprioceptive or combined targets before and after an adaptation to a visual distortion in two directions was compared. They showed that people adapt their pointing behaviour to visual targets more, when the displacement was in depth. The contrary was true for displacements in azimuth; here the adaptation was bigger for proprioceptive targets, but less for visual targets. That is, the weight of visual information is strong in azimuth, but weak in depth, whereas the reverse is true for proprioception. Van Beers et al. argue that the precision of vision and proprioception on a horizontal plane is not uniformly distributed, but is described by two orthogonal ellipses (Figure 1).

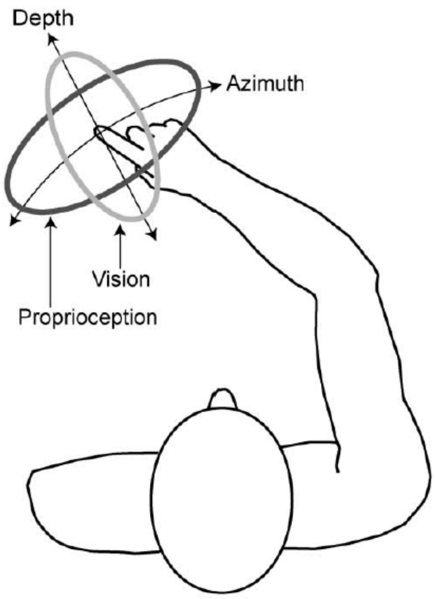

Figure 1. Direction-dependent precision of visual and proprioceptive localisation. Ellipses demonstrate schematically how precision varies with direction when pointing to visual or proprioceptive targets (van Beers et al., 2002).

For vision it is more difficult to make estimates in depth than in azimuth, whereas the contrary is true for proprioception. For vision to make accurate position estimations in azimuth, shifting the gaze is good enough. But for depth uncertain measurements such as vergence and disparity, as well the viewing condition and the vertical level have to be taken into account. Proprioception on the other hand must rely on its joint angles that seem to be more accurate in extension than in rotation (van Beers, Wolpert, & Haggard, 2002). van Beers et al. show that since the precision of proprioception in depth is increased and that of vision is decreased, the integration after adaptation relies more on proprioception, whereas the contrary is true for azimuth adaptation. Since the modality weighted more will adapt less (Ghahramani, Wolpert, Jordan, & Walpert, 1997), proprioceptive adaptation is smaller in depth than in azimuth (van Beers et al., 2002).

1.1 Touch perception

But what about touch? Intuitively we would say that touch would follow proprioceptive adaptation, since its main receptive organ is the skin that surrounds our limbs and is therefore following them where ever they are located. However, tactile events seem to be represented in a discrete anatomical, skin-based reference frame independent from limb location and need to be remapped to external coordinates by taking the current posture into account (Driver & Spence, 1998). It could be thought that these abstract spatial frames of references might help to plan, predict and execute a possible motor movement to a tactile stimulus' location (Brozzoli, Makin, Cardinali, Holmes, & Farnè, 2012). Therefore touch seems to have its own merit. Crossed hand experiments delivered good examples for the difference between touch perception and proprioception. In these experiments the skin-based and limb-based reference frames are brought into conflict in order to study the coordinate transformation of tactile events. For example when subjects cross their hands over body midline, they tend to misjudge the order of tactile events (Röder, Rösler, & Spence, 2004). This has been tested by applying the temporal order judgment (TOJ) task, where subjects are asked to detect the order of two tactile events delivered to the index finger of each hand. According to Yamamoto and Kitazawa the minimal interval to judge the order of two tactile events is about 70 ms if the hands are in an uncrossed position. If the subjects crossed their hands, the minimal interval to detect the order had to be increased to 1’500 ms (Yamamoto & Kitazawa, 2001). In another experiment, a tactile cue to a right hand crossed towards the left workspace, produced faster reaction times to visual stimuli in the anatomical side when very short cue-target onset asynchronies (CTOA) where applied. This so called cueing effect was reversed when the CTOA were respectively longer than 200 ms (Azañón & Soto-Faraco, 2008). This suggests, that first there is an automatic, unconscious sweep of bottom-up alignment of touch in a skin-based reference frame to the anatomical congruent side. Later in the coordinate transformation, actual body posture is taken into account and the haptic stimuli is remapped and converted to the external reference frame (Azañón & Soto-Faraco, 2008; Yamamoto & Kitazawa, 2001). On the other hand, when subjects are asked to consciously report the location of a touch in the same short intervals but before a visual cue, no inverse cuing effect was observed, suggesting that they did not base their judgment on an anatomical reference frame in the first place (Azañón & Soto-Faraco, 2008). A current and dominant view of multisensory integration proposes that the brain accomplishes coordinate transformation by converting different types of spatial information into a common reference frame. According to this view, the crossed hands produce impairment in coordinate transformation. However, more recent research suggests that the brain might be able to represent several reference frames in parallel. The reference frames influence behaviour in a weighted manner that is modulated through a top-down process, based on the context of the task (Heed, Buchholz, Engel, & Röder, 2015).

Another interesting finding was that presenting the subject with a pair of plastic rubber hands in an uncrossed position over their own crossed but unseen hands, ameliorated the crossed-hands deficit (Azañón & Soto-Faraco, 2007). The authors showed how adaptation to alternated visual information can influence the perception about body schema and can overrule the delayed remapping of touch to an external frame of reference caused by proprioception. Therefore both vision and proprioception can influence haptic perception.

These findings suggest that an optimal sensory integration is influenced by all the sensors included, and that their influence depends on the reliability attributed to the individual sensory feedback in a given context. Moreover the integration seems to be influenced by both internal acquired knowledge, as it is the case of the anatomical reference frames, and as well external feedback, as in the case of visual cuing or visual alterations. The interaction between these two can be modulated through adaptation or calibration.

1.2 Multisensory integration and adaptation

A recent study by Burge et al. sheds light on these assumptions. They propose that an optimal multisensory integration relies on two mechanisms; internal consistency and external accuracy. Internal consistency ensures that estimates from different sensory modalities about an external property agree with each other. External accuracy ensures that the estimates lead to the desired goal: for instance a successful reach towards a target taking external feedback into account. They conducted an experiment that focused on adaptation in internal consistency in the absence of external feedback, by presenting the subjects with a discrepancy between vision and touch and measuring the relative adaptation. They found that haptics adapted to vision, if vision was more reliable in the adaptation phase. The contrary was true when reliability for vision in the adaptation phase was low, then vision adapted to match haptics (Burge et al., 2012).

On the other hand the van Beers et al. study tested the adaptation in sensory reliability in external accuracy by exposing subjects to a mismatch between proprioception and vision and measuring in the relative adaptation of these two senses in different directions. Measuring the relative adaptation revealed that vision adapted more after shifts in depth where proprioception seems to be more reliable. The contrary was true for shifts in azimuth where more reliability is applied to vision.

But what if the reliability of three senses, vision, proprioception and touch need to be combined? In a more real world scenario we would rely most likely on all three senses in order to obtain a coherent perception of the environment. It would be interesting to see how the three modalities influence each other and how relative adaptation is modulated; if a mismatch between them is introduced.

The following study developed a new scenario based on the experiment of van Beers et al. by incorporating touch as a third sense besides vision and proprioception. Through this procedure we can imagine the following outcomes. The relative adaptation of touch follows the pattern of proprioception, since Burge et al. showed that if vision becomes less reliable, as it is in the case of shifts in depth, the other senses gain more weight and are more resilient to adaptation. Or it follows vision, as it is a dominant sense that has the ability to capture other senses, therefore modulating the adaptive behaviour of touch. A further outcome could be that touch is resilient to adaptation in this scenario, maintaining the internal consistency. It could be thought that the anatomical frame of references of touch belongs to the internal consistency mechanism that needs to be aligned with proprioception by incorporating external accuracy mechanisms, such as visual feedback about current body posture. As vision and proprioception are in conflict, touch does not take the external feedback into account contributing the most to internal consistency. Lastly, it could be hypothesised that touch adaptation shows no modulation by task specific alternations, and adaptation occurs to both experienced shifts. In sum we investigate if touch leads internal consistency and is resilient to external manipulation of accuracy. Or else, if on the contrary touch adapts, does it follow vision or proprioception depending on the task context.

2 MATERIAL AND METHODS

2.1 Participants

25 subjects (13 female), mean age 33 years (SD 5.9 years), participated in the experiment. The majority were right handed (three left handed) and all had normal or normal-to corrected vision. Prior to the experiment they gave their written consent and were naïve to the purpose of the experiment.

2.2 Task

Subjects performed a reach and point task in a virtual reality (VR) environment. They were asked to point with their left hand where they thought a target, which could be the own right hand, a tactile stimulation on their own right hand, a visual stimulus or a combination of the three was located in space. The subjects performed two modality-sessions each consisting of a pre adaptation, an adaptation and a post adaptation block. The pre and post adaptation blocks always consisted of four conditions with the different types of targets mentioned. In the two adaptation blocks only one type of target is shown, but once with a shift of visual feedback in azimuth and once in depth. Before and after each modality the subjects attended a washout block where no perturbation was applied. The perturbation was introduced in a way to avoid the subject's awareness about the conflict (see methods below). Before starting the experiment and during the pre and post adaptation blocks, each target condition was repeatedly explained to the subjects in order to guide them through the task. All subjects followed the same procedure during the experiment which is described in Table 1.

Table 1. Experimental procedure, numbers in the top row indicate the respective block. The order of the modalities (azimuth or depth) and the target conditions were randomized between the subjects.

<table>
<tr><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th></tr>
<tr><td rowspan="6">Training</td><td colspan="3">Azimuth</td><td rowspan="6">Washout</td><td colspan="3">Depth</td><td rowspan="6">Washout</td></tr>
<tr><td>Pre target conditions</td><td rowspan="5">Adaptation</td><td>Post target conditions</td><td>Pre target conditions</td><td rowspan="5">Adaptation</td><td>Post target conditions</td></tr>
<tr><td>Visual</td><td>Visual</td><td>Visual</td><td>Visual</td></tr>
<tr><td>Proprioception</td><td>Proprioception</td><td>Proprioception</td><td>Proprioception</td></tr>
<tr><td>Haptic</td><td>Haptic</td><td>Haptic</td><td>Haptic</td></tr>
<tr><td>Combined</td><td>Combined</td><td>Combined</td><td>Combined</td></tr>
</table>

a) Pre and post adaptation blocks: target conditions

In order to determine if tactile stimuli follow visual or proprioceptive adaptation patterns, the subjects were presented with the following four target conditions in the pre and post adaptation blocks in a randomized order:

1. **Visual targets**: The right hand remained at the starting position. A visual target at three possible target positions in the left workspace appeared on the screen. Then the subjects were asked to point with the unseen left hand to where they believed the visual target was in space.
2. **Proprioceptive targets**: The right hand reached to the imaginary target location in the left workspace (subjects were asked to reach to the experienced target position they performed before). The movement of the right hand was not visible to the subjects. Then the subjects were asked to point with the unseen left hand to where they believed the right hand was in space.
3. **Haptic target:** The right hand was passively placed on the target position in the left workspace (the position was marked by the experimenter on the table). The movement was not visible to the subjects. A tactile stimulation to one of three possible locations on the palm was delivered. Then the subjects were asked to point with the unseen left hand to where they believed the tactile stimulus occurred in space.
4. **Combined target**: The right hand had to reach to a visual target at three possible target positions in the left workspace. The movement of the right hand was visible to the subjects. A haptic and visual feedback was delivered when the subjects correctly reached the target. Then the subjects had to point with the unseen left hand to where they believed the target was in space.

The subjects performed each target condition nine times. After each trial the subjects were asked to return their hands to the virtual start positions. The four target conditions in the pre and post blocks as well the modality (azimuth or depth) were presented to the subjects in a random order. Besides being instructed verbally each target condition was announced with a text in the VR environment in order to indicate which target type would appear next.

b) Adaptation phase

During adaptation the subjects performed the same task as described in the combined target condition. However, during the session, the visual feedback about the target and the moving virtual right hand was progressively displaced to a maximum of 5 cm over the first five trials, either in azimuth or in depth. This was intended to induce an adapted pointing behavior when participants used their left hand to locate the target. The adaptation phase consisted of nine trials whereas the adaptation was gradually introduced in the first five trials. This progressive perturbation approach was used to prevent subjects' awareness about the discrepancy between vision and the other modalities and to achieve a more complete adaptation (Ingram et al., 2000). After the adaptation phase the subjects performed the post adaptation phase with the different target conditions without any displacement, just as in the pre adaptation block.

2.3 Materials and Set Up

a) Set up

The subjects were placed at an acrylic table in front of a desktop PC (Sony Vaio touch screen desktop, www.sony.com) and wore an Oculus Rift (Oculus VR, www.oculus.com) that occluded the vision of their real limbs and converted the task into a fully virtual 3D scene. Thanks to the Oculus Rift, the visual feedback that was given to the subject could be alternated as required in the adaptation blocks. The motion of the subject's limbs was tracked through a Microsoft Kinect (Kinect for Microsoft v2, www.microsoft.com/en-us/kinectforwindows) and was mapped to virtual arms of an avatar. Tactile stimulation was delivered through a custom made haptic glove that incorporated three small vibration motors (LilyPad Vibe Boards lilypadarduino.org) that could stimulate three positions on the subject's right palm. The setup of the experiment can be seen in Figure 2. A detailed description of the custom made glove can be found in Appendix a).

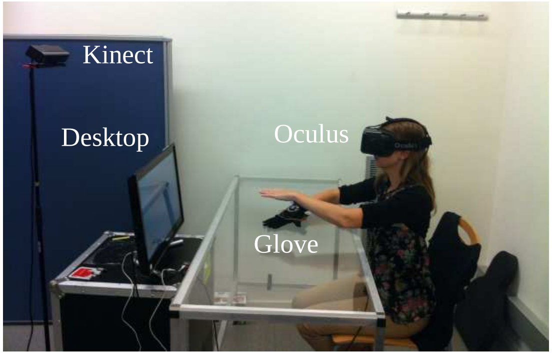

Figure 2. Experimental setup. It consisted of a desktop PC for running the task program, a Kinect to track the movement of the subject's upper limbs and an Oculus Rift for displaying the virtual task scenario. The haptic glove that was worn on the right hand received wireless signals from the task scenario when required and converted them into tactile vibrations on the subject's palm.

b) Scenario and Stimuli

The subjects performed the task in a virtual 3D environment. Except for the visual and haptic target conditions the participants always put first their right hand in the target location followed by the pointing with the left hand. Their upper limb movement was mapped onto a virtual avatar whose limbs could be made visible or not to the subject depending on the conditions (see description of target conditions). In order to start a trial, the subjects had to place their hands on virtual start positions on either side of their bodies. When the hands were close to the starting positions, the subjects always saw their virtual hands in order to facilitate positioning and avoid adaptive drift. Opposed to the right hand, the following reach with the left hand was never made visible to the subjects (Figure 3). The movement of the virtual hands was restricted to the horizontal plane, facilitating user experience.

Depending on the condition and block, the trial scene varied in its visual appearance. An overview of the combination of conditions/blocks and their features can be found in Table 2. In conditions where a visual target was presented, a blue capsule of 3 cm in diameter would appear at three possible locations on a virtual surface that were very close to each other. They were on the corners of an imaginary triangle with side lengths of 2.8x4x2.8 cm that was located about 40 cm in front and 10 cm to the left of the subject's body midline. This was necessary to induce some variance and avoid repetitive or automatic behavior. The target locations were sufficiently far from each other to provide some small pointing variation but close enough to be perceived by the subject as one target, in order not to interfere with the shift that was introduced in the adaptation blocks. The target was visible for 3 seconds. After that a sound indicated to the subjects to return their hands to the start positions; whether the subjects were able to reach for the target during this time or not.

The haptic stimuli were delivered to three positions on the palm that corresponded to the visual target positions, forming as well a small triangle on the subject's hand (see Appendix a)). These stimuli were the same in the haptic target condition in the pre and post adaptation block but without a visual target and without the subjects moving their arms. In conditions like these where the vision had to be occluded from the participants, a black screen appeared as soon as the subjects left the start positions.

In the adaptation blocks the visual target and virtual right hand was gradually displaced in the first trials, either to 5 cm in depth (forward, away from the subject) or in azimuth (leftwards). The virtual right hand was displaced in order to prevent the subjects from shifting as well the real hand and to observe a change in pointing errors due to adaptation in the post adaptation blocks. The perturbation in the virtual hand was zero at the start position and fully introduced at the final location of the hand.

An illustration of the VR-environments' coordinate system that defined left, right, azimuth and depth and be found in appendix III.

Table 2. Overview of conditions / blocks and their corresponding activated features in the task, indicated by an “X”.

Scene / Condition	Left visible?	Right visible?	Right moves?	Haptic feedback	Visual feedback	Visual target	Black screen
Visual		X				X	
Proprioceptive			X				X
Tactile				X			X
Combined		X	X	X	X	X	
Adaptation		X	X	X	X	X	
Washout		X	X	X	X	X	
Trial start	X	X					

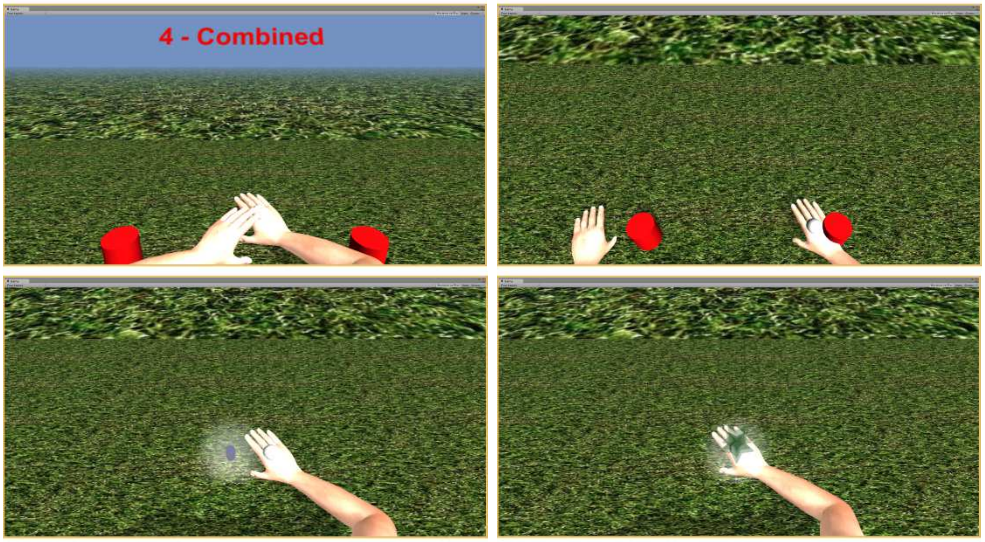

Figure 3. Representative screenshots of the virtual task scenarios as they were presented to the subjects. Every trial started when both hands were correctly placed on the start positions. Depending on condition / block, the vision of certain features or the whole scene was occluded.

c) Data obtained

All the events and kinematic movements of the real and virtual limbs during the whole experiment were logged and stored. From this the pointing behaviour of the left hand relative to the target in all blocks could be obtained. This allowed comparing pre adaptation target conditions to post adaptation target conditions and to determine in which conditions the subjects showed a change in pointing behaviour from which the relative adaptation for each sense can be obtained. No systematic qualitative data was obtained but the subjects were asked by the experimenter informally about their experience and if they had noticed anything unusual in the experiment.

3 RESULTS

For analysing the log files and plotting the data, Matlab was used. The statistical tests were run in SPSS. For the analysis the data of 17 subjects was used. The first four participants were excluded as they served as pilot tests after which the experimental design, the instructions to the subjects and the scenery was changed so that these participants' data are not comparable to the data of the others. Besides this, the remaining two left handed subjects were removed, as well as a subject that continuously touched her hands during the experiment and another one that reported to have noticed the visual manipulation of the target and the right hand. Moreover, the first analysis and the experimenter's observation showed that all participants had to become accustomed to the task in the virtual environment. Therefore the first (training) and the second block (pre adaptation) were not representative examples of the performance of the subjects as they contained too few valid trials. It was therefore decided to take from each participant only the second modality-session, once they were accustomed to the task. This decision changed the design from a repeated measure to a mixed one (mixed factorial ANOVA / GLM 5). Due to the exclusion of participants, the azimuth-modality contains data from nine and the depth-modality from eight participants. For the analysis only the visual, haptic and proprioceptive target conditions are used, as they should show the sensory dependent adaptation.

3.1 Constant Error

The mean constant error refers to the mean pointing error that subjects made in each target condition in the pre and post adaptation blocks for each modality. The mean pointing error (mean of constant errors for each target position, see the explanation of the variable error in the next section) per modality, condition and subject, was taken from the difference in x-coordinate (azimuth) respectively z-coordinate (depth) between the own left hand position and the target position for each trial (please see appendix III for description of the coordinate system). The mean constant errors for all subjects in pre and post conditions in depth and azimuth are shown in Figure 4. The detailed formula for calculating the constant error can be found in appendix II.

To determine the adaptation, the difference in mean constant error between pre and post adaptation for visual targets (ΔV), proprioceptive targets (ΔP) and haptic targets (ΔH) per modality and subject was obtained (Gaveau, Prablanc, Laurent, Rossetti, & Priot, 2014; McIntyre, Stratta, & Lacquaniti, 1997; van Beers et al., 2002); whereas resulting positive values indicate if an adaptation occurred in the expected direction of the visual distortion. The following figure (Figure 5) shows the mean difference in constant error for all subjects in the given modality.

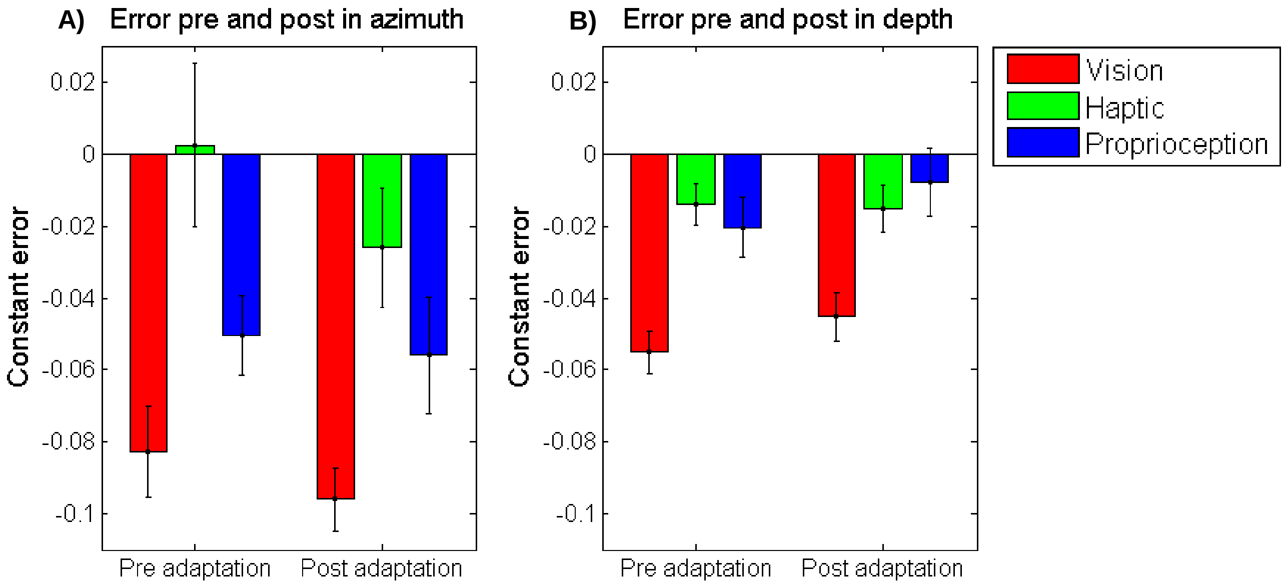

Figure 4. Mean constant errors in pre and post adaptation blocks in azimuth (A) and depth (B) for the three target conditions (vision, haptic and proprioception). Negative values in azimuth indicate rightward, negative values in depth indicate towards subject. Error bars represent standard errors.

In order to test if there was a significant difference between the modalities (between subjects), target condition and pre and post adaptation blocks (both within subject), a mixed factorial ANOVA on the constant errors was performed. The analysis revealed that there was a significant main effect of target condition $F(1.29, 19.36) = 7.28$, $p<0.05$. As Mauchly's test indicated that the assumption of sphericity had been violated, $\chi2(2) = 11.19$, $p < .05$, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .65$). The constant errors for the visual target condition were significantly higher than for proprioceptive, $F(1,15) = 22.28$, $p<0.001$ and haptic, $F(1,15) = 10.58$, $p<0.01$. All other effects showed no significance: no significant (ns) main effect of modality $F(1,15)$, <1, *ns*, no significant (ns) main effect in pre and post adaptation blocks $F(1, 15)$, <1, *ns*, no significant (ns) interaction between target condition and modality $F(2, 30)$, <1, *ns*, no significant (ns) interaction between pre and post blocks and modality $F(1, 15)$, <1, *ns*, no significant interaction between pre and post blocks and target condition $F(2, 30)$, <1, *ns* and no significant interaction between all three variables $F(2,30)$,<1,*ns*.

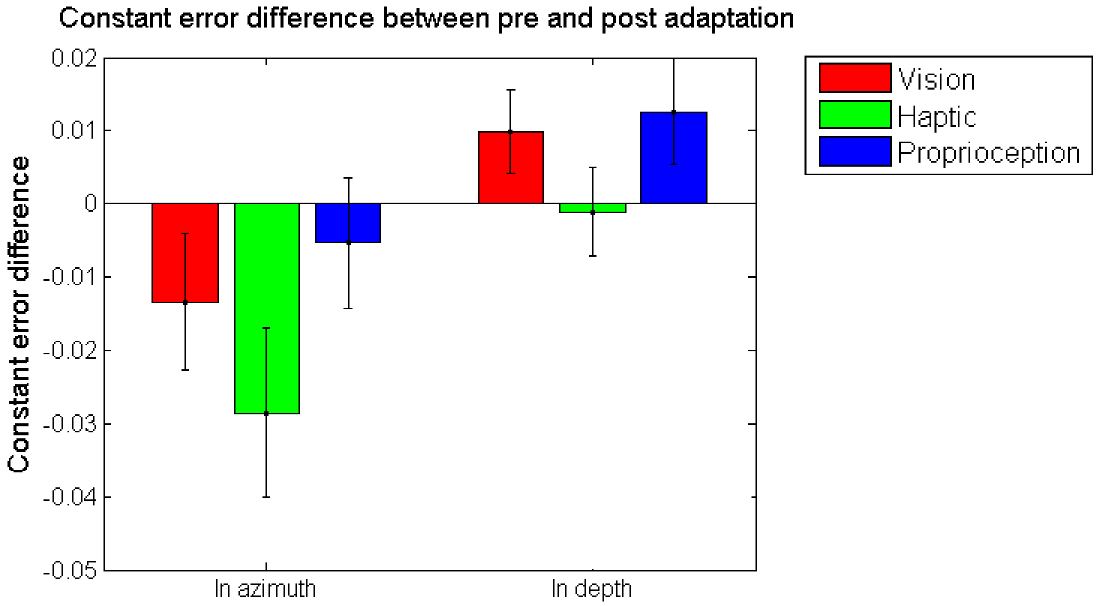

Figure 5. Mean difference between pre and post adaptation constant error for visual, haptic and proprioceptive target conditions over all subjects. Error bars represent standard errors.

In order to test if there was a significant difference between the modalities (between subjects) and the target conditions (within subjects), a mixed factorial ANOVA on the difference on the constant error was performed. The analysis revealed no significant (ns) main effect of modality, $F(1,15) < 1$, *ns*, no significant (ns) main effect of target condition, $F(2,30)$, <1, *ns* nor a significant (ns) interaction between modality and target condition, $F(2,30)$, <1, *ns*.

3.2 Variable Error

The variable error describes the variance that underlies the constant errors that were obtained from the differences between hand positions and the three target positions. This was calculated in order to verify that the pooling of the constant errors for the different target positions is justified respectively that the three target positions were sufficient close to each other. If the variance in the hand positions for each given target position is too different from the variance in the constant errors, and moreover if constant error variance is higher than variable error variance, the target positions themselves would have influenced the pointing behaviour and were maybe not perceived as a group. The detailed formula for calculating the variable error can be found in appendix II. The following figure (Figure 6) shows the mean variable error per subject, per target condition and modality in pre and post adaptation blocks in relation to the variance in the constant error.

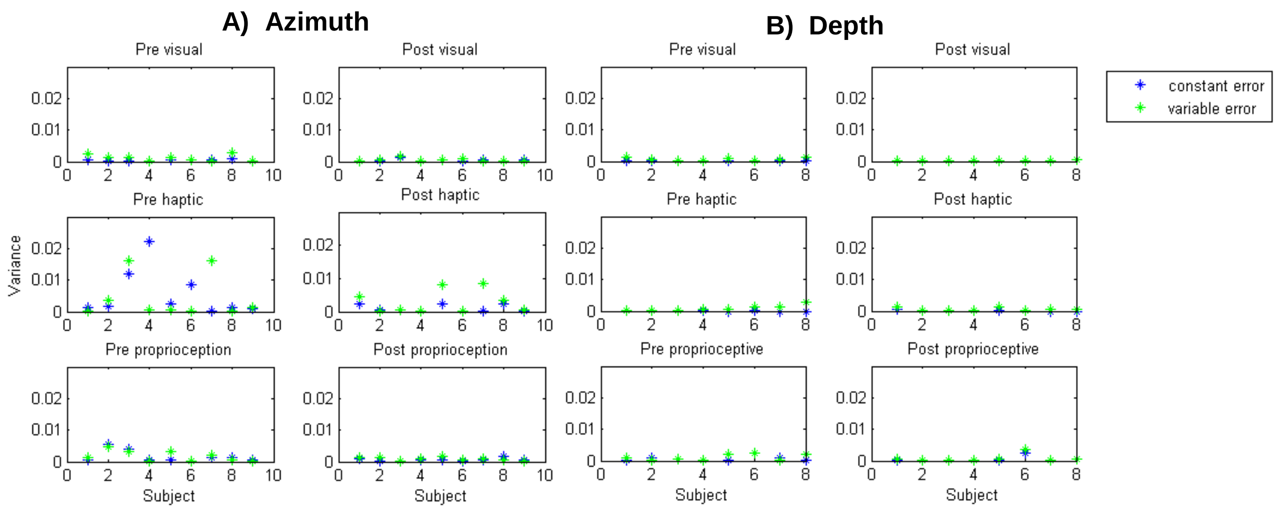

Figure 6. Mean variable error in hand position (green) in relation to the variance in constant error (blue) per subject in the pre and post blocks of all target conditions in the azimuth modality (A) and depth modality (B).

All mean variable errors seem to be almost the same or slightly higher than the constant error obtained for each subject, except for the haptic target conditions in the azimuth modality where some subjects show a higher variance in variable error and constant error.

3.3 Relative adaptation

Relative adaptation is a ratio that expresses the fraction of the adaptation of each target condition to the total adaptation in the given modality. The relative adaptation was obtained by taking the difference in constant error from pre to post adaptation and placed it in relation to the total adaptation. The relative adaptation for each subject and modality was calculated for vision as $\Delta V/(\Delta V+\Delta P+\Delta H)$, for proprioception $\Delta P/(\Delta V+\Delta P+\Delta H)$ and for haptics $\Delta H/(\Delta V+\Delta P+\Delta H)$. Here the directionality of the adaptation was not taken into account, therefore all constant errors were converted into positive values. The following figure (Figure 7) shows the mean relative adaptation for each condition and modality over all subjects.

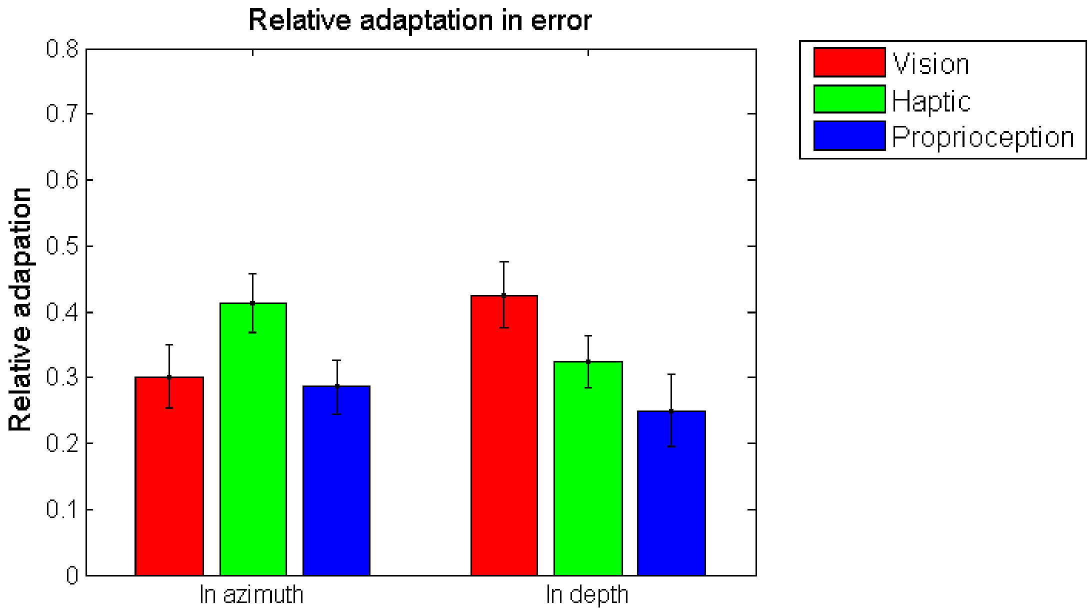

Figure 7. Mean relative adaptation over all subjects to visual, haptic and proprioceptive targets in both modalities. Error bars represent standard errors.

In order to determine the relative proportions of visual, proprioceptive and haptic adaptation, the ratio between these target conditions across modality was calculated. The ratio between vision, haptic and proprioceptive adaptation in azimuth (left column) was 30:41:29. The ratio between vision, haptic and proprioceptive adaptation in depth (right column) was 43:32:25.

To test if there was a significant difference between the modalities (between subjects) and the target conditions (within subjects), a mixed factorial ANOVA on the difference on the constant error was performed. For this the data was first transformed into arcsine values. The analysis revealed no significant (ns) main effect of modality, $F(1,15) < 1$, *ns*, no significant (ns) main effect of target condition, $F(2,30)$, <1, *ns* nor a significant (ns) interaction between modality and target condition, $F(2,30)$, <1, *ns*.

4 DISCUSSION AND CONCLUSION

In the following section the results are discussed, followed by a critical review of the problems faced by the study. The report is summarized with a conclusion and a proposal for future work.

4.1 Discussion of the results

Although the experiment failed to produce significant results, the data shows some interesting trends that can interpreted in the light of the introduction.

a) Overall adaptation

First we look at the overall adaptation behavior shown by the subjects. If we look at the constant error differences (Figure 5) and the relative adaptation (Figure 7) we can say, yes the subjects adapted and the adaptation appears to be different for each target condition, and modality but also that there is a puzzling contradictory effect. Figure 5 shows that adaptation in azimuth goes in the opposite direction of the adaptation in depth. This means that in depth the subjects adapted in the direction of the shift that was induced, while in azimuth they seem to have adapted in the opposite direction of the shift (remember that positive values were given for adaptation in the expected direction of the shift). This is in contrast to the study of van Beers et al. and what one would intuitively expect; but there are some explanations that might clarify this effect.

Indeed some studies have shown that an optical shift with prisms can induce an adaptation in the contrary direction of the shift (Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004; Rossetti, Rode, Pisella, Farne, & Lyon, 1998). Besides being used to treat patients with left sided spatial neglect, these studies showed that leftwards optical shifts induce rightward biases in healthy people when performing a haptic or proprioceptive task. The directionality of adaptation seems not to be dependent only on the direction of the shift but might be influenced by other factors. Although the experiment in this study is quite similar to van Beers et al. there are conceptual differences; like the visibility of an avatar hand, an entire virtual 3D environment and a total free movement of head and limbs that might be more similar to a prism intervention (because it is more natural) than to the set-up used by van Beers et al. In contrast to the prism studies, we observed as well a contra-directional shift in visual adaptation. A possible explanation could be that the 3D environment is not perceived as truly visual, leaving the subject to rely more on kinematics and internal representations of space. As prism adaptations seem to demonstrate plasticity in coordinate transformation it could be hypothesized that the azimuth shift introduced in the current experiment alternated internal visual and proprioceptive reference frames responsible for a compensation in the opposite direction (Rossetti et al., 1998). Moreover a study by Cameron et al. showed exactly the opposite effect of van Beers et al. findings. They observed heavier weighting, and therefore less adaptation of vision in depth, and heavier weighting of proprioception in azimuth. They explain the difference as well due to features of the task. It would therefore be interesting to test each task's features contribution and influence to the adaptation effect.

b) Visual dominance versus relative reliability

As shown in other studies, we observed that vision seems not to be dominant over the other senses. The constant errors and the relative adaptation to visual targets appear to be quite different as compared to the other target conditions. When looking at the constant errors (Figure 4) we can see that the subjects produced the greatest errors in the visual target condition. The test revealed that the difference between the target conditions was significant, so we can conclude that the subjects were the least accurate in the visual target condition as compared to the other conditions. However, this does not necessarily mean that vision was deemed to be the least reliable. When looking at the relative adaptation between the different target conditions and modalities we see that vision follows a pattern other than proprioception and haptic. Although not significant, the pattern across modality as shown in Figure 7 resembles the results presented in the study by van Beers et al. with vision adapting less in azimuth but more in depth, as opposed to the adaptation shown for proprioception, replicating that the task context might influence the weight applied to each sense. Haptic adaptation seems in general to follow proprioceptive adaptation, adapting more in azimuth than in depth. This could be interpreted that the lower reliability of vision in the depth modality increased the weights of both proprioception and haptics. If we look at the azimuth modality we do not see that proprioception adapted relatively more than vision as shown by van Beers et al. however haptic adaptation seem to be greater in relation to vision and proprioception.

c) Proprioceptive versus haptic adaptation

There are also differences between haptic and proprioceptive adaptation. When looking at Figure 4 and Figure 5 it can be seen that the mean pointing behaviour towards haptic targets changed a lot in the azimuth modality while there is almost no change in the depth modality. The pointing behaviour towards proprioceptive targets changed in the azimuth modality but as well in depth modality, although to a lesser extent. This could point to an integration hierarchy that is a result of the weights assigned to each modality that needs to be integrated in the given context. If we look at Figure 6 we see that the pointing behaviour to haptic targets in azimuth showed some variance in variable and constant errors as compared to all other conditions and modalities, possibly making the haptic sense in azimuth the least reliable. This could possibly link back to the findings in the crossed hand experiments where subjects seem to have difficulties to localize tactile events when the hand shifts in the cross-anatomical workspace impairing internal consistency. However, in the depth modality no variance is present in any target condition. So why does the pointing behaviour to haptic targets shows still more adaptation than the pointing behaviour to proprioceptive targets in depth?

A study by Newport et al. might help to clarify this question. They showed that in a task where subjects had to match the orientation of two bars, haptic matching errors varied with workspace location and orientation of the stimuli and that they were greatest for horizontal positions in the most leftward location (most far away from the reference limb and stimulus) of the workspace. Vertical positions did not yield the same effects (Newport, Rabb, & Jackson, 2002). Moreover they showed that the availability of non-informative visual information does positively influence the accuracy of haptic perception, depending on whether the subjects had to base their judgment on extrinsic (visual) or intrinsic (limb-based) coordinates. In the current study the same factors might have influenced the difference in haptic adaptation between azimuth and depth and its relativity to proprioceptive adaptation. Since the azimuth modality meant a shift to the leftward horizontal space, pointing to haptic targets might have per se produced greater errors that are also reflected in the variance shown in Figure 6. The absence of non-informative visual information (vision was completely occluded) may have further pronounced the errors: because the left limb was repositioned in a way that joint angles became extreme, the azimuth modality could have induced a coding of movement in extrinsic coordinates, reducing positional proprioceptive accuracy and therefore influencing haptic perception. Non-informative visual information would in this case have helped to decrease the errors (Rossetti, Meckler, & Prablanc, 1994). In contrast, shifts in vertical direction favored haptic accuracy, which might have been further promoted by the absence of non-informative visual information in this case. As left hand position in the depth modality was shifted forward, the posture of both hands was more homologous promoting an intrinsic coordination coding in which the absence of non-informative visual information favors haptic accuracy as shown by Newport et al. These circumstances might have favored the perception of touch, reducing its constant error in depth below proprioception.

4.2 Problems faced by the study

Besides the explanations given above, several factors of the experiment itself might have influenced the results and need to be taken into account when interpreting them. First, several subjects reported experiencing difficulties in executing the different target conditions properly, especially in the beginning, when the subjects did the target conditions for the first time. They often failed to do the reach and point task as requested, even though continuous verbal instruction was provided. It would be necessary to include a training phase in the procedure, but this would extend the experiment time to over half an hour, which may be excessive. The best solution would be to conduct the experiment over two days. This would allow for a proper training period, more trials that would intensify the adaptation effect and also assure that there is no remaining adaptation effect in the second modality. Moreover, a different tracking system should be considered that would allow for doing the pointing with the left hand under the acrylic table. Tests in the development phase revealed that the tracking of the Kinect was not stable enough to follow the left hand under the table; therefore the subjects had to lift the left hand over the right hand in order to avoid contact with it. As some subjects reported that this was tiring for them, the lifting of the left hand could have influenced the concentration and subsequently the adaptation process of the subjects. The tracking system only allowed tracking a point on the subject's hand, which could have influenced accuracy. Tracking individual points on the hand or the fingers would enhance accuracy and lessen variance. Besides this, the virtual environment might not have induced the body ownership necessary for proper adaptation. The tracking system and the head mounted display needed a special configuration of the virtual camera perspective that is not exactly the same as in reality, possibly creating a different depth and azimuth perception. The avatar used was a generic one that did not have the exact measurements of the subjects. Lastly, perhaps the dimensions used for placing the targets and the shifts were not suitable for this kind of virtual environment. Although they were taken over from the study of van Beers et al., they should have been tested beforehand with a separate set of subjects in order to verify whether they met the requirements to induce the expected adaptation effects.

4.3 Conclusion and future work

Multisensory integration is a complex process, whose basic mechanism of reliability estimation in order to create a coherent perception is influenced by many factors. The results of the present study showed some tendencies of previous findings in this field but also indicated some new and contradictory aspects especially regarding touch adaptation and integration, although not on a significant level.

We found that the subjects showed a diverse adaptive behavior to different kinds of target conditions and direction modalities. However, in contrast to the study of van Beer et al., which served as an inspiration for the present work, the adaptation in azimuth was in the contrary direction of the shift. One possible explanation could be that the task activated the same mechanisms as observed in prism intervention studies where a similar effect is observed.

Like other studies we found as well that there is no visual dominance over other senses. Depending on the reliability attributed to each sense that needs to be integrated, other sensory modalities might be assigned with higher weights and therefore capture vision following an optimal integration model. Our results showed that the pointing to visual targets induced the greatest constant errors, in both directional modalities. Vision alone was therefore not the most precise sense in this scenario. Nevertheless, its relative adaptation is modulated as predicted by the study from van Beers et al. by direction, adapting less in azimuth and more in depth. Less accuracy therefore doesn’t necessarily mean less reliability.

Haptic adaptation seems to follow the pattern of proprioceptive adaptation across modality but is different from proprioception within modality. In azimuth, touch shows the greatest change in constant errors of all the senses, whereas almost no change is visible in the depth modality. This might reveal a hierarchy in the reliability of the involved senses in this given context where the individual reliability can be explained by the sensors’ characteristics (e.g. presence of anatomical frame of reference in touch), and by the interaction conditions (e.g. availability of non-informative visual information). Touch therefore seems to be the least reliable in azimuth but gains reliability in depth.

Despite these interesting trends the current study has to be seen clearly as a pilot, given all the limitations as outlined in section 4.2. There are not many studies that attempted to investigate complex processes such as adaptation and multisensory integration by applying relatively novel, low cost technologies. Although they offer many advantages to existing approaches, their influence and scientific validity has not been extensively studied yet. For future work we therefore see two opportunities. Firstly an attempt should be made to replicate the results of this study with a more controlled version of the experiment that overcomes the mentioned limitations, foremost the tracking system. Secondly it would be interesting to study specifically the impact of novel technologies on sensor characteristics and interaction conditions that underlie multisensory integration.

Bibliography

Alais, D., & Burr, D. (2004). Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*, *14*(3), 257–262. doi:10.1016/S0960-9822(04)00043-0

Azañón, E., & Soto-Faraco, S. (2007). Alleviating the “crossed-hands” deficit by seeing uncrossed rubber hands. *Experimental Brain Research*, *182*(4), 537–48. doi:10.1007/s00221-007-1011-3

Azañón, E., & Soto-Faraco, S. (2008). Changing reference frames during the encoding of tactile events. *Current Biology : CB*, *18*(14), 1044–9. doi:10.1016/j.cub.2008.06.045

Brozzoli, C., Makin, T. R., Cardinali, L., Holmes, N. P., & Farnè, A. (2012). Chapter 23 Peripersonal Space - A Multisensory Interface for Body-Object Interactions. In *The Neural Base of Multisensory Processes*.

Burge, J., Girshick, A. R., & Banks, M. S. (2012). Visual-Haptic Adaptation Is Determined by Relative Reliability. *Journal of Neuroscience*, *29*(6), 997–1003. doi:10.1016/j.biotechadv.2011.08.021.Secreted

Driver, J., & Spence, C. (1998). Attention and the crossmodal construction of space. *Trends in Cognitive Sciences*, *2*(7), 254–262. doi:10.1016/S1364-6613(98)01188-7

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. doi:10.1038/415429a

Gaveau, V., Prablanc, C., Laurent, D., Rossetti, Y., & Priot, A.-E. (2014). Visuomotor adaptation needs a validation of prediction error by feedback error. *Frontiers in Human Neuroscience*, *8*(November), 1–15. doi:10.3389/fnhum.2014.00880

Ghahramani, Z., Wolpert, D. M., Jordan, M. I., & Walpert, D. M. (1997). Computational models of sensorimotor integration. In *Self-Organization, computational maps and motor control* (pp. 117–147). doi:10.1016/S0166-4115(97)80006-4

Girardi, M., McIntosh, R. D., Michel, C., Vallar, G., & Rossetti, Y. (2004). Sensorimotor effects on central space representation: Prism adaptation influences haptic and visual representations in normal subjects. *Neuropsychologia*, *42*(11), 1477–1487. doi:10.1016/j.neuropsychologia.2004.03.008

Hay, J., Pick, H., & Ikeda, K. (1965). Visual capture produced by prism spectacles. *Psychonomic Science*, *2*(8), 215–216. doi:10.2466/pms.1965.20.3c.1070

Heed, T., Buchholz, V. N., Engel, A. K., & Röder, B. (2015). Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends in Cognitive Sciences*, *19*(5), 251–258. doi:10.1016/j.tics.2015.03.001

Ingram, H. a, van Donkelaar, P., Cole, J., Vercher, J. L., Gauthier, G. M., & Miall, R. C. (2000). The role of proprioception and attention in a visuomotor adaptation task. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *132*(1), 114–126. doi:10.1007/s002219900322

McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology*, *78*(3), 1601–1618.

Mon-Williams, M., Wann, J. P., Jenkinson, M., & Rushton, K. (1997). Synaesthesia in the normal limb. *Proceedings. Biological Sciences / The Royal Society*, *264*(1384), 1007–1010. doi:10.1098/rspb.1997.0139

Newport, R., Rabb, B., & Jackson, S. R. (2002). Noninformative vision improves haptic spatial perception. *Current Biology*, *12*(19), 1661–1664. doi:10.1016/S0960-9822(02)01178-8

Posner, M. I., Nissen, M. J., & Klein, R. M. (1976). Visual dominance: an information-processing account of its origins and significance. *Psychological Review*, *83*(2), 157–171. doi:10.1037/0033-295X.83.2.157

Redding, G. M., & Wallace, B. (1996). Adaptive spatial alignment and strategic perceptual-motor control. *Journal of Experimental Psychology. Human Perception and Performance*, *22*(2), 379–394. doi:10.1037/0096-1523.22.2.379

Rock, I., & Victor, J. (1964). VISION AND TOUCH: AN EXPERIMENTALLY CREATED CONFLICT BETWEEN THE TWO SENSES. *Science (New York, N.Y.)*, *143*, 594–596. doi:10.1126/science.143.3606.594

Röder, B., Rösler, F., & Spence, C. (2004). Early Vision Impairs Tactile Perception in the Blind. *Current Biology*, *14*(2), 121–124. doi:10.1016/j.cub.2003.12.054

Rossetti, Y., Meckler, C., & Prablanc, C. (1994). Is there an optimal arm posture? Deterioration of finger localization precision and comfort sensation in extreme arm-joint postures. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *99*(1), 131–136. doi:10.1007/BF00241417

Rossetti, Y., Rode, G., Pisella, L., Farne, A., & Lyon, D. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, *395*(September), 8–11.

Van Beers, R. J., Sittig, A. C., Denier van der Gon, J. J., Elliott, M. T., Wing, A. M., Welchman, A. E., … Braun, D. A. (1999). Integration of Proprioceptive and Visual Position-Information : An Experimentally Supported Model Integration of Proprioceptive and Visual Position-Information : An Experimentally Supported Model. *Journal of Neurophysiology*, (81), 1355–1364.

Van Beers, R. J., Wolpert, D. M., & Haggard, P. (2002). When feeling is more important than seeing in sensorimotor adaptation. *Current Biology*, *12*(10), 834–837. doi:10.1016/S0960-9822(02)00836-9

Welch, R. B., Widawski, M. H., Harrington, J., & Warren, D. H. (1979). An examination of the relationship between visual capture and prism adaptation. *Perception & Psychophysics*, *25*(2), 126–132. doi:10.3758/BF03198798

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, 1–7.

Appendix

I. Haptic Glove

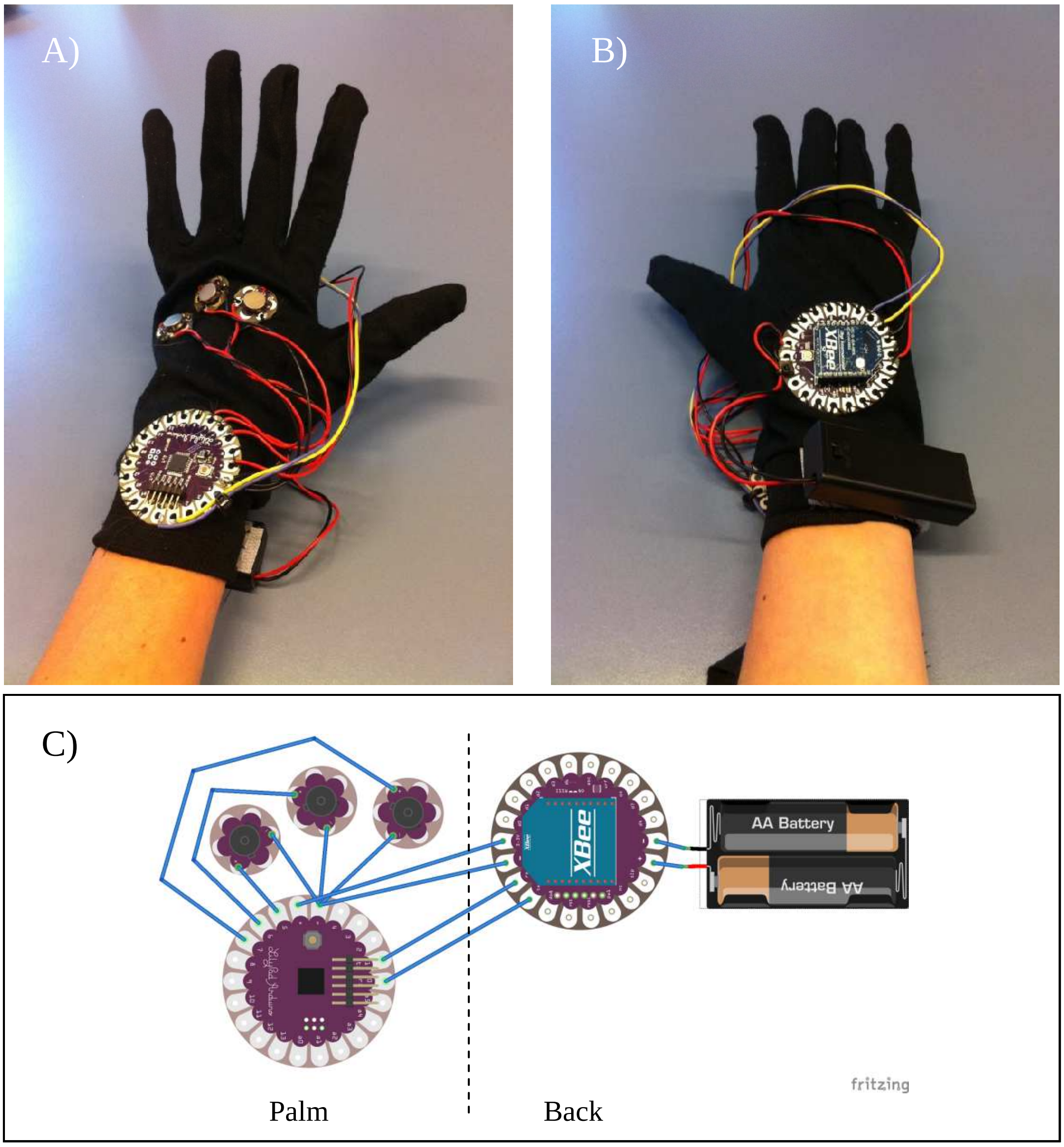

Figure 8. Custom made haptic glove. The glove received signals from the virtual task scenario wirelessly (via two XBee Series 1 chip antennas) (B) and converted them into haptic stimuli that were delivered through three vibration motors (all sewable electronic modules were from LilyPad Arduino) on three locations on the subject's right palm (A). In figure C the schema of the electronic circuit as it is placed on the gloves back and front (palm) side is shown. The Xbee antenna on the back of the palm received the wireless signals from the second Xbee that was attached to the desktop PC where the virtual task was running.

II. Constant and variable error equations

The constant error was calculated by applying the following equation (1), taken from the study by McIntyre et al (McIntyre et al., 1997). The constant error $e^i$for target i is given by the expression

$$e^i = \bar{p}^i - t^i \tag{1}$$

where t^i is the position of the target i, and p_j^i is the final position of the left hand for trial j to target i. The final position of the left hand was computed as the 2D point where the hand's velocity was the lowest in its maximal extend. The error Δ_j^i for a single trial was the difference in x-position for azimuth and z-position in depth for the final hand position and the target. The average final position for n^i repetitions to target i is denoted by $\bar{p}^i$. The deviation δ from the mean for a given trial is defined as

$$\delta_j^i = p_j^i - \bar{p}^i \tag{2}$$

The variable error $V^i$for a single target was given by the equation

$$V^i = \frac{1}{N-1} \sum_{j=1}^{N} |A_i - \bar{p}^i|^2 \tag{3}$$

Where A_i is a variable vector containing all final positions p_j^i for n^i repetitions to target i. In order to compare the variable errors $V^i$of the final positions to the constant errors $e^i$of the targets, the variance $V^k$of B_k a variable vector containing all constant errors for all targets in block k, was calculated with the following equation

$$V^k = \frac{1}{N-1} \sum_{k=1}^{N} |B_k - \bar{e}^k|^2 \tag{4}$$

The overall average constant error $\bar{e}^k$ for all targets was the average constant error over all three target positions in one block k. The data over all three target positions was combined as it was assumed that if they were sufficient close to each other errors produced to each target in a given block would be similar (McIntyre et al., 1997).

III. VR-environment coordinates

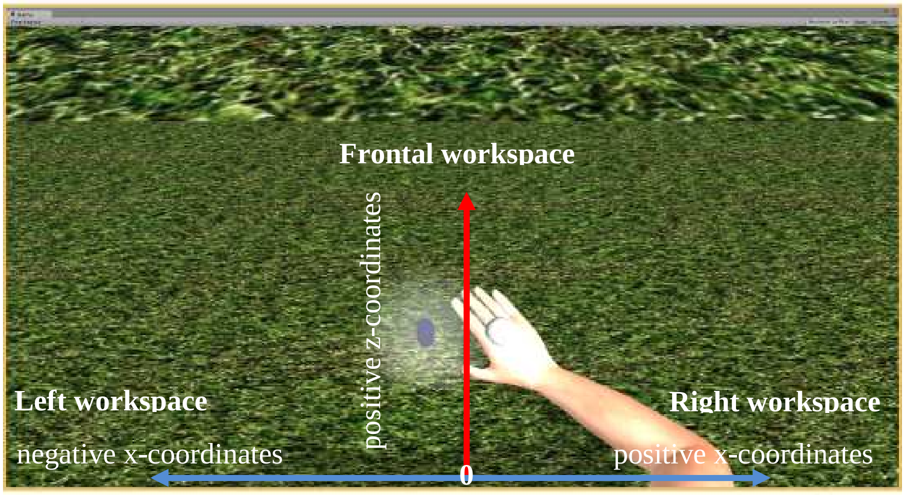

Figure 9. Coordinates in VR-Scenario. The blue line indicates azimuth that uses x-coordinates, whereas negative x-values indicate the left side of the workspace and positive x-values indicate the right side of the workspace. The red line indicates depth that uses z-coordinates, positive z-values indicate forward (away from the subject); negative z-values would be behind the subject. For illustrative purposes the body midpoint (0) is shown a bit in front of the subject. When the target positions where displaced in azimuth they shifted more to the left (greater negative x-coordinates). When the target positions were displaced in depth, they shifted more forward (greater positive z-coordinates) away from the subject.