Representations of space based on haptic input

Voorstellingen van de ruimte op grond van haptische input

(met een samenvatting in het Nederlands)

Proefschrift

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Table of contents

Voor Eelke en Siem

Chapter 1| Introduction

Introduction

We live in a visual world, and what we experience seems to be dominated by what we see. Even when we close our eyes our minds seem filled with visual images. Moreover, many of our daily life actions seem to be guided by vision: retrieving that red Corvette, reaching for one of its doors, navigating from work to our homes, avoiding collisions with other drivers. However, beneath that overwhelming visual top layer, there is a whole - more or less hidden – world of touch, of which we are often hardly aware. This world, conveyed to us by the so-called "haptic system" is crucial for our daily functioning. Basically, by telling us where our hands are, where they are going and what they are touching, our haptic system allows us to perform actions and interactions with objects without having to use vision. Consequently, by performing actions like "looking" for the car keys in our pockets, opening the car door, adjusting our seats, finding the ignition, shifting gear, the haptic system literally allows to look ahead and plan our next move.

Normally, the visual and the haptic systems work together smoothly and efficiently. But what happens when the eyes are turned off before spatial knowledge can be acquired visually? What do we "see" when we close our eyes and explore an unknown environment with our hands? Somehow we manage to form mental representations of the objects around us, their locations, their orientations. But how do we achieve this? What are the characteristics of these representations, and what processes and mechanisms in the brain underlie them? How can we examine these processes and mechanisms? And, importantly, considering the dominance of vision, what is the influence of vision on the characteristics of these representations? These are some of the basic questions that are addressed in the current thesis, which, more formally, is on the representations of grasping space (i.e., the space we can reach without having to move through space) based on haptic, or active touch, input. In order to be able think along, the reader may benefit from an introduction of some of the basic assumptions and previous studies underlying the experimental work presented in the following chapters. In this introduction chapter, I therefore shortly discuss the input channels involved in haptic spatial perception, haptic spatial performance in previous studies and some general assumptions and central concepts of spatial cognition. In addition, blind people's haptic performance, and the possibly important roles for visual as well as haptic experience are addressed. Finally, possible sex differences in haptic spatial performance and their promise for revealing haptic spatial processing mechanisms are discussed.

Haptics as a spatial sense

Basically, to build a mental representation of objects and their locations in grasping space using active touch input alone requires knowing where our hands are, where they are going and what it is they touch. Where our hands are and where they are going is conveyed to our brains by so-called proprioceptive input coming from little organs in the muscles and tendons in our arms and hands. What our hands touch, is conveyed by tactile input coming from different sorts of mechanoreceptors in the skin of the hand. But to make sense of what we touch, we need movement. Without pressing the hand on an object or moving over it, no information will come in on the identity of the object. Therefore, in order to identify both *what* it is we touch, and to know *where* it is, proprioceptive and tactile information need to be integrated.

Both the proprioceptive and tactile input enter the brain at the brain's relay station, the thalamus. The thalamus sends the information coming from any modality up to the appropriate cortical brain regions which make sense of the information. In the case of haptics, the thalamus sends the proprioceptive and haptic information up to the primary somatic sensory cortex (or SI, Brodmann areas 1,2 and 3, see Figure 1). From here, the information is conveyed to the secondary somatic sensory cortex (or SII, Brodmann area 43) and the posterior parietal cortex (Brodmann's areas 5 and 7), which also receives direct input from the thalamus. In these cortical regions the proprioceptive and tactile information is integrated, forming the basis of haptic spatial processing (See Gardner, Martin & Jessell (2000), Gardner & Martin (2000) and Gardner & Kandel (2000) to learn more about the neural mechanisms underlying the processing of touch input). Figure 1 shows a schematic picture of the information flow in the brain underlying motor actions based on haptic information.

Importantly, the processing of proprioceptive and tactile information has been found to result in experiences that do not match the actual, physical space around us. Tactile size perception, for example, has been found to depend on the density of mechanoreceptors in the skin, resulting in different tactile size perceptions for different body sites (Weber 1834; Green 1982; Marks et al. 1982). Also proprioceptive localization has been found to be systematically incorrect, and to be different for the hands (Haggard, Newman, Blundell & Andrew, 2000). In addition, the perceived position of a hand has been shown to drift towards the body (Wann & Ibrahim, 1992). Since, as mentioned above, haptic spatial representation depends on the integration of tactile and proprioceptive input, it should not come as a surprise that also haptic spatial tasks like judging line or path length, identifying shape, or matching orientations have been shown to be liable to systematic distortions (line length: Lanca & Bryant, 1995; Marks & Armstrong, 1996; path length: Lederman, Klatzky & Barber, 1985; shape: Henriques & Soechting, 2003; orientation: (Blumenfeld, 1937; Kappers & Koenderink, 1999; Kappers, 1999).

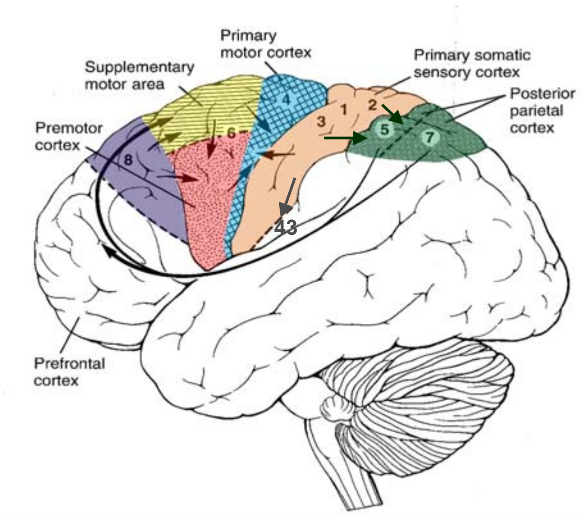


Figure 1. Schematic picture of cortical brain areas underlying haptic processing. Digits represent Brodmann areas. The arrows represent the information flow in the brain underlying motor actions based on haptic input.

A basic assumption for the research presented in this thesis is that studying the characteristics of systematic distortions in performance on simple spatial tasks like those mentioned above, and identifying the exact circumstances under which they occur, provides us with information about the underlying mechanisms and processes of haptic spatial representation in the brain. In this respect, clear and consistent performance patterns resulting from haptic orientation perception tasks have appeared particularly promising (Kappers & Koenderink, 1999; Kappers, 1999). Figure 2 shows a typical deviation pattern of performance on the so-called parallel-setting task. In this task, comprising haptic orientation perception, blindfolded participants are instructed to rotate one or more bars parallel to a bar with a certain reference orientation (Kappers & Koenderink, 1999; Kappers, 1999). Strikingly, in spite of the seemingly simple instruction, anyone who performed this task up until this day made (often large) systematic errors, like the ones displayed in Figure 2. Given that orientation is a very basic spatial property which may well play a role in deviations of higher level properties like angle, shape, path length, it may well be that uncovering the mechanisms and processes involved in orientation representation touches upon many aspects of haptic spatial representation. Therefore, the present thesis has predominantly focused on those factors that modulate haptic orientation perception in order to uncover the mechanisms underlying it. In our approach, we have turned to some of the general principles of spatial cognition which predominantly find their origin in research in the visual domain, and to findings resulting from spatial performance by the blind.

Figure 2. Large deviations in the haptic perception of parallelity.

Spatial reference frames

Spatial cognition research is aimed at identifying the characteristics of the mental representations of space, and the underlying processes, mechanisms and brain areas involved. One of its foundations is the concept of the spatial reference frame. Spatial reference frames may be described as the anchors to which new incoming spatial information is related. The central idea is that an object is always somewhere in relation to something else: your coffee cup is somewhere in relation to your tabletop, the phone, your mouth, your hand. Critically, in order to be able to function as a spatial reference frame, the location or orientation of the object to which the incoming information is linked has to be known to some extent. Otherwise, of course, using it as a reference frame would be useless. In short, an object without a spatial reference frame does not have a location or orientation.

The literature distinguishes between two types of reference frames, egocentric reference frames and allocentric reference frames, which have been suggested to be processed in different brain areas, and to fulfill different functions (e.g. Milner & Goodale, 1995). Employing egocentric reference frames comprises relating incoming spatial information to (parts of) the own body (*ego* = Greek for "self"), which is believed to be especially relevant when a goal-directed action is required: e.g., in order to grab an object, it is particularly useful to know where that object is with respect to yourself, or more specifically, with respect to your grasping hand. In contrast, the employment of allocentric reference frames comprises relating spatial information to objects other than the self (*allo* = Greek for "other"), which is particularly useful when a more absolute, map-like representation of objects is required, i.e., a representation independent of the positioning of the observer's body (parts).

Reference frames in haptics: the hand, the body

One can imagine that in haptics, representations of space particularly rely on egocentric reference frames, even when the task at hand requires a representation of objects in an allocentric spatial map, and independent of the positioning of the limbs or the body. In order to represent space by using touch, we simply cannot get around using our bodies. In particular, the hand and the body may be involved: touching objects with our hands, and at the same time knowing where the hands are and what their orientations are with respect to the body should provide us with all the spatial information we need. But, importantly, as mentioned in the previous paragraph, our conscious interpretation of where our hand is in space may be systematically wrong (Haggard, Newman, Blundell & Andrew, 2000; Wann & Ibrahim, 1992), which may bias our representation of the hand's location and orientation. Now, look at Figure 2 again. Seen in this light, it should not come as a surprise that the performance pattern on the haptic parallel-setting task, has been suggested to stem from biases in egocentric referencing. Perfect performance in this task requires an allocentric representation of the bars in space, i.e., a representation of the bars independent of the positioning of one's body or limbs. Yet, the only way to achieve an internal representation of the bars' orientations without peeking, is through using body and limbs. In other words, the orientation of a bar may be systematically misperceived due to systematic biases in relating the orientation of a bar to egocentric reference frames like the hand and/or the body. Indeed, inspection of Figure 2 seems to suggest that the deviations in haptic orientation perception may stem from the relating of the bar orientation to the hand and/or the body. One may claim that the larger the orientation difference between the hands, the larger the deviation in parallelity perception. On the other hand, the deviation pattern seems to revolve around the body, as if the orientations of the bars have been related to the body.

Irrespective of whether the hands or the body are responsible for the deviations in haptic parallelity perception, it is very likely that relating the incoming haptic orientation information to an (or more) egocentric reference frame(s) forms the basis of these deviations. But how can we be (more) sure? Interestingly, it has been found that whereas immediate goal-directed pointing movements in the visual and proprioceptive modalities employ egocentric reference frames, delaying the pointing movement by just a couple of seconds after perception results in *allocentric* reference frame employment (Rossetti & Régnier, 1995; Rossetti, Gaunet & Thinus-Blanc, 1996). When participants pointed directly after the perception of one of six target locations together forming an arc-shape, the pattern of landing points around the target location was in the direction of the pointing movement, reflecting egocentric reference frame use. In contrast, after 8 seconds delay, the landing points were aligned with the arc-shape of the target locations. This suggests that the delayed pointing movement was based on a representation of target locations with respect to each other, which would indicate allocentric reference frame use. Since, as explained earlier, proprioceptive information is indispensable for haptic representations of space, it may be that a similar shift from egocentric to allocentric reference frame employment due to delay can be observed in haptic space representation. In the case of parallel-setting, a shift from biasing egocentric reference frame towards absolute allocentric reference frame employment would lead to an *improvement* of performance. Whether the introduction of a delay between the perception of a reference bar and the rotation of a test bar indeed results in a (maybe counterintuitive) improvement of parallel-setting performance, is revealed in *Chapter 2*.

The issue of whether relating haptic orientation input to the hands or the body (or both) is responsible for the deviation pattern found in orientation perception tasks is addressed in *Chapter 3*. In this chapter, we introduce the so-called verbal judgment task, in which participants are to verbally assign a number of minutes to a haptically explored bar orientation. In this task, bars at locations fixed with respect to the body are perceived by either the right or the left hand, which should allow us to decide whether the orientation of the hand or the location of a bar with respect to the body determines the deviation.

Haptic space representation: the possible role of vision and consequences for the blind

In contrast to the haptic sense, vision has been claimed to be particularly apt when forming allocentric representations of space; whereas haptic spatial exploration is sequential, visual exploration allows the more or less instantaneous integration of large amounts of spatial information from close by as well as far away, making it easier to represent space in a more absolute fashion. In addition, it has been claimed that visual memories, which may be activated when we close our eyes ("visuospatial imagery"), affect how we interpret what we feel (or hear) around us. As such, these visual spatial memories may help us when we represent space using our haptic sense: it may be that knowing what our hands look like in different spatial locations and orientations affect our internal representation of our hands in space. In other words, vision - and consequently visual memories - can provide us with a (more or less) instant context with which we can interpret incoming spatial information from any modality, and a different internal "view" on our hands and bodies in space. (See Thinus-Blanc & Gaunet, 1997, for a review on the importance of the visual modality on spatial performance).

Importantly, haptic tasks may differ in the extent to which visual memories are activated and visual context is available. Consequently, the foregoing implies that specific task characteristics may largely affect haptic performance. For one, we would expect that task characteristics that stimulate the generation of visuospatial images may improve the ability to represent space more allocentrically. In addition, we would expect that providing (visual) allocentric context to a (haptic) perception would improve performance on haptic orientation perception tasks like the parallel-setting task. In *Chapter 3*, in addition to allowing us to determine the influences of hand- and body-centered reference frames on the deviation in orientation perception (see p.8), the verbal judgment task is employed to study the effects of stimulating allocentric reference frame use on haptic orientation perception. In contrast to the parallel-setting task, we would expect this task to stimulate allocentric reference frame employment, as to be able to name a number of minutes, participants are forced to both form a (visuo)spatial image of a haptically perceived bar on a clock face, and to use the edge of the stimulus table as a mental allocentric reference frame. In order to examine to which extent performance on this task depends on (visuo)spatial imagery we correlated it to performance on a visuospatial imagery task called the mental clock test (Paivio, 1978). In *Chapter 4*, we examine the effects of visual context on haptic parallel-setting performance (cf.

Newport, Rabb & Jackson, 2002), as well as its dependence on where you look. In this chapter, blind-folded performance is contrasted to performance in circumstances in which the bars, hands and body are concealed by a cloth.

But what about the blind? During my PhD project, many people have asked me about the blind and their performance on haptic orientation perception tasks. Of course the blind are an important group for haptic (spatial) tasks, and although one may intuitively expect their haptic experience to improve their haptic spatial abilities, the foregoing suggests otherwise. Indeed, it has been long claimed that the blind, and those that are born blind in particular, have a diminished tendency and/or ability to form allocentric representations of space, and a larger tendency to use egocentric (movement) coding (e.g. Millar 1981, 1988, 1994). Apparently, living with haptic input may tune the blind to represent space egocentrically. This would suggests that the blind (and particularly those who were born blind) may not at all do better than the sighted on the parallel-setting task. Considering their trouble generating representations of space, it is also of interest whether or how delay affects their performance: do they show a similar shift from egocentric to allocentric reference frame use? Previous studies in the proprioceptive domain suggest not. Using the proprioceptive pointing study discussed above, Rossetti and colleagues have shown that blind people do not show the transition from egocentric to allocentric reference frame employment (Rossetti, Gaunet & Thinus-Blanc, 1996;

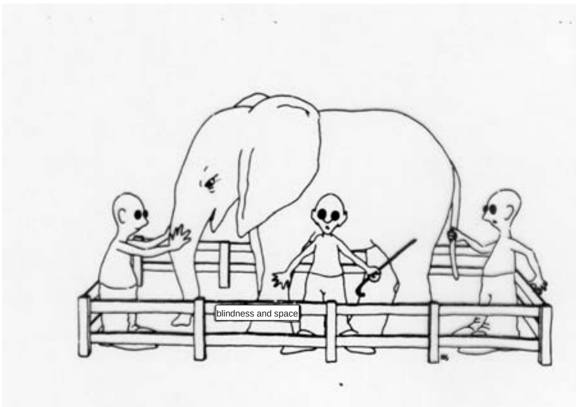


Figure 3. The blind often experience problems integrating multiple pieces of spatial information.

Gaunet & Rossetti, in press). Performance of the blind (both congenitally and late blind) on the non-delayed and delayed parallel-setting task is examined in Chapter 5. Also in this Chapter, we examine blind people's performance on the verbal judgment task, in order to investigate the effects of visual experience on a haptic task in which allocentric reference frame employment and visual imagery is explicitly stimulated

Haptic space representation: the blind and a possible role for haptics

Maybe somewhat surprising to some readers, we seem to expect no advantages of the blind on the haptic spatial tasks we have discussed up until now. But one may question the relevance of the ability to rotate bars parallel for the blind, and argue that spatial tasks that resemble those performed by the blind in daily life, should result in clear advantages for the blind, irrespective of whether they require allocentric or egocentric representation. For example, one may expect that recognizing objects and learning where they are located would result in clear advantages for the blind. Although we share these intuitions, again, the literature seems to decide otherwise, at least at first sight. The accuracy of haptically identifying familiar objects or their depictions seem to favor the visually experienced, when participants have to name the object (Morrongiello, Humphrey, Timney, Choi & Rocca, 1994; Heller, 1989; Shimizu, Saida & Shimura, 1993). Importantly, however, Heller (1989) found that the blind are faster, but not more accurate, when matching simple abstract shapes. This suggests that the accuracy of specifically familiar object identification benefits from a visual memory representation of that object, and that haptic experience may result in a faster identification of abstract haptic shapes, like square, ellipse, triangle etc.

Also with respect to the localization of multiple objects, visual experience rather than haptic experience has been found to improve task performance, particularly after rotation of the object configuration, for which an allocentric representation of the objects is required (Ungar, Blades & Spencer, 1995; Hollins & Kelley, 1988). Importantly, however, the respective roles of visual and haptic experience have been subject of study only under conditions in which participants were given unlimited time to explicitly learn the objects and locations by heart before the actual experiments began. If indeed, the blind are faster at identifying abstract familiar shapes, however, one would expect blind people to be faster in tasks in which the locations of such shapes are learned by, for example, matching them to cutouts in a board, as fast as possible. In *Chapter 6*, we examined the differences between the early blind, the late blind and the sighted in the speeded learning of abstract familiar shapes and their locations, and the accuracy and characteristics of the resulting spatial representations using different (motor and verbal) response methods.

Haptic space representation and the sexes

In addition to individual differences resulting from visual experience, differences between the sexes have long been a matter of interest in spatial cognition research. Remarkably, sex differences in the haptic domain have been examined surprisingly sparsely. In the visual modality, however, sex differences have been well documented. Generally these differences favor males, who have been proposed to have a superior understanding of Euclidean space and a related tendency to employ more allocentric reference frames (for elaborate overviews of sex differences in spatial performance see Voyer, Voyer & Bryden (1995) and Ecuyer-Dab & Robert (2004)). Although these differences may well apply to haptic spatial perception, haptic and visual perception differ in crucial aspects, which may result in a different expression of these sex differences. For one, although males seem to have a larger tendency to employ allocentric reference frames, haptic input – in contrast to visual input - is egocentric, which may affect their advantage. In addition, spatial functions (spatial attention (Kinsbourne, 1987), spatial representation (e.g., Kosslyn, Koenig, Barrett, Cave, Tang & Gabrieli, 1989)) have been found to be distributed differently over the brain's right and the left hemispheres for men and women. Basically, due to these differences, particularly males have been found to judge the left side of space larger than the right (Kinsbourne, 1987), and we may expect males to be more accurate specifically with their left hands. In addition, since the hands - in contrast to the eyes - can be moved into the opposite side of space, this may result in interesting modulations of possible attentional and/or hand effects, which may differ for the sexes. In *Chapter 7*, we examined sex differences on the parallel-setting task in both non-delay (cf. Kappers 2003) and delay conditions, the verbal judgment task, and a production of orientation task.

Finally, the findings of *Chapters 2* through *7* are summarized and discussed in *Chapter 8*.

References

Appelle, S., & Countryman, M. (1986). Eliminating the haptic oblique effect: Influence of scanning incongruity and prior knowledge of the standards. *Perception, 15,* 325-329.

Blumenfeld, W. (1937). The relationship between the optical and haptic construction of space. *Acta psychologica, 2,* 125-174.

Ecuyer-Dab, I., & Robert, M. (2004). Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition, 91,* 221-257.

Gardner, E.P., Kandel, E.R. (2000). Touch. In E.R. Kandell, J.H. Schwarz, T.M. Jessell (Eds). *Principles of neural science* (4th edition, pp. 451-471). New-York: McGraw-Hill.

Gardner, E.P., Martin, J.H., & Jessell, T.M. (2000). The bodily senses. In E.R. Kandell, J.H. Schwarz, T.M. Jessell (Eds). *Principles of neural science* (4th edition, pp. 430-450). New-York: McGraw-Hill.

Gardner, E.P., & Martin, J.H. (2000). Coding of sensory information. In E.R. Kandell, J.H. Schwarz, T.M. Jessell (Eds). *Principles of neural science* (4th edition, pp. 411-429). New-York: McGraw-Hill.

Gaunet, F., & Rossetti, Y. (in press). Effects of visual deprivation on space representation: Immediate and delayed pointing towards memorized proprioceptive targets, *Perception.*

Green B.G. (1982). The perception of distance and location for dual tactile pressures. *Perception & Psychophysics, 31,* 315-323.

Haggard, P., Newman, C., Blundell, J., & Andrew, H. (2000). The perceived position of the hand in space. *Perception & Psychophysics, 62,* 363-377.

Heller M.A. (1989). Picture and pattern perception in the sighted and the blind: the advantage of the late blind. *Perception, 18,* 379-389.

Henriques, D.Y., & Soechting, J.F. (2003). Bias and sensitivity in the haptic perception of geometry. *Experimental Brain Research, 150,* 95-108.

Hollins, M., & Kelley, E.K.(1988).Spatial updating in blind and sighted people. *Perception and Psychophysics, 43,* 380-388.

Kappers, A.M.L. (1999). Large systematic deviations in the haptic perception of parellelity. *Perception, 28,* 1001-1012.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 114,* 131-145.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Kinsbourne, M. (1987). Mechanisms ofunilateral neglect. In M. Jeannerod (Ed.) Amsterdam: North Holland. *Neurophysiological and Neuropsychological Aspects of Spatial Neglect.*

Kosslyn, S.M., Koenig, O., Barrett, A., Cave, C., Tang, J., & Gabrielig, J.D.E. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate spatial relations. *Journal of Experimental Psychology: Perception and Performance, 15,* 723-735.

Lanca, M., Bryant, D.J. (1995). Effect of orientation in haptic reproduction of line length. *Percept Mot Skills, 80,* 1291-1298.

Lederman, S.J., Klatzky, R.L., Barber, P.O. (1985). Spatial and movement-based heuristics for encoding pattern information through touch. *Journal of Experimental Psychology: General, 114,* 33-49.

Marks, L.E., Armstrong, L. (1996). Haptic and visual representations of space. In T. Inui, & J.L. McClelland (Eds.) *Attention and performance 16: Information integration in perception and communication* (pp 263-287). Cambridge, MA, USA: Mit Press.

Millar, S. (1981). Self reference and movement cues in coding location by blind and sighted children. *Perception, 10,* 255-264.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England: Clarendon Press/Oxford University Press.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* Oxford, England UK: Oxford University Press.

Morrongielo, B.A., Humphrey, K., Timney, B., Choi, J., & Rocca, P.T. (1994). Tactual object exploration and recognition in blind and sighted children. *Perception, 23,* 833-848.

Newport, R., Rabb, B., & Jackson, S.R. (2002). Non-informative vision improves haptic spatial perception. *Current Biology, 12,* 1661-1664.

Paivio A. (1978). Comparisons of mental clocks. Journal of Experimental Psychology: Human Perception and Performance, 4, 61-71.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Rossetti, Y., & Régnier, C. (1995). Representations in action: pointing to a target with various representations. In B.G. Bard, R.J. Bootsma, & Y. Guiard (Eds.)

Studies in Perception and Action III (pp. 233-236). Mahwah, NJ: Laurence Erlbaum Associates Inc.

Shimizu, Y., Saida, S., & Shimura, H. (1993). Tactile pattern recognition by graphic display: Importance of 3-D information for haptic perception of familiar objects. *Perception & Psychophysics, 53,* 43-48.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-44.

Ungar, S., Blades, M., & Spencer, C. (1995). Mental rotation of a tactile layout by young visually impaired children. *Perception, 24,* 891-900.

Voyer, D., Voyer, S., & Bryden, M.P. (1995). Magnitude of sex differences in spatial abilities: a meta-analyses and consideration of critical variables. *Psychological Bulletin, 117,* 250-270.

Wann, J.P., & Ibrahim, S.F. Does limb proprioception drift? *Experimental Brain Research, 91,* 162-166.

Weber, E.H. (1834). *De pulsu, resorptione, auditu et tactu: Annotationes anatomicae et physiologicae.* Leipzig : Koehler.

The sighted

Chapter 2 | Delay improves performance on a haptic spatial matching task

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). *Experimental Brain Research, 149,* 320-330.

Abstract

Systematic deviations occur when blindfolded subjects set a test bar parallel to a reference bar in the horizontal plane using haptic information (Kappers & Koenderink, 1999; Kappers, 1999). These deviations are assumed to reflect the use of a combination of a biasing egocentric reference frame and an allocentric, more cognitive one (Kappers, 2002). In two experiments, we examined the effect of delay between the perception of a reference bar and the parallel setting of a test bar. In both experiments a 10-seconds delay improved performance. The improvement increased with a larger horizontal (left-right) distance between the bars. This improvement was interpreted as a shift from the egocentric towards the allocentric reference frame during the delay period.

Introduction

The haptic sense forms a critical source of information about the space around the body. As such, it is striking that, at least under some circumstances, our experience of space based on haptic information differs from physical space. Various studies have revealed distortions in the reproduction, matching or judgment of spatial properties, like line length (Marks & Armstrong, 1996; Lanca & Bryant, 1995), path length in peripersonal space (Lederman, Klatzky & Barber, 1985), and orientation (e.g. Blumenfeld 1937; Lechelt, Eliuk & Tanne, 1976; Lechelt & Verenka, 1980; Appelle & Countryman, 1986; Gentaz & Hatwell, 1998, 1999; Kappers & Koenderink, 1999; Luyat, Gentaz, Corte & Guerraz, 2001). Interestingly, Kappers and Koenderink (1999) and Kappers (1999) have pointed out not only that haptic peripersonal space in the horizontal plane deviates from physical space, but also that it does so in a systematic way over multiple locations for different tasks. Consistent patterns of deviations resulting from the unimanual and bimanual parallel-setting of two bars, the collinear-setting of two bars, and pointing a test bar in the direction of a marker suggest that these three tasks call on the same specific egocentric and allocentric reference frames. The goal of the present study was to shed more light on the involvement of these reference frames in the haptic spatial representation of orientation in a horizontal plane.

On the basis of both patient and experimental data, Milner and Goodale (1995) proposed egocentric and allocentric reference frames to be distinct, emphasizing their functional and neuroanatomical independence in the visual modality. In their view, processing in the so-called 'dorsal stream' mediates sensorimotor representations that are used in goal-directed action. These representations are thought to be implicit, short-lived and based on *egocentric* reference frames. Processing in the so called 'ventral stream' and the hippocampal region, however, is thought to mediate conscious perception of space and objects, and is assumed to generate longer lasting representations available for cognitive processing (i.e. declarative memory). The latter representations are thought to take longer to generate and to be based on *allocentric* reference frames. Studies with so-called 'numb-sense' patients, who appear to have implicit, but no conscious knowledge of tactile (Paillard, Michel & Stelmach, 1983; Rossetti, Rode & Boisson, 1995) or proprioceptive (Rossetti, Rode & Boisson, 1995) input, have indicated that the functional and neuroanatomical separation may also apply to these non-visual modalities. Given that proprioceptive and tactile input are both indispensable for haptic spatial representations, the intriguing question arises whether the separation is also applicable to the haptic sense. Recent visual and proprioceptive studies have shown that the introduction of a delay period between perception and action changes the contributions of egocentric and allocentric reference frames involved (e.g. Rossetti, Gaunet & Thinus-Blanc, 1996; Rossetti & Régnier, 1995; Bridgeman, Peery & Anand, 1997; Milner, Paulignan, Dijkerman, Michel & Jeannerod, 1999). In the present study we examined whether this change in contributions of reference frames can also be observed in the haptic modality. In two experiments in which a bimanual parallel-setting task (cf. Kappers, 1999) was used, we examined the effect of delay between the perception of a reference bar and the parallel-setting of a test bar on the pattern of deviations.

In the literature ample evidence can be found for the existence and use of intermediate or combinations of reference frames. In goal-directed action tasks, typically multiple egocentric reference frames are employed (Paillard 1991). In turn, in mental imagery and mental manipulation tasks, combinations of allocentric reference frames are addressed (Wraga, Creem & Proffitt, 1999). Over the last couple of years it has also become clear that *interactions* between egocentric and allocentric reference frames occur in various tasks. It has been claimed that in both the visual (Bridgeman, Peery & Anand, 1997; Rossetti, Pisella & Pelisson, 2000; Milner, Paulignan, Dijkerman, Michel & Jeannerod, 1999) and proprioceptive modality (Rossetti & Régnier, 1995; Rossetti, Gaunet & Thinus-Blanc, 1996) *allocentric* representations of space can be employed in goal-directed action by exploiting the differences in temporal characteristics of the representations involved. For example, Milner and colleagues (1999) found that optic ataxia patient A.T.'s pointing to a visual stimulus paradoxically *improves* when she is required to wait for 5 seconds. The authors suggested that the delay enables A.T. to employ a different, more flexible visuospatial coding system than her damaged visuomotor system. Importantly, Rossetti and colleagues (Rossetti & Régnier, 1995; Rossetti et al., 1996) and showed that, with healthy subjects, the introduction of a delay period of 8 seconds between perception of a proprioceptive target at a certain location and the movement directed at this location, does not only result in generally less accurate performance, but also in a *qualitatively* different error distribution than when an immediate movement is performed. In one of the experiments, the targets were presented in an arc array. Whereas the endpoint distributions of pointing actions were aligned with the direction of the movement in the non-delay condition, they tended to be aligned with the target array in the delay condition (i.e. perpendicular to the movement). The former errors were associated with an underlying egocentric frame, whereas the array-based deviations were thought to reflect the employment of an allocentric representation.

Furthermore, recent studies have indicated that in tasks that require conscious processing - and thus in Milner and Goodale's view (1995) would employ an allocentric reference frame - *egocentric* processing can play a role. For example, Dijkerman and Milner (1997) showed that visual form agnosia patient D.F. can perform a perceptual task like copying a line of a certain orientation by using motor imagery, without being able to perceptually discriminate between different lines. In addition, Sterken and colleagues (Sterken, Postma, De Haan & Dingemans, 1999) showed that verbal judgment of the allocentric position of a stimulus was influenced by egocentric information, which suggests that both allocentric and egocentric reference frames can be involved in an allocentric task. In line with this, there is evidence that conscious tasks like matching or comparing vary in their recruitment of different frames, i.e. the relative contribution of egocentric and allocentric frames appears to be task-dependent. An experiment investigating visual perception of slant has suggested dissociation between *motor* matching responses and *verbal* matching responses (Creem & Proffitt, 1998). The motor matching response appears to lie somewhere in-between 'pure' goal-directed action tasks and perceptual tasks like verbally matching or judging. This suggests the use of a combination of an egocentric and an allocentric reference frame in motor matching tasks. The haptic parallel-setting task (Kappers & Koenderink, 1999; Kappers, 1999, 2002), in which subjects have to match the orientation of a test bar to that of a reference bar by means of a motor response using conscious haptic perception, can be considered a motor matching task. If the characteristics of haptic space as found by Kappers and Koenderink (1999) and Kappers (1999, 2002) indeed reflect the use of a combination of an implicit egocentric reference frame and an allocentric one representing space in a more cognitive way, it would be of interest to try to experimentally change the contribution of the two frames in this task by means of a delay (cf. Bridgeman et al., 1997; Rossetti et al., 2000; Milner et al., 1999; Rossetti and Régnier 1995; Rossetti et al., 1996).

Analyses of the deviation pattern found in both the unimanual and the bimanual version of the task in the horizontal (Kappers & Koenderink, 1999; Kappers, 1999) as well as the midsagittal plane (Kappers, 2002) indeed suggest the involvement of an egocentric frame work and an allocentric one representing physical space. In fact, in Milner and Goodale's view (1995) outlined above, the nature of the parallel-setting task would presuppose the use of an allocentric reference frame, as matching of spatial information based on conscious perception is required to live up to the cognitive notion of parallelity. Allocentric space in haptic perception, however, is not as straightforward as it is in vision. It is unknown whether in haptic space the processing of allocentric and egocentric information happens in parallel, as is assumed to be the case in visual space (Milner & Goodale 1995). Considering the properties of haptic input, it may be that conscious haptic spatial processing is based on more serial processing of information, with egocentric referencing partly preceding the construction of allocentric space. In other words, in order to form a cognitive allocentric representation to perform the task, it might be necessary to integrate information coming from several egocentric frames. This issue, however, is beyond the realm of this paper. For the sake of transparency, we assume that without biasing implicit egocentric reference frames, performance would be veridical as is our cognitive notion of parallelity. We will use the term 'allocentric reference frame' to address the sum of all explicit reference frames, employed to live up to the cognitive notion of parallelity.

In the unimanual and bimanual haptic parallel-setting task in both the horizontal (Kappers & Koenderink, 1999; Kappers, 1999) and in the midsagittal plane (Kappers, 2002) performance has been shown to be systematically and consistently deviating from physical space. As, of course, subjects are not aware of these errors, they appear to be caused by - obviously implicit - egocentric reference frames. In the horizontal plane the deviation pattern for both unimanual (Kappers & Koenderink, 1999) and bimanual parallel-setting (Kappers, 1999) showed the following characteristics: if the test bar was on the right side of the reference bar the deviations were in clockwise direction; if the test bar was to the left of the reference bar the deviations were counter-clockwise. The size of these deviations (up to 62º!) depended on the horizontal (left - right) distance between the reference bar and the test bar: the larger this distance, the larger the deviation. Vertical distance (towards - away from the body) between the bars did not significantly affect deviation size. Kappers (2002) noted that a frame of reference intermediate to a biasing one fixed to the test hand (i.e., an egocentric frame of reference) and one fixed in space (i.e., an allocentric frame of reference) would not only adequately describe the deviation patterns found for all tasks in the horizontal plane, but also those in the midsagittal plane. However striking, this does not necessarily mean that the test hand indeed forms a prominent egocentric reference frame in biasing performance. Yet, as it has been suggested that both visual and tactual stimuli are represented in an egocentric co-ordinate system anchored to the body part used in stimulus manipulation (Graziano, Hu & Gross, 1997; Ládavas, Pellegrino, Farnè & Zeloni, 1998), a reference frame centered on the hand is a plausible implicit egocentric reference frame in causing a bias in the perception of bar orientation, and in performing the parallel-setting action as such. Although other implicit egocentric reference frames (like the arms, shoulders, the body mid-line) may contribute to the biased performance as well, it is likely that two hand-centered reference frames play a role, both biasing the perceived orientation of their bar. However interesting, the issue of which egocentric reference frames make up the frame work that biases performance is not directly relevant to the hypothesis of a delay causing a shift in the relative contributions of an egocentric framework and an allocentric one. Therefore, we will simply speak of "the egocentric reference frame" when referring to the implicit frame work that in our view systematically biases performance[1].

In short, we assume that in the haptic parallel-setting task a combination of an egocentric and an allocentric reference frame is used and that this combination results in a egocentrically biased production of haptic parallelity. The introduction of a delay between the perception of a reference bar and the parallel-setting action then would lead to a shift in the relative contributions of the biasing implicit egocentric reference frame and the allocentric one representing space in a more cognitive way, towards the latter. This then would result in a (counterintuitive) improvement of performance.

We conducted two experiments in which we used bimanual versions of the haptic parallel-setting task in the horizontal plane (Kappers, 1999). In both experiments, a delay was introduced between the exploration of a reference bar (perception) and the parallel-setting of a test bar to the reference bar (action). Experiments by Rossetti with numb-sense patient J.A. suggest that the crucial shift from an egocentric sensorimotor representation to an allocentric cognitive one, would be between 1 and 2 seconds for the tactile modality, and about 4 seconds for the proprioceptive modality (Rossetti, 1998). Consequently, in both experiments the delay period was varied (0 s and 10 s) in order to capture the hypothesized shift from a predominantly egocentric (0 second delay) towards a more allocentric reference frame (10 seconds delay) in the deviation patterns. We expected the 10-seconds delay period to minimize the contribution of the ego-centric reference frame, and to prevent the allocentric representation from decaying. The 0-second delay period was expected to lead to the predominant employment of the egocentric frame. In addition, we examined a possible influence of the duration of the exploration period on the contribution of the reference frames in the first experiment by using both a short (1 s) and a longer exploration time (5 s). Response time (i.e. the time allowed for parallel-setting) was held constant in both experiments (1.4 s).

[1] As pointed out by an anonymous referee, the hand-centered frame might also be considered external to the body, and thus in a sense could form an allocentric reference instead. Here we will stick to the more classical approach, that whenever a part of the body is used to link features in space to, it is taken as an egocentric reference.

The aim of the first experiment was to give an overall impression of the effect of delay on the characteristics of haptic space in the horizontal plane. In the second experiment we addressed the question whether the delay effects found in experiment 1 depend on horizontal distance per se or on the positioning of the bars with respect to the body as well.

Experiment 1

Method

Design
Delay time (0 s and 10 s) and exploration time (1 s and 5 s) were varied. Response time was held constant (1.4 s). Combining these time restrictions left us with four conditions.

Apparatus
The same setup as in the studies by Kappers and Koenderink (1999) and Kappers (1999) was used. The stimuli were presented on a table with an iron tabletop (161 cm x 81 cm). It was covered by a plastic layer on which fifteen protractors (diameter 20 cm) were printed (the circles and discs in Figure 1). In the present experiment, those protractors indicated by the open circles were used. Two aluminum bars with a length of 20 cm and a diameter of 1.1 cm were used as reference and test bars. A small pin attached to the middle of the bars fit exactly into holes in the centers of the protractors. A bar placed on the table with the pin in a hole could be rotated without being displaced. Small magnets fixed to the bars were used to increase the resistance to movement (hence the use of the iron tabletop). Two magnets were fixed to the bar that acted as test bar, whereas four magnets were fixed to the reference bar. At both ends the bars were tapered off, allowing the experimenter an accurate reading of their orientation (uncertainty of about 0.5º). An Apple Macintosh computer was used to provide the time restriction signals.

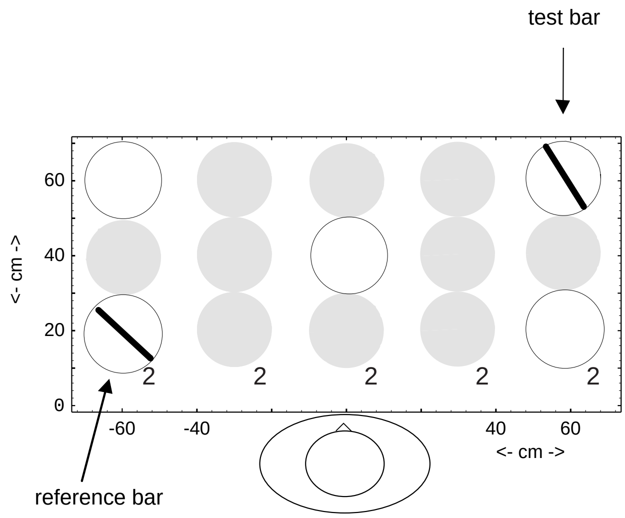


Figure 1. Top view of the table. The 5 open circles indicate the positions used in experiment 1. The 5 circles indicated by "2" were the positions used in experiment 2. The horizontal (left-right) distance between the bars in both experiments was either 60 cm or 120 cm.

Stimuli

The five locations indicated by the open circles in Figure 1 were chosen as positions for the reference and test bars to give us a global indication of the effect of delay on horizontal peripersonal haptic space. A bar on one side of the body had to be handled by the hand on that side of the body. Given the position for the reference bar, all remaining positions could be used as test bar locations, with one exception: when one of the lateral positions was occupied by the reference bar, the other lateral position on this side was not used as a test bar location, for this would lead to uncomfortable positions for the subjects. Thus, horizontal distance (which proved to have an effect on the error size in the experiments by Kappers and Koenderink (1999) and Kappers (1999)) between the bars was either 60 cm or 120 cm. The reference bar appeared randomly under one of four possible orientations in every trial: 0º, 45º, 90º, 135º (0º is parallel to the long side of the table; increasing orientation values signify a rotation in counterclockwise direction). The presentation of four orientations served above all to provide variation in the presentation of the reference bar. We expected that varying the locations and orientations of the stimuli would prevent the subjects from deducing that (only) four orientations were used as these orientations were experienced differently at different distances in the original studies. We had no particular predictions concerning the effect of orientation.

The total number of combinations was: 4 (lateral positions of reference bar) x 3 (positions of test bar locations) x 4 (reference orientations) + 1 (central reference bar location) x 4 (positions of test bar locations) x 4 (reference orientations) = 64. For each of the four conditions all combinations were presented three times in random order, adding up to a total of 192 trials per condition. The order was randomized and different for each subject. Conditions were blocked.

Subjects

Six paid undergraduates of Utrecht University (three male and three female, aged 18 - 24 years), who gave their informed consent prior to inclusion in the study, participated in the experiment. They were naive to all aspects of the task, that is, they had never seen the set-up, knew nothing about the reference orientations or locations, were unaware of the experimental purposes, and were never given any feedback. Five subjects were strongly right-handed and one female subject was strongly left-handed as assessed by means of a standard questionnaire (Annett, 1970).

Procedure

The blindfolded subjects were seated on a stool with their navels at coordinates (0,0), i.e. in front of the middle of the table. The experimenter positioned the reference bar in a predetermined orientation and the test bar in a random orientation, in this case an orientation corresponding to the orientation of the seconds-hand of his watch at that particular time. Next, he took the hand that had to explore the reference bar in that particular trial while saying (the Dutch equivalent of) "here is the reference bar" and left it to float about 5 cm above the reference bar. He then took the subject's other hand, saying "here is the test bar" and left it to float about 5 cm above the test bar. After this, the experimenter started the timed sequence. A sampled male voice uttered the numbers "one", "two", "three" and "four" in a timed sequence to indicate which action was desired from the subject. In the non-delay trials (i.e. delay time is 0s) "one" signified the start of the exploration period of the reference bar. "Two" signified both the end of the exploration period and the start of the setting of the test bar. "Three" signified the end of the setting of the test bar. In the delay trials, "one" signified the start of the exploration period of the reference bar. "Two" signified the end of the exploration period and the start of the 10-seconds delay period. At "three" the subject was required to start the parallel-setting, and "four" was the signal to terminate the parallel-setting.

Subjects had to stick to the time restrictions when they explored the reference bar with one hand, waited, or rotated the test bar with the other. In the exploration and response phase, the subjects were free in their choice of strategy but were not allowed to touch the edges of the table with their hands or arms and had to remain seated. After exploration of the reference bar, the reference hand had to be returned to the body without touching the edge of the table. The subjects were instructed to rotate the test bar in such a way that they thought it was parallel to the just felt reference bar orientation. When the subject finished the trial, the experimenter noted down the orientation of the test bar and positioned the bars for the next trial. See Figure 2 for an impression of subject actions in a delay trial.

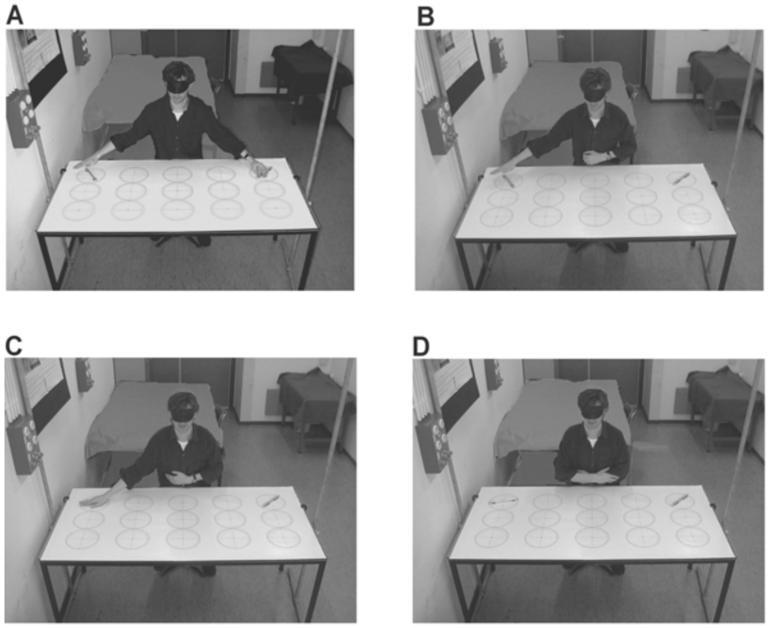


Figure 2. Figures A through D show the sequence of subject actions in a delay trial. 2A: Exploring the reference bar; 2B: 10 seconds delay period; 2C: Response; 2D: The result.

The subject was instructed to do the parallel-setting as accurately as possible, and to finish at the latest when he/she heard the last signal (either "three" in non-delay conditions or "four" in delay conditions). Occasionally 1.4 seconds turned out to be too narrow a time window to perform the parallel-setting action. These trials (approximately 5% of the trials in all conditions) were discarded and presented again at a later time during the session.

The duration of an experimental session was between 1.5 and 2.5 hours with a short break in the middle of the session to avoid weariness. Different sessions took place on different days over a period of a few weeks. Each session consisted of one condition. Before the start of every session, the subjects performed a series of 5 random practice trials to get used to the temporal sequence in which they had to perform the actions. A balanced Latin square fixed the order of conditions. All subjects took about 9 hours to complete all trials.

Data analysis

For all analyses below we computed mean signed average errors in degrees. A positive value signifies a deviation in the expected direction, i.e. the direction of the deviations found in the previous studies (Kappers & Koenderink, 1999; Kappers, 1999); a negative value expresses an error in the opposite direction. Although orientation served merely to provide variation in the reference bar presentation, we included it in our analyses as an exploratory measure.

Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction. For post-hoc testing, Bonferroni correction of the significance criterion α was applied.

Results

Figure 3 shows the average deviations for all test and reference bar combinations for all non-delay trials (lines), and the amount improvement after delay (numbers, in degrees). All these average errors (for non-delay as well as delay trials) were in the same direction as reported by Kappers (1999) and Kappers and Koenderink (1999).

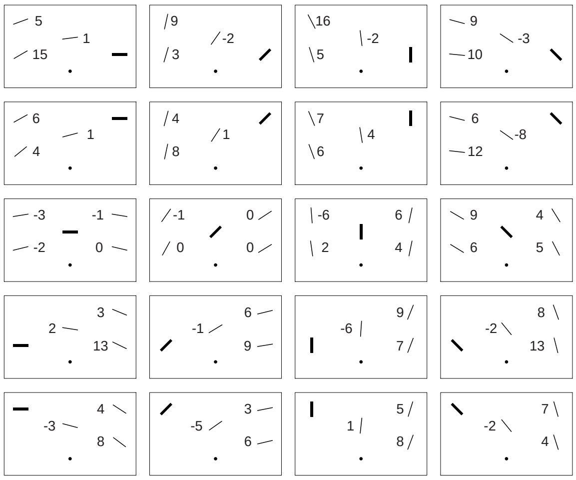


Figure 3. Representation of the average deviations in experiment 1. In each square, the thick line represents the reference bar and the dot indicates the position of the subject. The thin lines depict the average test bar orientations for all non-delay trials corresponding to that particular reference bar orientation. The numbers represent the average amount of improvement in performance after delay for that particular reference bar - test bar combination, in degrees. A negative value signifies a worsening in performance.

A 2 (delay) x 2 (horizontal distance) x 2 (exploration time) x 4 (orientation) within-subjects ANOVA was conducted for the mean signed errors. Significant main effects were found for delay: $F(1,5) = 36.5$, $p = .002$; horizontal distance: $F(1,5) = 34.9$, $p = .002$; exploration time: $F(1,5) = 7.8$, $p = .038$; and orientation: $F(3,15) = 4.7$, $p = .017$. The main effect of delay was a reduction of the size of the error, i.e. the mean signed error was 18.6° and 15.2° for non-delay and delay trials, respectively. The main effect of horizontal distance was an increase in error size for the 120-cm measurements, as compared to the 60-cm measurements: 23.1° and 10.6°, respectively. The main effect of exploration time was a reduction of the size of the error when exploration was 5 seconds, as compared to when exploration time was 1 second: 15.6° and 18.2°, respectively. The main effect of orientation was expressed in different deviations for the four reference bar orientations: 18.8°, 20.8°, 12.4° and 15.5° for 0°, 45°, 90°, and 135°, respectively. The main effect of orientation is caused by performance on reference orientations of 90° and 45°. This is verified by contrast analyses. Performance for reference bar orientations of 90°

was significantly better than performance on reference bar orientations of 0º and 45º (F(1,5) = 10.8, p = .022). In addition, performance on 45º was significantly worse than performance on 90º and 135º (F(1,5) = 16.6, p = .01. No interaction effects involving orientation were found.

An interaction effect was found for delay x horizontal distance, F(1,5) = 38.1, p = .002. A further post-hoc analysis of this interaction effect using two separate 1 (delay) x 2 (horizontal distance) within-subject ANOVA's with Bonferroni correction lowering significance criterion α to .0125 showed that delay improved performance at a horizontal distance of 120 cm, 26.4º(non-delay) and 19.8º (delay) (F(1,5) = 48.9, p = .001), but not at 60 cm, 10.7º (non-delay) and 10.6º (delay) (F(1,5) = .08, p = .79). See Figure 4. The overall pattern of Figure 4 (clear improvement at 120 cm and no or marginal improvement at 60 cm after delay) was found for all six subjects. The overall improvement at 120 cm ranged from 4.5º to 10.1º for the subjects. At 60 cm the average performance of all subjects ranged from 1.7º improvement to 1.4º deterioration.

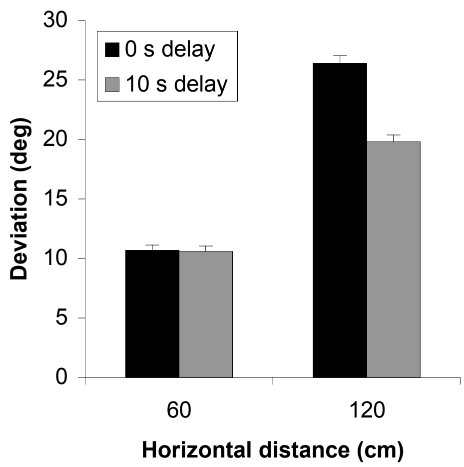


Figure 4. The differential effect of delay on deviation size in experiment 1 for both horizontal distances between bars. The error bars show +/- 1.0 standard error of mean.

Also an interaction effect was found for exploration time x horizontal distance, F(1,5) = 10.6, p = .022. A further post-hoc analysis of this interaction effect using two separate 1 (exploration) x 2 (horizontal distance) within-subject ANOVA's showed that there was a trend of improvement of performance with a 5 seconds exploration time only at the horizontal distance of 120 cm, 25.1º (1 s exploration time) and 21.1º (5 s exploration time), $F(1,5) = 13.0$, $p = .015$ and not at 60 cm, 11.2º (5 s exploration time) and 10.0º (1 s exploration time), $F(1,5) = 1.7$, $p = .25$. No interaction was found for delay x exploration, $F(1,5) = .436$, $p = .54$.

To examine possible effects of the factors delay, exploration time and horizontal distance on the variability of the data, we conducted a 2 (delay) x 2 (exploration time) x 2 (horizontal distance) within-subjects ANOVA on the mean standard deviations of 24 measurements (3 (replications) x 2 (reference hand) x 4 (orientation)). The overall mean standard deviation for this analysis was 16.6˚. A main effect of horizontal distance signified a larger standard deviation at 120 cm than at 60 cm: 19.4˚ and 13.9˚ respectively , $F = 44.6$, $p = .001$. The fact that the mean signed errors were much larger at 120 cm (23.1˚) than at 60 cm (10.6˚) might account for this difference, as one would expect that the relative variability is more of less constant. No main effects were found for delay ($F = .56$, $p = .49$) or exploration time ($F = 3.5$, $p = .121$). No interaction effects were found.

Another 2 (delay) x 2 (vertical distance) x 2 (exploration time) x 4 (orientation) within-subjects ANOVA showed that vertical distance did not significantly affect performance, $F(1,5) = 1.9$, $p = .23$. We used only the largest vertical distance (40 cm) and the smallest vertical distance measurements (0 cm) between bars for this particular analysis to keep vertical distance effects separate from horizontal distance effects: the 0 and 40-cm vertical distances are always 120-cm horizontal distances and the 20-cm vertical distance is always 60-cm horizontal. We examined the effect of delay on 40-cm and 0-cm vertical distances and 20-cm distance independently. The 2 (delay) x 2 (vertical distance) x 2 (exploration time) x 4 (orientation) within-subject ANOVA showed no interaction effects between vertical distance and delay, exploration time or orientation for 40-cm and 0-cm vertical distances between bars, nor did a 2 (delay) x 1 (vertical distance) x 2 (exploration time) x (orientation) within-subjects ANOVA for 20-cm vertical distance between bars.

Discussion of Experiment 1

The most important finding of this first experiment with regard to our hypothesis was that a delay of 10 seconds between the perception of a reference bar and the parallel-setting of a test bar improved performance. Based on our reasoning in the introduction, this improvement is interpreted as the expression of a shift in the relative contributions of an egocentric and an allocentric reference frame, towards the latter. Exploring the reference bar for 5 seconds improved performance, as compared to an exploration period of 1 second, but the effects of delay and exploration time on performance appeared to be independent. This suggests that a 5 second exploration time resulted in better encoding of the orientation, which led to better performance. The orientation of the reference bar, which was varied to provide variation in stimulus presentation, had an effect on performance as well. With 90º angles, performance was relatively spared, whereas with 45º angles it was worse. The deviations on all orientations, including those on 90º, however, were in the expected direction which suggests that all were subject to the same biasing egocentric reference frame.

Interestingly, delay improved performance only at the larger of the two horizontal distances between the bars. A similar trend of exploration time improving performance only at the larger horizontal distance was found. This suggests that the shift in the relative contributions of the egocentric and allocentric frameworks might depend on time rather than on delay, independent of enduring perception of the reference bar. In addition, it implies that the occurrence of the shift depends on horizontal distance between the bars. Another factor that could be responsible is the positioning of the bars with respect to the body; at the horizontal distance of 120 cm, either bar was on another side of the body, whereas when the horizontal distance was 60 cm, one bar was right in front of the body and the other one was at a location lateral to the body.

We thus conducted a second delay experiment in order to examine whether the shift in the relative contributions of an egocentric and an allocentric framework on performance for the two horizontal distances is due to the horizontal distance between the bars, or to the difference in the positioning of the bars with respect to the body. Since the effects of delay appeared to be independent of exploration time, and the effect of delay seems slightly more pronounced in the 1-second exploration time, we eliminated the 5-second exploration time for this second experiment.

We expected to replicate the results of our first experiment concerning the 60-cm asymmetrical and 120-cm distance conditions. In addition, we were especially interested in the interaction of horizontal distance and delay; if horizontal distance is what differentially affects performance in a delay condition, we would expect the effect of delay on 60-cm asymmetrical to be no different from the effect on 60-cm symmetrical. If the positioning of the bars with respect to the body is what matters, we would expect a significant difference of the effect of delay on the two 60-cm conditions.

Experiment 2

Method

Design, experimental set-up, apparatus, stimuli, procedure and data analysis were as in experiment 1 with a few modifications. We used the circles in Figure 1 indicated by the "2", thus leaving out the vertical distance component, for it had no significant effect on performance in experiment 1. We combined the reference and test bar positions in such a way that it left us with the following horizontal distance conditions between the bars to examine: 120 cm symmetrical to the midsagittal plane, 60 cm asymmetrical and 60 cm symmetrical to the midsagittal plane. The total number of combinations was: 4 (reference orientations) x [2 (lateral positions of reference bar) x 2 (positions of test bar locations) + 1 (central reference bar location) x 2 (positions of test bar locations) + 2 (intermediate reference positions) x 1 (intermediate test bar positions)] = 32.

Another modification was that exploration time was not varied; exploration time was 1 second for all trials. The three horizontal distances were examined in two delay conditions: condition 1 consisted of a 1-second exploration period, 0-second delay (i.e. no delay) and a 1.4-seconds response period; condition 2 consisted of 1-second exploration period, 10-second delay and a 1.4-seconds response period. For both conditions, all combinations were presented three times in random order, adding up to a total of 96 trials per condition. Each subject performed two sessions. The duration of an experimental session was about 1 hour. Subjects thus took about 2 hours to complete all trials. In each session the subjects did one half of both conditions.

Subjects

Six new paid subjects (three male and three female undergraduates of Utrecht University, aged 19-26 years), who gave their informed consent prior to inclusion in the study, participated in the experiment. Again the subjects were naive to all aspects of the task. Five subjects were strongly right-handed and one female subject was strongly left-handed as assessed by means of a standard questionnaire (Annett, 1970).

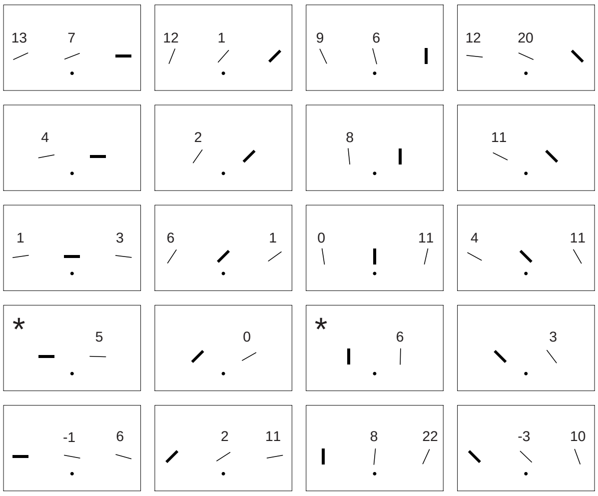


Figure 5. Representation of the average deviations in experiment 2. In each square, the thick line represents the reference bar and the dot indicates the position of the subject. The thin lines depict the average test bar orientations in the non-delay condition for that particular reference bar orientation. The numbers represent the corresponding shifts in test bar orientations after the 10 seconds delay, in degrees. A positive value represents a test bar shift after delay in the expected direction. In all reference bar - test bar combinations, except for the ones in the boxes indicated by "*", this corresponded to an improvement in performance. A negative value signifies a test bar shift after delay in the unexpected direction.

Results

Figure 5 shows that, in general, the average deviations were in the expected direction for non-delay trials, as were the shifts due to delay. A 2 (delay) x 3 (horizontal distance) x 4 (orientation) within-subjects ANOVA was carried out for the mean signed errors. Significant main effects were found for delay, $F(1,5) = 14.4$, $p = .013$, horizontal distance, $F(2,10) = 24.6$, $p = .003$, $\varepsilon = .56$, and orientation, $F(3,15) = 5.4$, $p = .01$. Delay reduced the size of the error, i.e. 15.5° and 8.8°, for non-delay and delay trials, respectively. The effect of horizontal distance reflects a difference in deviation size for the three distance conditions: 9.1° for 60 cm asymmetrical, 6.7° for 60 cm symmetrical, and 20.6° for 120 cm symmetrical. Contrast analysis showed that there is a significant difference between the two 60 cm distances and the 120 cm, $F(1,5) = 26.9$, $p = .004$, but no significant difference between the 60 cm distances, $F(1,5) = 5.8$, $p = .061$. The main effect of orientation was expressed in different deviations for the different reference bar orientations:

10.0º, 15.3º, 8.1º and 15.2º were found for 0º, 45º, 90º, and 135º, respectively. These means suggest that the main effect of orientation is particularly caused by the differences between the right and the oblique angles. Contrast analyses showed that it is particularly performance on 0º that differs significantly from performance on 45º ($F(1,5) = 7.1$, $p = .045$) and 135º ($F(1,5)= 10.4$, $p = .023$) reference bar angles. For performance for 90º angles only trends can be reported for differences from performance on 45º ($F(1,5) = 6.4$, $p = .053$) and 135º ($F(1,5) = 6.3$, $p = .051$).

In addition to these main effects an interaction effect was found for delay x horizontal distance, $F(2,10) = 8.7$, $p = .03$, $\varepsilon = .52$ (see Figure 6). Inspection of Figure 6 suggests that the effect of delay is proportionally larger for the 120-cm distance than the two 60-cm conditions. Contrast analysis showed that the difference in the reduction of the error due to delay between the shorter horizontal distances, i.e. 3.8º for 60 cm asymmetrical and 4.4º for 60 cm symmetrical, was not significant: $F(1,5)$, $p = .29$. Contrasting the reduction of the error due to delay on these 60 cm distances together with the reduction of the error size for the 120 cm distance (11.9º), indeed revealed a significant difference: $F(1,5)$, $p = .031$.

In addition paired t-tests on the mean errors revealed that the effect of delay reducing the mean signed error is significant for every horizontal distance condition. For 60 cm asymmetrical we found 11.0º (non-delay) and 7.2º (delay), with $t(5) = 2.9$, $p = .033$. For 60 cm symmetrical: 8.9º (non-delay) and 4.5º (delay), with $t(5) = 4.7$, $p = .005$. For 120 cm we found 26.5º (non-delay) and 14.6º (delay), with $t(5) = 3.5$, $p = .017$.

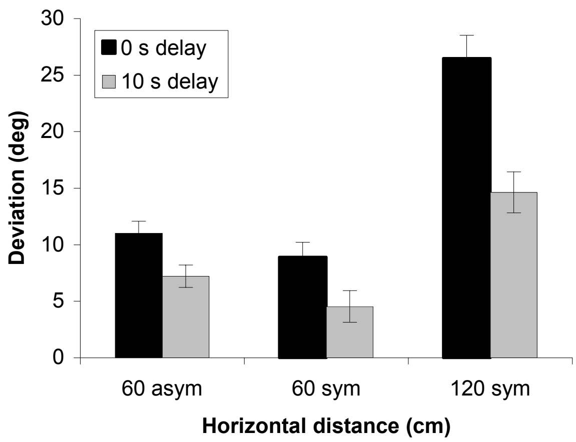


Figure 6. The effect of delay for each distance condition in experiment 2. The error bars show +/- 1.0 standard error of mean.

Another interaction effect was found for horizontal distance x orientation: $F(6,30) = 2.6$, $p = .038$. A further post-hoc analysis of this interaction effect with three separate 1 (horizontal distance) x 4 (orientation) within-subject ANOVA's with Bonferroni correction lowering significance criterion α to .0125, showed that this interaction effect was due to an effect of orientation only on the 60 cm symmetrical, $F(3,15) = 8.0$, $p = .002$. An inspection of the mean signed error sizes, suggests that there is a difference in error size for right (4.1º for 0º, and 2.8º for 90º) and oblique orientations (13.2º for 45º , 9.6º for 135º).

Discussion of Experiment 2

In experiment 2, again, delay between the perception of a reference bar and the parallel-setting of a test bar improved performance. The delay effect was now present for all distance conditions and improvement after delay at the 60-cm conditions was proportional to the improvement at 120 cm. Interestingly, we found no differential effects of delay for symmetrical and asymmetrical positioning of the bars with respect to the midsagittal plane. In short, in experiment 2 the improvement in performance after a 10-seconds delay appeared to depend on the horizontal distance between the bars.

In addition, orientation of the reference bar orientation appeared to affect performance, and it particularly did so for the 60 cm symmetrical horizontal distance. The results suggest that right angles in particular resulted in smaller deviation sizes than the oblique angles. This would imply that at this distance right angles are easier to encode or to produce, or both. At this distance, the natural orientation of the hands is more or less orthogonal to the edge of the table which might have improved the quality of encoding and / or reproduction.

Comparison and integration of Experiments 1 and 2

Superficial comparison of the results of experiments 1 and 2 suggests that somehow the effect of delay was more pronounced in experiment 2 than in experiment 1: the improvement after delay on the 120-cm distance seems to be larger in experiment 2 than in experiment 1 and whereas delay did not affect performance for 60-cm horizontal distance between bars in experiment 1, it did in experiment 2.

In order to investigate the differences and similarities between experiments 1 and 2 concerning the effect of delay, an ANOVA was performed on all data of both experiments (12 subjects) with delay and horizontal distance as within-subjects factors and experiment as between-subjects factor. To this end, the 60-cm conditions of experiment 2 were combined and treated as one condition, as were the vertical distance conditions of experiment 1, and the trials with exploration times of 1 or 5 seconds of experiment 1.

Results and discussion

A main effect of delay ($F(1,10) = 26.2$, $p < .001$) was found, which was not different for both experiments ($F(1,10) = 4.3$, $p = .065$). The main effect of horizontal distance ($F(1,10) = 60.7$, $p < .001$) was also found to be no different in the two experiments: $F(1,10) = .002$, $p = .96$. Furthermore, the interaction between horizontal distance and delay ($F(1,10) = 25.5$, $p < .001$) signifying a larger reduction of the mean signed error on the 120-cm distance as compared to the 60-cm condition, appeared to be no different for both experiments ($F(1,10) = .22$, $p = .65$). In sum, it appears that the results of both experiments concerning delay and horizontal distance are comparable.

General discussion

In the present study, we carried out two experiments to examine the effect of delay on the systematic deviations that occur in a haptic parallelity matching task in the horizontal plane. It has been suggested that the deviations are caused by the combinational use of a biasing egocentric and a more cognitive allocentric reference frame (Kappers, 2002). In both experiments we showed that a 10-seconds delay period between the perception of a reference bar and the parallel-setting of a test bar i*mproved* performance (i.e. performance became more similar to physical space), as compared to a 0-second delay. The amount of improvement depended on the horizontal distance between the bars: the larger this distance, the larger the improvement. We interpret this improvement to reflect a shift in the contributions of a biasing implicit egocentric reference frame and a more cognitive allocentric one, towards the latter during the delay period of 10 seconds (cf. Bridgeman et al., 1997; Rossetti & Régnier, 1995; Rossetti et al., 1996). In the following section we will make some suggestions concerning the mechanisms involved in this shift, integrating evidence coming from haptic and tactile studies, and studies with blind people.

It is likely that the retention of haptic information after perception requires effortful processing or is at least under conscious cognitive control. A study by Gentaz and Hatwell (1999) showed that attentional resources are indeed necessary to overcome or prevent distortions in the representation of oblique orientations. In their experiments, verbal as well as haptic interpolated tasks during delay periods of 5 or 30 seconds resulted in increased errors in reproduction of oblique orientations in the horizontal plane, whereas the 'oblique effect' was absent after unfilled delays. This has been interpreted as subjects' involvement in active rehearsal processes during the delay period. It is likely that also in our haptic parallel-setting task, effortful rehearsal processes play an important role in the retention of orientation during the delay. Yet, as in our task an *improvement* is observed after delay, we feel that rehearsal processes alone are not sufficient to explain our data.

The amount of effortful processing by the subject might not only be important in rehearsal processes, but also a prominent factor in bringing about the proposed shift. Since the allocentric representation is thought to be a conscious, more cognitive representation, its quality is likely to depend on the amount of cognitive effort in encoding and retaining the perceived orientation, as well as cognitively elaborating on its spatial representation during the delay, e.g. by relating it to other, more allocentric reference frames, or - as it could be that in haptic spatial perception egocentric referencing partly precedes generation of an allocentric frame - integrating information from egocentric reference frames in a more allocentric frame. Hence, in our task, active cognitive processing during encoding and delay periods probably results in a more veridical representation of the perceived orientation, which in turn results in an improved performance.

An intrinsic component of haptic perception in sighted people and a likely candidate to support not only rehearsal processes but also effortful encoding and elaboration processes, is visual imagery. It has been claimed that sighted persons invariably translate tactile-kinesthetic information into visual imagery (Worchel, 1951), and that haptic (and auditory) information is processed and organized in a visual map or reference frame (Pick, Warren & Hay, 1969; Pick, 1974). Selfreports by our subjects (in both experiments 1 and 2) support this idea: all subjects claimed that they tried to visualize the orientation of the reference bar. Furthermore, there is evidence for the involvement of the visual cortex in tactile tasks from both a functional imaging study (Sadato et al., 1996) and transcranial magnetic stimulation (TMS) studies (Zangaladze, Epstein, Grafton & Sathian, 1999; Cohen et al., 1997). More specifically, it has been suggested that visual cortex is involved especially in more complex, spatial tactile tasks. Zangaladze and colleagues (1999) showed that TMS applied to the occipital or lateral occipital cortex impaired performance on a task involving tactile discrimination of orientation, whereas it did not in a simple tactile detection task. As the processing of tactile spatial information is indispensable for haptic spatial representations, it is likely that visual cortex is also involved in the processing of orientation in the haptic parallel-setting task.

Integration of haptic information with a visual representation might be an important mechanism in achieving the allocentric (re)coding of this information, since a number of studies have suggested a close connection between visual and allocentric reference frames. Studies concerning spatial behavior of blind people have shown that early and congenitally blind persons do not perform as well as late blind or sighted persons specifically in tasks that are thought to require allocentric representation (Millar, 1988, 1994; Thinus-Blanc & Gaunet, 1997). In addition, it has been claimed that vision is the most appropriate modality to employ when an allocentric representation is needed, as it allows a more simultaneous perception of the (distant as well as peripersonal) environment (e.g. Foulke, 1982; Millar, 1981; Cornoldi, Cortesi & Preti, 1991). In short then, it might be that over (delay) time, visual, more allocentric representations are allowed to play a more prominent role, which results in a counterintuitive improvement in performance on our task.

In sum, we propose that the representation of orientation in a horizontal plane is based on two reference frames: an egocentric and an allocentric frame. The egocentric reference frame biases our haptic perception and / or the reproduction of orientation, whereas the allocentric reference frame is, in principle, capable of partly overcoming this biasing effect. With a 10-seconds delay between perception and action a shift seems to occur towards the allocentric representation. Future research might further focus on the mechanisms and transformations involved in this shift, as well as on the underlying neuroanatomical circuits. One of the leads to go on is the possible role of visual reference frames in the shift towards an allocentric representation. A logical sequal would be to study the performance of early and late blind people on similar haptic tasks. Another would be to interfere with visual processing by means of TMS at visual brain areas during the delay period.

References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61,* 303-321.

Appelle, S., & Countryman, M. (1986). Eliminating the haptic oblique effect: Influence of scanning incongruity and prior knowledge of the standards. *Perception, 15,* 325-329.

Bridgeman B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics, 59,* 456-469.

Cohen, L., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., & Catala, M.D. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature, 389,* 180-183.

Cornoldi, C., Cortesi, A., & Preti, D. (1991). Individual differences in the capacity limitations of visuospatial short-term memory: Research on sighted and totally congenitally blind people. *Memory & Cognition, 19,* 459-468.

Creem, S.H., & Proffitt, D.R. (1998). Two memories for geographical slant: Separation and interdependence of action and awareness. *Psychonomic Bulletin & Review , 5,* 22-36.

Dijkerman, H.C., & Milner, A.D. (1997). Copying without perceiving: Motor imagery in visual form agnosia. *Neuroreport, 8,* 729-732.

Foulke, E. (1982). Perception, cognition and the mobility of blind pedestrians. In M. Potegal (Ed). *Spatial abilities: Development and physiological foundations* (pp 55-76). San Diego, CA, USA: Academic Press.

Gentaz, E., & Hatwell, Y. (1998). The haptic oblique effect in the perception of rod orientation by blind adults. *Perception & Psychophysics, 60,* 157-167.

Gentaz, E., & Hatwell, Y. (1999). Role of memorization conditions in the haptic processing of orientations and the 'oblique effect'. *British Journal of Psychology, 90,* 373-388.

Graziano, M.S.A., Xin Tian Hu, & Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology, 77,* 2268 - 2292.

Kappers, A.M.L. (1999). Large systematic deviations in the haptic perception of parellelity. *Perception, 28,* 1001-1012.

Kappers, A.M.L. (2002). Haptic perception of parallelity in the midsagittal plane. *Acta Psychologica, 109,* 25-40.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Ládavas, E., di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience, 10,* 581-589.

Lanca, M., & Bryant, D.J. (1995). Effect of orientation in haptic reproduction of line length. *Perceptual & Motor Skills, 80,* 1291-1298.

Lechelt, E.C., Eliuk, J., & Tanne, G. (1976). Perception orientational asymmetries: A comparison of visual and haptic space. *Perception & Psychophysics, 20,* 463-469.

Lechelt, E.C., & Verenka, A. (1980). Spatial anisotropy in intramodal and cross-modal judgments of stimulus orientation: The stability of the oblique effect. *Perception, 9,* 581-589.

Lederman, S.J., Klatzky, R.L., & Barber, P.O. (1985). Spatial and movement-based heuristics for encoding pattern information through touch. *Journal of Experimental Psychology: General, 114,* 33-49.

Luyat, M., Gentaz, E., Corte, T.R., & Guerraz, M. (2001). Reference frames and haptic perception: body and head tilt effects on the oblique effect. *Perception and Psychophysics, 63,* 541-554.

Marks, L.E., & Armstrong, L. (1996). Haptic and visual representations of space. In T. Inui & J.L. McClelland (Eds.) *Attention and performance 16: Information integration in perception and communication* (pp. 263-287). Cambridge, MA, USA: Mit Press.

Millar, S. (1981) Cross modal and intersensory perception and the blind. In H.L. Pick & R.D. Walk (Eds.). *Intersensory perception and sensory integration.* New York, USA: Plenum Press.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England, UK: Clarendon Press/Oxford University Press.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* Oxford, England UK: Oxford University Press,

Milner, A.D., Paulignan, Y., Dijkerman, H.C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London. Series B, Biological Sciences, 266,* 2225-2229.

Paillard, J. (1991). Motor and representational framing of space. In J. Paillard (Ed.) *Brain and space* (pp. 163-182). Oxford, England UK: Oxford University Press.

Paillard, J., Michel, F., & Stelmach, G. (1983). Localization without content. A tactile analogue of 'blind sight'. *Archives of Neurology, 40,* 548-551.

Pick, H.L., Warren, D.H., & Hay, J.C. (1969). Sensory conflict in judgments of spatial direction. *Perception and Psychophysics, 6,* 203-205.

Pick, H.L. (1974). Visual coding of non-visual spatial information. In R.B. Macleod & H. Pick (Eds.) *Perception: essays in honor of J.J. Gibson* (pp 153-165). Ithaca, NY, USA: Cornell University Press.

Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness & Cognition: an International Journal, 7,* 520-558.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Rossetti, Y., Pisella, L., & Pelisson, D. (2000). New insights on eye blindness and hand sight: Temporal constraints of visuo-motor networks. *Visual Cognition, 7,* 2785-2808.

Rossetti, Y., & Régnier, C. (1995). Representations in action: pointing to a target with various representations. In B.G. Bardy, R.J. Bootsma & Y. Guiard (Eds.) *Studies in Perception and Action III* (pp. 233-236). Mahwah, NJ: Laurence Erlbaum Associates Inc.

Rossetti, Y., Rode, G., & Boisson, D. (1995). Implicit processing of somaesthetic information: A dissociation between where and how? *Neuroreport, 6,* 506-510.

Sadato, N., Pascual-Leone, A., Grafman, J., Ibanez, V., Deiber, M.P., Dold, G., & Hallett, M. (1996). Activation of primary visual cortex by Braille reading in blind subjects. *Nature, 380,* 526-528.

Sterken, Y., Postma, A., de Haan, E.H.F., & Dingemans, A. (1999). Egocentric and exocentric spatial judgements of visual displacement. *Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology, 52A,* 1047-1055.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-42.

Worchel, P. (1951). Space perception and orientation in the blind. *Psychological Monographs, 65,* 1-28.

Wraga, M., Creem, S.H., & Proffitt, D.R. (1999). The influence of spatial reference frames on imagined object- and viewer rotations. *Acta Psychologica, 102,* 247-264.

Zangaladze, A., Epstein, C.M., Grafton, S.T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature, 401,* 587-590.

Chapter 3 | Effects of hand orientation and delay on the verbal judgment of haptically perceived orientation

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2005). *Perception, 34*, 741-755.

Abstract

The current study examined the haptic perception of single bar orientations throughout the horizontal plane using a verbal response: participants were to assign a number of minutes to a bar orientation defined with respect to the stimulus table. Performance was found to be systematically biased. Deviations were consistent with, yet much smaller than those resulting from haptic motor matching tasks. The size and direction of the deviations were found to correlate with hand orientation, and not to depend on spatial location per se, suggesting a role for hand-centered reference frames in biasing performance. Delaying the response by 10 seconds led to small improvement of only right hand perceptions, indicating different hemispheric involvement in processes involved in retaining and/or recoding of haptic orientation information. Also the haptic oblique effect was found with the current verbal response. Importantly, it was not affected by hand orientation nor by delay, suggesting the oblique effect to be independent of the aforementioned deviations in orientation perception.

Introduction

The haptic sense provides us with essential information about the spatial layout of the world surrounding us, especially when we lack visual input. Interestingly, our haptic perception of various spatial properties like line length (Lanca & Bryant, 1995; Marks & Armstrong, 1996), path length (Lederman, Klatzky & Barber, 1985) and orientation (e.g. Blumenfeld, 1937; Appelle & Countryman, 1986; Gentaz & Hatwell, 1998, 1999; Lechelt, Eliuk & Tanne, 1976; Lechelt & Verenka, 1980; Luyat, Gentaz, Corte & Guerraz, 2001) has been shown to be liable to distortions. Most studies dedicated to the haptic perception of orientation have concentrated on the factors involved in the so-called haptic "oblique effect", a distortion in the haptic (re)production of orientation characterized by larger variability for oblique orientations as compared to vertical and horizontal orientations. In these studies, typically, the location of the stimuli in peripersonal space is regarded as irrelevant. Fairly recently, however, it has been suggested that the location of a stimulus systematically affects the perception of its orientation: Kappers and Koenderink (1999) and Kappers (1999, 2002, 2003) demonstrated that blindfolded subjects instructed to rotate bars until they are parallel or collinear, make consistent matching errors that vary systematically in magnitude and direction throughout peripersonal space. As this sort of matching tasks requires a *relative* motor judgment, the question whether the *absolute* perception of a single bar orientation also depends on its spatial location, still goes unanswered.

To address the question of where the systematic distortions resulting from haptic matching tasks come from, recent studies have focused on the tasks' requirements and on analyses of the deviation patterns. With respect to the task requirements of haptic parallel- or collinear setting, it has been suggested that perfect performance on these tasks require allocentric (or extrinsic) representation, as veridical performance is achieved when reference and test bar(s) are in the same orientation within physical space. Biases in performance then are likely to result from distortions in egocentric referencing. Analyses of deviation patterns support this assumption (Kappers, 1999, 2002, 2003): the deviation patterns can be adequately described by the use of a reference frame intermediate to an allocentric reference frame and an egocentric reference framework comprising the hands and/or the trunk. Moreover, recent experimental evidence has provided further support for the employment of both an egocentric and an allocentric framework: presenting subjects with a 10-seconds delay between the perception of the reference bar and the parallel-setting of the test bar led to an *improved*, but still biased, performance (Zuidhoek, Kappers, Van der Lubbe & Postma, 2003). We have interpreted this improvement to reflect a shift from an egocentric towards a more allocentric spatial representation over delay time, similar to findings of several visual and proprioceptive spatial studies (cf. Bridgeman, Peery & Anand, 1997; Milner, Paulignan, Dijkerman, Michel & Jeannerod, 1999; Rossetti, Thinus-Blanc & Gaunet, 1996; Rossetti & Régnier, 1995). Delayed performance being still egocentrically biased, suggests an egocentric-allocentric continuum rather than a binary spatial coding system.

Although the aforementioned studies provide evidence that performance on haptic matching tasks is based on the combined use of ego- and allocentric reference frames, the identity of the egocenters making up the biasing egocentric reference frame has not yet been established. Considering the characteristics of the deviation patterns, it seems that two plausible egocentric reference frameworks may be considered. The first is one in which the orientation of a bar is related to the body of the subject, as the deviation patterns seem to revolve around the body. Interestingly, the body has also been implicated to be involved in the other known distortion in haptic orientation representation, the haptic oblique effect: a recent study suggests that it depends on a subjective gravitational reference frame comprising an allocentric gravitational reference frame and body- and head-centered reference frames (Luyat et al., 2001). Dependence of the location-based distortion on a body-centered reference frame may be indicative of a relationship between the two distortions.

A second plausible egocentric reference framework that may be involved in biasing haptic matching performance is one centered on the hand(s) with which the bars are perceived and rotated: it seems that, if, for example, a matching error at a particular location is in clockwise direction, the hand at that particular location is rotated clockwise with respect to that of the hand at the reference bar location. Moreover, the size of the deviation has been shown to depend on the distance between the bars, which is directly related to the orientation difference between the hands (Kappers, 1999, 2002, 2003).

Based on the foregoing, one could argue that to perform well on tasks that require absolute representation of space, the influence of biasing egocentric frames needs to be minimized. One way of doing this would be by removing response-related egocentric frames by choosing, for example, a verbal response. Another would be to increase the relative contribution of the allocentric reference frame, by stimulating its use or increasing its strength. As stated above, this can be achieved by delaying the response in motor matching tasks (Zuidhoek et al., 2003).[1] The responsible mechanism and whether the effect of delay also occurs in haptic spatial tasks other than motor matching tasks is unknown, however.

Interestingly, there are some indications that (mental) visual processing may play an important part in both producing or facilitating the shift in reference frame contributions, and in allocentrically representing (haptic) space in general. For example, in the proprioceptive modality, the transition from egocentric to allocentric representation has been found to depend on early visual experience (Rossetti et al., 1996). In general, late-blind and sighted subjects have often been found to outmatch congenitally blind subjects specifically on spatial tasks requiring an allocentric representation (Millar, 1988, 1994; Thinus-Blanc & Gaunet, 1997). Moreover, it has been shown that simply letting subjects view the region of peripersonal space directly above the workspace also improves haptic parallel-setting (Newport, Rabb & Jackson, 2002; Zuidhoek, Visser, Bredero & Postma, 2004). Interestingly, mental models based on visual imagery have been suggested to account for the haptic oblique effect (Appelle & Countryman, 1986; Appelle & Gravetter, 1985). In contrast, however, Gentaz and Hatwell (1998) found early visual experience to have no effect on the haptic oblique effect in a study with early and late blind participants.

The current study focused on the reference frames involved in the absolute haptic perception of a single bar orientation throughout peripersonal space. We examined the unimanual haptic perception of a single bar orientation in four locations in peripersonal space. By letting an orientation at a particular location be perceived by both the right and the left hand without changing the body's position and posture, we were able to study the influences of hand orientation and that of stimulus position with respect to the body on perception. As we reasoned that the customary motor response would trigger an egocentric representation of the bar, and may lead to response-related egocentric biases while we were interested in the absolute perception of orientation, we chose a *verbal* response in contrast to all previous studies on haptic orientation perception: blindfolded participants assigned a number of minutes on an imagined clock to the orientation of a perceived bar orientation (cf. Haber, Haber, Penningroth, Novak & Radgowski (1993), who had blind people use this verbal response to indicate the egocentric direction to auditory

[1] Note: An alternative view on attenuating distortions in haptic perception - namely by instructing the explicit use of body-centered reference frames - has recently been put forward (e.g. Millar and Al Zatar, 2002). This view will be shortly discussed in Discussion.

targets). The orientation of a bar was defined in relation to an extrinsic, allocentric frame of reference, namely the stimulus presentation table. Although, arguably, using a verbal response may introduce new, unknown biases, we would expect these to be independent of spatial location or hand use as they would arise from the process of relating the input to the image of a clock face and not from the perception of the orientation itself.

Our first goal was to establish to what extent hand- and body-centered reference frames are involved in the absolute haptic perception of a single bar orientation in the horizontal plane. We expected performance to reveal systematic biases throughout the horizontal plane consistent with the aforementioned matching studies. With respect to a *body-centered* reference frame biasing perception, the aforementioned matching studies would predict orientations presented left from the midsagittal plane to result in a clockwise perceptual bias (corresponding to an overestimation of the presented number of minutes), whereas orientations presented to the right would lead to a bias to perceive the bar as if rotated counterclockwise from their true orientation (i.e., an underestimation of the presented number of minutes). The biases would be independent of hand use and hand orientation. In case of a *hand-centered* reference frame biasing perception, however, the perception of a bar orientation at a particular location would depend on the orientation of the hand at that particular location, with hands pointing leftward from alignment with the midsagittal plane resulting in clockwise perceptual deviation (overestimation of the number of minutes), and hands pointing rightward of midsagittal plane alignment resulting in a counterclockwise perceptual deviation (underestimation). With deviation size totally depending on hand-midsagittal plane misalignment, a linear relationship between the two would be expected, with deviations becoming larger with larger hand-midsagittal plane misalignment.

A second goal was to shed light upon the role and characteristics of an *allocentric* reference frame in the absolute perception of the orientation of a single bar throughout peripersonal space. More specifically, we examined the possible shift in the relative contributions of ego- and allocentric reference frames with a delay between perception and response. With the orientation explicitly defined in an allocentric reference frame (i.e., the stimulus table), and the verbal response minimizing the egocentric reference frame involvement, we expected performance to be relatively spared, and thus leaving less room for improvement with delay as compared to matching tasks (cf. Zuidhoek et al., 2003). As a consequence, we would predict improvement with a 10 seconds delay to be attenuated or even absent. In addition, we anticipated that performance may depend considerably on (visuo)spatial imagery ability since the verbal response required the translation of the haptic input to a (visuo)spatial image of a clock, which – as discussed above –in turn may affect the ability to form an allocentric reference frame as well. To investigate this, we assessed this ability with a revised version of the mental clock test introduced by Paivio (1978) – which also requires the imagery of clock faces - , and correlated it to performance on the main task, which we coined the verbal judgment (of haptic orientation perception) task.

A further interest concerned the oblique effect. Importantly, the present study was the first to examine the oblique effect with a verbal (i.e., a non-motor) response. In other words, we were able to address the question whether the haptic oblique effect as reported in former studies is indeed caused by a bias in perception and not merely by egocentric frames involved in performing and feeding back the motor response. Delaying this verbal response may have different effects than delaying a motor response (which - with unfilled delays - has been found not to affect performance (Gentaz & Hatwell, 1999)), since a motor response may stimulate movement coding and motor memory, whereas the current verbal response may stimulate (visuo)spatial imagery. In addition, the present study allowed us to examine the oblique effect systematically throughout peripersonal space, which should be informative not only with respect to the haptic oblique effect phenomenon in general, but also to its possible relationship to the systematic distortion of haptic orientation perception throughout peripersonal space. Furthermore, relating haptic oblique effect size to visuospatial imagery ability could provide valuable information concerning the role of mental orientation models based on visual imagery in the haptic oblique effect (cf. Appelle & Countryman, 1986; but see Gentaz & Hatwell, 1998).

General Method

Participants

Sixteen paid undergraduates of Utrecht University (eight male, eight female, 19 - 25 years of age, all native Dutch speakers) participated. They were naive to all aspects of the tasks, i.e., they were unaware of the experimental purposes, had never seen the haptic setup, knew nothing about the orientations or locations used, and were never given any feedback. All were right-handed as assessed by means of a standard questionnaire (Annett, 1970; all scores > +10).

Procedure
The experiment consisted of 2 sessions. The duration of an experimental session was about 1.5 hours including a short break in the middle to avoid weariness. Different sessions took place on different days. The participants were first tested on the mental clock test. This took about five to ten minutes. After this they were presented with the first of two sessions of the verbal judgment of orientation perception task.

Verbal judgment of orientation task

Design
The experiment had a within-subjects design and comprised two conditions, i.e. immediate and delayed judgment of haptically perceived orientation (resp. 0s and 10s delay). Haptic exploration time (1s) and verbal response time (1.4s) were held constant[1]. These time restrictions for exploration, delay and response, were the same as in Zuidhoek et al. (2003), parallel-setting experiment 2. Hand use (2), stimulus location (4) and bar orientation (8) were varied, resulting in a total number of combinations of 64 per condition. For both conditions (0 or 10 seconds delay between perception and response), all combinations were presented three times in random order, adding up to a total of 192 trials per condition. The order of presentation was random and different for each subject.

Apparatus
A table with an iron table top covered by a plastic layer (depicted in Figure 1) was used for stimulus presentation. The stimuli were four aluminum bars with a length of 20 cm and a diameter of 1.1 cm presented on the four protractors (diameter 20 cm) indicated by the circles in Figure 1. A small pin attached to the middle of a bar fitted exactly into the hole in the center of a protractor. Small magnets attached to the bars increased their resistance to movement. At both ends the bars were tapered

[1] Note: A relatively short haptic exploration time was chosen (1s) in order to capture a possible shift from egocentric towards more allocentric reference frames involvement over time. One might argue that this exploration period is too short to lead to reliable response behavior or to be called 'normal' haptic exploratory behavior. In a previous haptic parallel-setting study, however, 1s exploration periods were found to provide a clearer delay effect than 5s exploration periods, without affecting the variability of the data (Zuidhoek et al., 2003). This suggests that a haptic exploration period of 1s suffices to generate a representation of orientation.

off, allowing the experimenter an accurate reading of their orientation (uncertainty of about 0.5º). An Apple Macintosh computer was used to provide the time restriction signals.

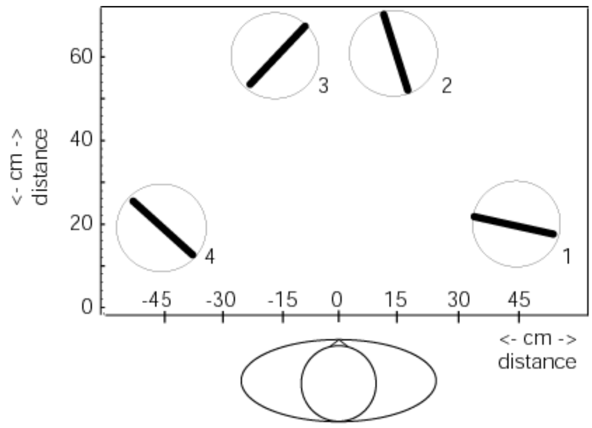


Figure 1. Top view of the experimental set up of the verbal judgment of haptic orientation experiment. The 4 circles indicate the stimulus positions.

Stimuli

The four positions indicated by the open circles in Figure 1 were chosen as stimulus locations. Stimuli on these locations were explored unimanually by either hand. The bars appeared under one of eight possible orientations, in random order. The orientations were chosen in such a way that they corresponded to whole minutes. In addition, we made sure they did not correspond to multiples of 5 minutes to avoid response biases affecting the data. The following minutes were presented: 1, 4, 8, 12, 16, 19, 23, 27, corresponding to the following orientations of 84º, 66º, 42º, 18º, 174º, 156º, 132º, 108º (where 0º is parallel to the long side of the table, and on the right side of a protractor (participant's perspective); increasing orientation values signify a rotation in counterclockwise direction).

Procedure

The subjects were blindfolded and seated on a stool in front of the stimulus presentation table as depicted in Figure 1. They were told that they were sitting at a table and that they were about to repeatedly feel the orientation of a bar on different locations on the table with either their left or right hand. They were instructed to keep their exploring limb in a natural position and to think of the felt bar as the minutes hand of a clock, and to assign a number of minutes to its orientation. They were told that all ‘clocks’ on the table were positioned in such a way that when the minutes hand signified 15 minutes (or 45 minutes), it was parallel to the side of the table they were sitting on. To make sure that they understood this, the subjects were asked to place a pen on a table in the orientation corresponding to 15 and 45 minutes. They were instructed to respond as accurately as possible in whole minutes within a response range of 0 to 60 minutes.

Before the start of a trial, the experimenter positioned the bar in a predetermined orientation. Next, he took the hand with which the bar was to be perceived in that particular trial, saying (the Dutch equivalent of) "here is the bar" and left it to float about 5 cm above the bar. After this, the experimenter started the timed sequence. A sampled male voice uttered the numbers "one", "two", "three" and in delay trials also "four" in a timed sequence indicating which action was desired from the subject. In non-delay trials (i.e. delay time is 0s) "one" signified the start of the 1-second exploration period of the bar. "Two" signified the end of the exploration period and also the start of the period in which the verbal response had to be given. "Three" signified that the response period (1.4s) was over. In delay trials, "one" again signified the start of the exploration period of the bar. "Two" signified its end and the start of the 10-seconds delay period. Between the counts of "three" and "four" the response had to be given (1.4s).

Subjects had to obey the time restrictions when exploring the bar, waiting, or verbally responding. In addition, they were not allowed to touch the edges of the table during the trials and had to remain seated the way they were. In between trials they were allowed to touch the table to check their positioning with respect to the table, which happened only occasionally. Trials in which these restrictions were not met, as checked by the experimenter, were presented again at a later time during the session (approximately 5% of the trials). Subjects were free in choice of strategy when exploring the bar. In practice, subjects would press the hand on the bar and make a couple small finger, hand and arm movements. Occasionally, this was followed by a quick hand movement over the bar. After exploration of the bar in delay trials, the reference hand had to be returned to the body. After the subject had finished the trial by giving his verbal response, the experimenter noted it down and both continued with the next trial. After the very last trial, orientations of the left and the right hand of the (still blindfolded) subject were measured on all four positions, in order to be able to examine the effect of hand-midsagittal plane misalignment on deviation size.

The task was split up over two session. In each session, one half of both delay conditions was presented. Within a session, conditions were blocked. The sequence of conditions in the first session, was reversed in the second. Before the start of every new block, the subjects performed a series of 5 random practice trials to get used to the temporal sequence in which they had to perform the different actions.

Data analysis for establishment of egocentric reference frame involvement

For our analyses, we computed mean signed errors in minutes. A positive value signified an overestimation of the number of minutes on the haptically perceived clock, expressing the perception of the orientation of bars as if rotated clockwise from their 'true' orientations; a negative value signified an underestimation, expressing the perception of the orientation of bars as if rotated counterclockwise from their true orientations. As responses that were 15 minutes (i.e. 90º) off could signify an overestimation as well as an underestimation we had the intention to remove these responses from the analyses. In practice, no such responses were given. Comparative analyses necessary to discern between body-centered or hand-centered coding were planned. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction.

Data analysis oblique effect

Our stimuli did not contain purely horizontal (0°), vertical (90°) or "ideal" oblique (45°, 135°) orientations, as stimulus orientations corresponding to multiples of five minutes (0°, 90°) could have led to response biases, and 45° and 135° do not correspond to whole minutes (7.5 min and 22.5 minutes, respectively). However, the orientations we did use deviated only to a small amount from the "ideal" horizontal, vertical and oblique orientations. To examine whether the oblique effect holds for verbal judgments of haptically obtained orientation information, the four orientations closest to the horizontal (i.e. 174° and 18°), vertical (84° and 108°) and those four closest to the ideal oblique orientations (42°, 66°, 132° and 156°) were taken together to form groups of horizontal-vertical and oblique orientations, respectively, corresponding to the factor orientation type. For the analyses, mean *standard deviations* (sd, in minutes) were computed, to assess the variability for these orientation groups. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction.

Mental clock test

Procedure

Subjects were asked to imagine analogue clock faces of auditorially presented pairs of times, and judge which of these clock faces shows the greater angle between the hands. They were instructed to consider only the angles smaller than 180° and to respond as quickly and accurately as possible. Before the experiment started, they were to place their left index finger on the "f" and their right on the "j" on the keyboard of the computer. When the experiment started they closed their eyes to avoid visual distraction and interference. They had to push the "f" if the first mentioned time formed the greater angle, or the "j" for the second. Immediately after a key press, the next stimulus was presented.

Stimuli and apparatus

The stimuli were presented by a male voice, which had been recorded. The sound samples were of equal length (2.48 s), and represented 48 pairs of times involving only half-hours and whole hours (cf. Trojano et al 2000). Each stimulus consisted of clock times resulting in angles of different sizes on an analogue clock face. A number of measures was taken to discourage the use of strategies other than imagery (like mathematical, verbal or other) to decide which of the two angles was the greater. All 24 clock times were included and presented equally often, i.e., four times: twice as the first and twice as the second of a pair. In half of the trials, the numerically greater time of the pair showed the greater angle (e.g. 4 o'clock vs. 2 o'clock); consequently, in the other half the numerically smaller time corresponded to the greater angle (e.g. half past 2 vs. 9 o'clock) (cf. Trojano et al., 2000). The times were balanced for the side of the clock face on which the hands had to be imagined (cf. Trojano et al., 2000): for 12 pairs only the right side of the clock had to be imagined; for another 12 only the left; for the remaining 24, both sides of the clock had to be imagined. In the original paper, Paivio (1978) chose to present participants with 5 (30º, 60º, 90º, 120º, 150º; experiment 1) or 4 (30º, 60º, 90º, 120º; experiment 2) orientation differences. In the present study, meeting the criteria to minimize the use of strategies other than imagery inevitably resulted in 12 orientation differences with an unequal number of repetitions, with a maximum of 7 and a minimum of 1 repetitions (see Table 1).

Each subject was presented with the same randomized stimulus sequence. An IBM-compatible computer was used for auditory stimulus presentation as well as data collection. The stimuli were presented through earphones. Response time (RT) and accuracy were logged for each stimulus.

Data analysis mental clock test and correlation with verbal judgment task.
According to Paivio (1978), who interpreted his mental clock test as a psychophysical task, good imagery ability yields fast responses that show an inverse relationship with the orientation difference between the angles of the two clocks. Participants not showing this inverse relationship can not be considered to have purely used imagery to perform the task, and thus are likely to have used other strategies or have been guessing. Response accuracy is typically ignored in the mental clock test unless error rates are higher than 25 %, a common psychophysical criterion for discrimination threshold in dichotomous choice situations (Paivio, 1978), which reflects guessing and, in this case, very low imagery skills.

To evaluate the imagery ability of participants, we used Paivio's criteria concerning the inverse relationship between response time and orientation difference, average response time and response accuracy. To level equalize the number of repetitions per orientation difference, we created 3 orientation difference categories: small orientation difference (OD) (OD $<$ 60°; 15 repetitions), intermediate (60 $\leq$ OD $<$ 120; 18 repetitions), and large (OD $\geq$ 120°; 15 repetitions), respectively (see Table 1). The relationship between orientation difference category and correct reaction times was examined for every subject using a Spearman rank correlation. Participants showing a significant negative correlation between orientation difference category and reaction times to correct responses were considered imagers. Participants not showing this significant correlation were considered non- (or inconsistent) imagers, and were ranked lower than imagers by definition. Both imagers and non-imagers were ranked using mean response time, within their groups. The lower the mean response time, the higher the ranking. Participants with an error rate higher than 25% (i.e., more than 12 errors) were ranked lower than participants with an error rate lower that 25%, without further ranking on the basis of response time.

To investigate whether performance on the verbal judgment of haptic orientation task is related to visual spatial mental imagery abilities, we correlated the mean signed deviation sizes of participants on the verbal judgment of orientation task to their imagery ability ranking resulting from the mental clock test. In addition, we correlated the mean oblique effect sizes of participants (def. as mean sd for horizontal-vertical orientations minus mean sd for oblique orientations) to their ranking on the mental clocktest. For both analyses, a Spearman rank order correlation was computed.

Table 1. The orientation differences (ODs) occurring in the mental clock task, their number of repetitions and their categorization into three OD-categories: small, intermediate and large.

Or. difference	Nr. of repetitions	OD-Cat.
15°	6	small
30°	7	small
45°	2	small
60°	5	interm.
75°	4	interm.
90°	5	interm.
105°	4	interm.
120°	2	large
135°	4	large
150°	4	large
165°	4	large
180°	1	large

Results

Verbal judgment task

Egocentric reference frame involvement

A 2 (hand) x 4 (positions) x 2 (delay) x 8 (orientation) within-subjects ANOVA was conducted for the mean signed errors. Only one main effect was found: position affected judgment of orientation, $F(1.3,19.3) = 7.0$, $p = .011$, $\varepsilon = .429$, which was expressed in the following mean signed errors for the four positions: $M_{pos1} = -.68$, $M_{pos2} = -.09$, $M_{pos3} = .199$, $M_{pos4} = .917$. No main effect of hand was found, suggesting that performance had been equally good for both hands. Yet, an interaction effect was found for hand x position, $F(3,45) = 5.5$, $p = .003$, which suggests that differences in performance found for the positions can be explained by hand use (see Figure 2).

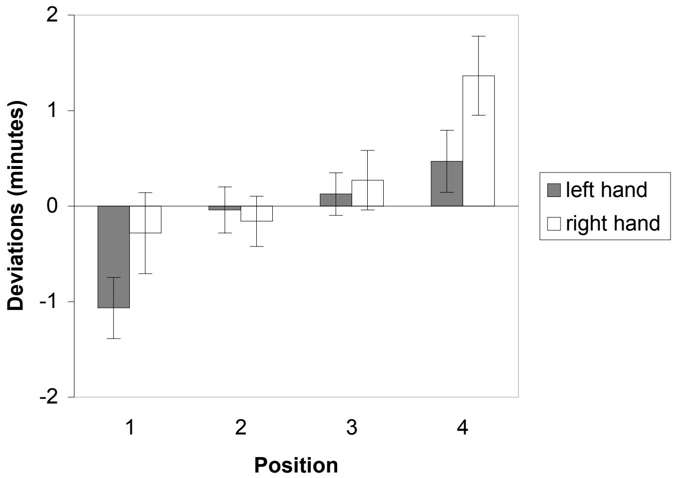


Figure 2. The interaction effect of hand x stimulus position on deviation size. Error bars show +- 1.0 standard error of mean. The main effect of position depends on hand (orientation).

Visual inspection of Figure 2 suggests that particularly the right hand at position 4, and the left hand at position 1 were responsible for this interaction effect. Analysis of the interaction using four paired-samples t-tests showed that hand had an effect at positions 1 ($t(15) = -2.3$, $p = .033$) and 4 ($t(15) = -2.3$, $p = .034$), and not at positions 2 ($t(15) = .5$, $P = .64$) and 3 ($t(15) = -.4$, $p = .7$). As shown in Table 2, at positions 1 and 4, the orientation difference between the hands is particularly large.

Table 2. Average hand-midsagittal plane misalignments for the left and right hand on the four stimulus positions over all subjects in degrees. Hand orientations misaligned to the left were attributed a positive sign; rightward hand-midsagittal plane misalignments were attributed a negative sign.

Position	Left hand	Right hand
1	-63	-19
2	-14	-6
3	8	16
4	22	61

Moreover, as the large deviations seem to result from large hand-midsagittal plane misalignment, these results suggest a positive relationship between hand-midsagittal plane misalignment and deviation size which was expected in case of hand-centered reference frame use. We addressed this relationship by computing the Pearson correlation between hand-midsagittal plane misalignment and mean deviation size (both hands on all four locations for all subjects): $r = .471$, $p < .000$, which indicates a moderate, yet obviously linear relationship between hand orientation and deviation size (see Figure 3).

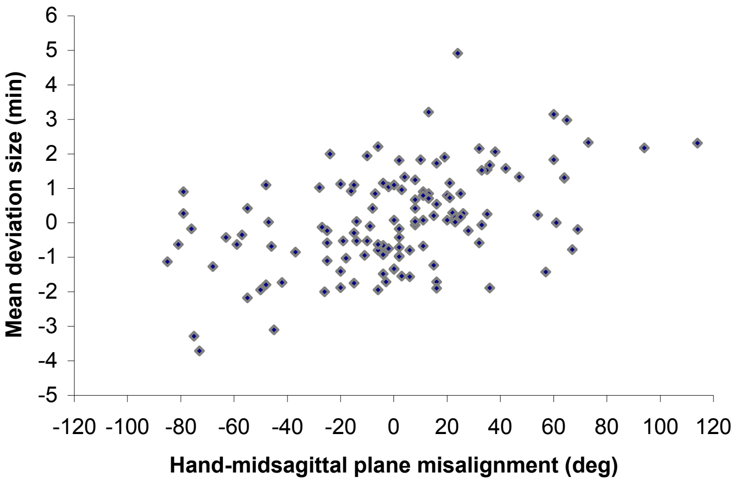


Figure 3. The relationship between hand-midsagittal plane misalignment and mean deviation size. Every dot represents the mean deviation size on one of the four stimulus locations for either right- or left hand performance of a particular subject plotted against the hand orientation of that subject on that location. Hand orientations misaligned to the left were attributed a positive sign; rightward hand-midsagittal plane misalignments were attributed a negative sign.

Interestingly, no main effect of delay was found. Yet, an interaction effect was found for hand x delay, $F(1,15) = 6.1$, $p = .026$, indicating that the effect of delay on mean signed error is different for right and left hand perceptions. Further examination of this interaction indicates that there is an effect of delay for right hand perceptions ($M_{\text{non delay}} = .48$, $M_{\text{delay}} = .12$; $t(15) = 2.4$, $p = .033$), and not for left hand perceptions ($M_{\text{non delay}} = -.12$, $M_{\text{delay}} = -.14$; $t(15) = .24$, $P = .81$), with delay bringing right hand perceptions up to left hand performance level.

Furthermore, a position x orientation ($F(21,315) = 5.3$, $p < .001$) interaction and a hand x position x orientation interaction ($F(21,315) = 3.1$, $p = .037$) were found, suggesting that orientations were judged differently at different positions due to hand use, and thus hand orientation. Figure 4 shows the interaction effect of hand x position x orientation. It suggests that the hand x position effect is mainly due to different performance for the hands on the orientations 18°, 42°, 66° and 84° at position 1, and the (more or less) corresponding orientations 108°, 132° and 156° at position 4. No further interaction effects were found.

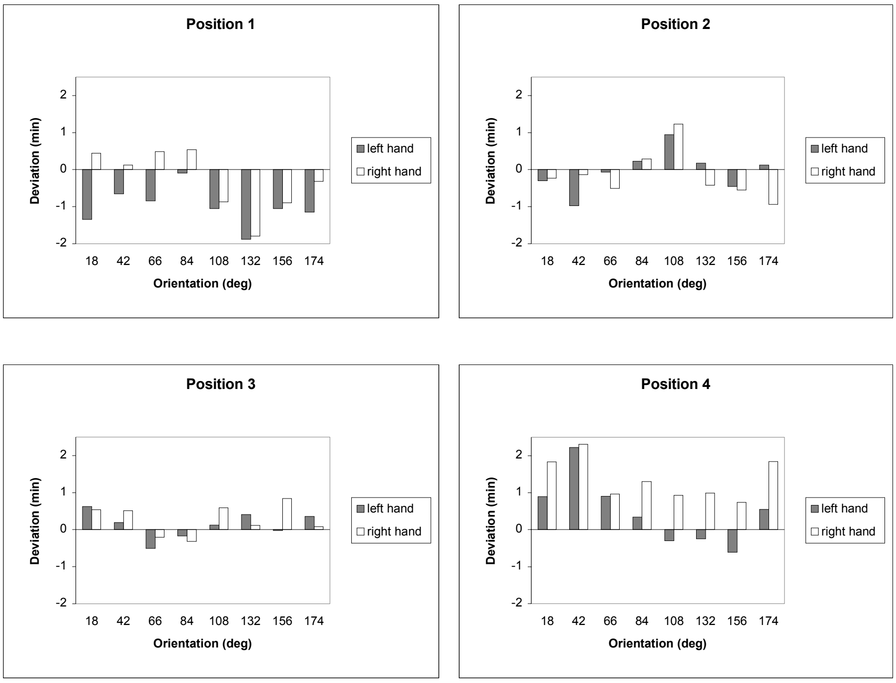


Figure 4. The hand x position x orientation interaction effect. Error bars are left out for reasons of clarity. The hand x position effect seems particularly due to different performance for the hands on the orientations 18°, 42°, 66° and 84° at position 1, and the (more or less) corresponding orientations 108°, 132° and 156° at position 4.

Oblique effect

A 2 (orientation type) x 2 (delay) x 2 (hand) x 4 (position) within-subjects ANOVA was performed on the mean standard deviation of the signed errors. The mean standard deviation for this analysis was 2.4°. A main effect for orientation type was found ($F(1,15) = 12.5$, $p = .003$) which signified a larger standard deviation for oblique orientations than for horizontal-vertical orientations: 2.6° and 2.3°, respectively, which corresponds to the classic oblique effect. In addition, a main effect of position was found, $F(1,15) = 6.0$, $p = .002$, signifying a location dependent difference in standard deviation size. Inspection of the means suggests that this effect is rooted in differences between the standard deviations at positions 1 and 4 and those at positions 2 and 3: $M_{pos1} = 2.6°$, $M_{pos2} = 2.2°$, $M_{pos3} = 2.3°$, $M_{pos4} = 2.6°$. No significant main effects were found for delay ($F(1,15) = .1$), and hand. However, the effect of hand did show a trend towards more variable performance with the right hand as compared to the left ($F(1,15) = 4.3$, $p = .055$), as expressed in mean standard deviation size ($M_{right} = 2.5°$, $M_{left} = 2.3°$). Importantly, no interaction effects were found, indicating that the oblique effect found, as expressed by the main effect of orientation type, was not modified by the other investigated factors.

Mental clock test and correlations with verbal judgment task

Table 3 shows the data used to rank participants. The participants ranked 1 through 7 were considered imagers according to the criteria explained in the data analysis section of the mental clock test. Participants ranked 8 through 15 were considered to be non-imagers or inconsistent imagers. Imagers as well as non-imagers were ranked on the basis of mean RT within their groups. One subject had an error rate higher than 25% (29%, 14 errors) and was ranked 16 for this reason.

To investigate whether performance on the verbal judgment of haptic orientation task was related to visuospatial mental imagery ability, we intended to correlate the rank score on the mental clock test to the mean signed deviation size on the verbal judgment of orientation task and to mean oblique effect size, as explained in the clock test's data analysis section. However, as right and left hand performance had led to differently signed errors on average (see also Figure 2), the mean deviation sizes (comprising both left and right hand performances) were close to zero. Considering the size of the deviations found for both hands, this would be no adequate reflection of verbal judgment task ability. Since oblique effect size

Table 3. The ranking of subjects on mental clock test performance. A low ranking number signifies high visual spatial imagery abilities; a high ranking number signifies low imagery abilities. For every subject, mean response times (RTs, in ms) for small, intermediate and large orientation differences (ODs), overall mean RTs, Spearman rank correlation coefficient, its P-value, group assignment (imagers = 1, non-imagers = 2), and number of errors are shown.

Ranking	RT_{small}	RT_{interm}	RT_{Large}	R_s	$P_{(Rs)}$	Group	Mean	Nr of err
1	5043	3763	4243	-0,28	0,041	1	4278	7
2	5246	4368	4256	-0,28	0,033	1	4579	5
3	5078	5093	4248	-0,29	0,033	1	4822	7
4	5602	4890	4639	-0,37	0,007	1	5012	3
5	6652	5263	4994	-0,32	0,018	1	5563	5
6	8218	6376	6319	-0,28	0,029	1	6918	2
7	9701	8575	6635	-0,26	0,046	1	8254	3
8	4048	4154	4082	0	0,496	2	4104	7
9	4209	4498	4107	-0,1	0,27	2	4287	7
10	4383	4441	4335	-0,04	0,416	2	4394	12
11	4899	5136	4900	0,03	0,433	2	4999	10
12	6710	5628	5560	-0,18	0,14	2	5902	8
13	5810	6901	5720	-0,04	0,397	2	6176	7
14	6360	6920	6617	0,02	0,454	2	6656	1
15	10643	11715	9013	-0,16	0,163	2	10623	10
16	4457	5189	4335	-0,12	0,247	2	4690	14

deals with standard deviations, which are always positively signed, the problem was specific to the mean deviation sizes. To provide a more meaningful measure for mean deviation size, left-hand errors were recoded into right-hand errors by changing their sign before computing the mean deviation size. This way, participants with a positively signed mean deviation reflected hand-related biases. Considering the allocentric frame as a counterweight to the egocentric frame as explained in the introduction, participants showing a negatively signed mean deviation should be interpreted to have performed allocentrically, and should be expected to do well on the mental clock test.

The Spearman rank order correlation (one-tailed), $r_S = .40$, $p = .06$, showed a trend suggesting the higher the ranking on the mental clock test, the smaller the average deviation on the verbal judgment of orientation task. Furthermore, we found no relationship between the size of the oblique effect in individuals and their ranking on the mental clock test, ($r_S = .17$, $p = .27$).

Discussion

The current study investigated the haptic perception of a single bar orientation throughout peripersonal space. A first goal was to examine whether the haptic perception of single bar orientation is systematically distorted throughout peripersonal space by hand- and/or body-centered reference frames. Importantly, we found evidence that the perception of the orientation of a haptically perceived bar systematically depends on the orientation of the perceiving hand with respect to the midsagittal plane, and not on spatial position with respect to the body per se: the larger the hand-midsagittal plane misalignment, the larger the deviation in verbal judgment. Moreover, these hand orientation related differences in perception depended on stimulus orientation, suggesting that the judgment of a particular stimulus orientation depends on its orientation with respect to the hand. In addition, an interaction between hand and delay was found, which is discussed at a later point in this discussion.

Although the data clearly indicate that the deviation in haptic orientation perception originates from the hand, one might argue, of course, that the hand is not the only egocentric reference frame with which a representation of stimulus orientation is formed: different parts of the limb (e.g. the elbow) and body (e.g. the shoulder, body-midline) are likely to be involved, and consequently may contribute to the deviation. We would like to argue, however, that essentially these body parts afford proprioceptive information concerning the placement of the hand in space, which permits the transformation of a hand-centered representation of bar orientation into a more absolute representation. As such, this information would help rather than distort the allocentric representation of orientation. Importantly, several recent studies have suggested that particularly the use of reference frames comprising the body midline may be vital for adequate spatial representations in certain haptic tasks. Haptic illusions (Millar & Al-Attar, 2002), and distortions in haptic location (Millar & Al-Attar, 2004) and symmetry perception (Ballesteros, Millar & Reales, 1998) have been shown to be attenuated by explicit instructions to use the body midline as a referent. Also with respect to haptic orientation perception the importance of a body-centered reference frame has been suggested (Heller, Brackett, Scroggs & Allen, 2001). Our present findings that hand orientations which were more aligned with the midsagittal plane yielded better performance, would fit with the idea that employment of a body-midline reference frame exerts an advantageous influence on haptic orientation perception.

A second goal concerned the role and characteristics of the allocentric reference frame complementing the aforementioned influence of egocentric reference frames. Interesting in this respect is the finding that the observed perceptual biases in orientation perception, although consistent with those resulting from haptic matching studies, were relatively small, even when we consider that matching studies comprise of two bars: whereas the maximum deviation in the present study was only about 1.2 minutes (or 7.2°) on average for extreme hand-midsagittal plane misalignments, matching studies with similarly extreme misalignments have reported average deviations as large 55° or more (Kappers, 1999; Zuidhoek et al., 2004). This may be explained by the required verbal response being explicitly defined in an allocentric frame of reference, which (in contrast to a motor response) is likely to stimulate allocentric reference frame generation and employment.

Anticipating small deviations, we expected a small or no effect of a 10 seconds delay between perception and response (cf. Zuidhoek et al., 2003). In addition, one could argue that the instruction to assign a number of minutes to the perceived orientation would trigger the retention of the orientation as verbal code, which may also obstruct further processing during delay. However, an improvement with delay was found. Surprisingly, the improvement was found exclusively for right hand performance, with delay bringing it up to the level of left hand judgments. This suggests that, for right hand perceptions, additional allocentric recoding of the egocentrically biased representation did occur during the delay period also in the current task. A possible interpretation is that for allocentric processing to be completed, the haptic information needs to be transferred to the right hemisphere. In support of this, the right parietal cortex has been argued to be involved in the integration of haptic information for both the left and the right side of the body (Knecht, Kunesch & Schnitzler, 1996).

To examine whether performance depended on visual spatial imagery ability, and to quantify the possible relationship between this ability and the ability to generate an allocentric representation of haptic orientation information, we had participants perform the mental clock test (Paivio, 1978) and correlated performance on this test with performance on the main task. The trend found suggests that there may be a moderate relationship. It should be considered, however, that in addition to the presupposed common imagery component, there may be some nontrivial differences between the tasks concerning the characteristics of the imagery process which may have obstructed the obtainment of a more clear and stronger relationship. For example, seen from a working memory point of view, constructing two images and actively comparing them, as in the mental clock test, involves more active central executive involvement than just constructing one image, as in the current haptic task (Cornoldi & Vecchi, 2003). Nevertheless, the results suggest that there may well be a connection between visuospatial imagery ability and the ability to generate an allocentric representation of space based on haptic input. It is clear, however, that more research is needed on the relationship between (mental) visual and haptic spatial processing.

Of further interest was the haptic oblique effect, with its possible dependence on hand- and/or body-centered reference frames and its manifestation with a verbal response as primary focuses. The oblique effect was found with the current verbal response method, which suggests that it is, indeed, a perceptual phenomenon, and not merely resulting from egocentric reference frames employed in performing and feeding back the motor response. Moreover, we observed that, at least in the horizontal plane, the oblique effect is independent of spatial location with respect to the body, hand orientation, and delay. These results are consistent with the view that the systematic hand orientation related deviation and the haptic oblique effect are independent, and thus employ different reference frames. Examination of a possible connection between visual imagery ability and the haptic oblique effect did not reveal any relationship. This particular result is in line with the finding by Gentaz and Hatwell (1998) that early blind individuals and late blind individuals produce similar oblique effects, and suggests that the haptic oblique effect can not be explained by mental orientation models based on visual experience or visual imagery (Appelle & Countryman, 1986; Appelle & Gravetter, 1985), but more likely results from a subjective gravitational frame (Luyat et al., 2001).

In sum, the present study has yielded new insights in haptic space perception. First, we found that the haptic perception of orientation depends on a reference frame centered on the hand performing the haptic inspection. Since, in contrast to previous studies, a verbal instead of a motor response was required, the effect of hand on performance can truly be said to be perceptual. Second, an improvement with delay suggests involvement of an allocentric frame, which acts as a counterweight to the hand-centered one; the extent to which an allocentric reference frame is involved may be linked to the ability to generate an internal visuospatial image of the haptic input. Third, the haptic oblique effect, which was found with a verbal response for the first time in the present study, appeared to be independent of the hand-centered bias in perception: it was not affected by hand orientation and delay, nor was it related to visuospatial imagery ability. Taken together, the current study suggests that our haptic perception of orientation in peripersonal space engages multiple ego- and allocentric reference frames, some of which may be functionally and possibly neurally independent. The employment of reference frames and their contributions seem to depend on the task (motor response vs. verbal response, non-delay vs. delay, extent of stimulating spatial imagery) and on the aspect (deviation size or variability) of the dependent measure under examination.

References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61,* 303-321.

Appelle, S., & Countryman, M. (1986). Eliminating the haptic oblique effect: Influence of scanning incongruity and prior knowledge of the standards. *Perception, 15,* 325-329.

Appelle, S., & Gravetter, F. (1985). Effect of modality-specific experience on visual and haptic judgment of orientation. *Perception, 14,* 763-773.

Ballesteros, S., Millar, S., & Reales, J.M. (1998). Symmetry in haptic and in visual shape perception. *Perception & Psychophysics, 60,* 289-404.

Blumenfeld, W., 1937. The relationship between optical and haptic construction of space. *Acta Psychologica, 2,* 125-175.

Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics, 59,* 456-469.

Cornoldi, C., & Vecchi, T. (2003). *Visuo-spatial working memory and individual differences.* Hove, UK: Psychology Press.

Gentaz, E., & Hatwell, Y. (1998). The haptic oblique effect in the perception of rod orientation by blind adults. *Perception & Psychophysics, 60,* 157-167.

Gentaz, E., & Hatwell, Y. (1999). Role of memorization conditions in the haptic processing of orientations and the 'oblique effect'. *British Journal of Psychology, 90,* 373-388.

Haber, L., Haber, R.N., Penningroth, S., Novak, K., & Radgowski, H. (1993). Comparison of nine methods of indicating the direction to objects: data from blind adults. *Perception, 22,* 35-47.

Heller, M.A., Brackett, D.D., Scroggs, E., & Allen, A.C. (2001). Haptic perception of the horizontal by blind and low-vision individuals. *Perception, 30,* 601-610.

Kappers, A.M.L. (1999). Large systematic deviations in the haptic perception of parallelity. *Perception, 28,* 1001-1012.

Kappers, A.M.L. (2002). Haptic perception of parallelity in the midsagittal plane" *Acta Psychologica, 109,* 25-40.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 144,* 131-145.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Knecht, S., Kunesch, E., & Schnitzler, A. (1996). Parallel and serial processing of haptic information in man: Effects of parietal lesions on sensorimotor hand function. *Neuropsychologia, 34,* 669-687.

Lanca, M., & Bryant, D.J. (1995). Effect of orientation in haptic reproduction of line length. *Perceptual and Motor Skills, 80,* 1291-1298.

Lechelt, E.C., Eliuk, J., & Tanne, G. (1976). Perception orientational asymmetries: A comparison of visual and haptic space. *Perception & Psychophysics, 20,* 463-469.

Lechelt, E.C., & Verenka, A. (1980). Spatial anisotropy in intramodal and cross-modal judgments of stimulus orientation: The stability of the oblique effect. *Perception, 9,* 581-589.

Lederman, S.J., Klatzky, R.L., & Barber, P.O. (1985). Spatial and movement-based heuristics for encoding pattern information through touch. *Journal of Experimental Psychology: General, 114,* 33-49.

Luyat, M., Gentaz, E., Corte, T.R., & Guerraz, M. (2001). Reference frames and haptic perception: Body and head tilt effects on the oblique effect. *Perception and Psychophysics, 63,* 541-554.

Marks, L.E., & Armstrong, L. (1996). Haptic and visual representations of space. In T. Inui & J.T. McClelland (Eds.) *Attention and performance 16: Information integration in perception and communication* (pp. 263-287). Cambridge, MA, USA: Mit Press)

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development**,** **11,*** 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England UK: Clarendon Press/Oxford University Press.

Millar, S., & Al-Attar, Z. (2002). The Müller-Lyer illusion in touch and vision: Implications for multisensory processes. *Perception & Psychophysics, 64,* 353-365.

Millar, S., & Al-Attar, Z. (2004). External and body-centered frames of reference in spatial memory: evidence from touch. *Perception & Psychophysics, 66,* 51-59.

Milner, A.D., Paulignan, Y., Dijkerman, H.C., Michel, F., & Jeannerod M. (1999). A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London, Biological Sciences, 266,* 2225-2229.

Newport, R., Rabb, B., & Jackson, S.R. (2002). Non-informative vision improves haptic spatial perception. *Current Biology, 12,* 1661-1664.

Paivio, A. (1978). Comparisons of mental clocks. *Journal of Experimental Psychology: Human Perception and Performance, 4,* 61-71.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Rossetti, Y., & Régnier, C. (1995). Representations in action: pointing to a target with various representations. In B.G. Bardy, R.J. Bootsma & Y. Guiard (Eds.) *Studies in Perception and Action III (*pp 233-236). Mahwah, NJ: Laurence Erlbaum Associates.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-42.

Trojano, L., Grossi, D., Linden, D.E.J., Formisano, E., Hacker, H., Zanella, F.E., Goebel, R., & Di Salle, F. (2000). Matching two imagined clocks: the functional anatomy of spatial analysis in the absence of visual stimulation. *Cerebral Cortex, 10,* 473-481.

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). Multisensory integration mechanisms in haptic space perception. *Experimental Brain Research, 157,* 265-268.

Chapter 4| Multisensory integration mechanisms in haptic space perception

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). *Experimental Brain research, 157,* 265-268.

Abstract

It has been argued that representations of peripersonal space based on haptic input are systematically distorted by egocentric reference frames (Kappers, 2003; Zuidhoek, Kappers, Van der Lubbe & Postma, 2003). Interestingly, noninformative vision (i.e. freely viewing the region above the haptic workspace) improves performance on the so-called haptic parallel-setting task (Newport, Rabb & Jackson, 2002), in which participants are instructed to rotate a test bar until it is parallel to a reference bar. In the present study, we made a start at identifying the different sensory integration mechanisms involved in haptic space perception by distinguishing the possible effects of orienting mechanisms from those of noninformative vision. We found that both the orienting direction of head and eyes and the availability of noninformative vision affect parallel-setting performance and that they do so independently: orienting towards a reference bar facilitated the parallel-setting of a test bar in both no-vision and noninformative vision conditions, and noninformative vision improved performance irrespective of orienting direction. These results suggest the effects of orienting and noninformative vision on haptic space perception to depend on distinct neurocognitive mechanisms, likely to be expressed in different modulations of neural activation in the multimodal parietofrontal network, thought to be concerned with multimodal representations of peripersonal space.

Introduction

Representations of peripersonal space based on haptic input are systematically distorted, as has been demonstrated with haptic matching tasks: blindfolded subjects instructed to rotate bars until they are parallel or collinear, make matching errors that vary systematically in magnitude and direction throughout peripersonal space (e.g. Kappers & Koenderink, 1999; Kappers, 2002). These errors have been shown to result from the use of biasing egocentric reference frames, where an allocentric one should have been used (Zuidhoek, Kappers, Van der Lubbe & Postma, 2003). Interestingly, a recent study by Newport and colleagues (Newport, Rabb & Jackson, 2002) demonstrated that freely viewing the region of space directly above the workspace reduced deviation size in haptic parallel-setting. The way in which this "noninformative" visual information exerted its effect is by no means clear, however. For one, considering that participants were allowed to freely move their heads and eyes during the task, it may be that orienting behavior during the task affected multimodal integration. In support of this, simple tactile detection and discrimination studies have shown that the orienting of head and eyes towards a tactilely stimulated body site *without* any visual input boosts tactile processing, which suggests hardwired multimodal connections between tactile, visual and proprioceptive processing (Honoré, Bourdeaud'hui & Sparrow, 1989; Driver & Grossenbacher, 1996).

The goal of the current study was to distinguish the possible effects yielded by orienting mechanisms from those of noninformative vision. The two factors might either show mutual dependencies or have independent effects. Discovering their relationship will give further insight in the mechanisms of multimodal integration and crossmodal facilitation. To this end, we examined the role of orienting direction in the bimanual haptic perception of parallelity of two bars in the horizontal plane, in no-vision and noninformative vision conditions. We reasoned that if the orienting direction of head and eyes affects haptic space perception, orienting to either of the hands handling the bars may improve the parallel-setting performance by enhancing tactile perception and possibly also proprioception (cf. Newport, Hindle & Jackson (2001), but see also Van Beers, Sittig & Denier van der Gon (1999)). A neutral fixation point straight ahead above the workspace served as a baseline.

Materials and methods

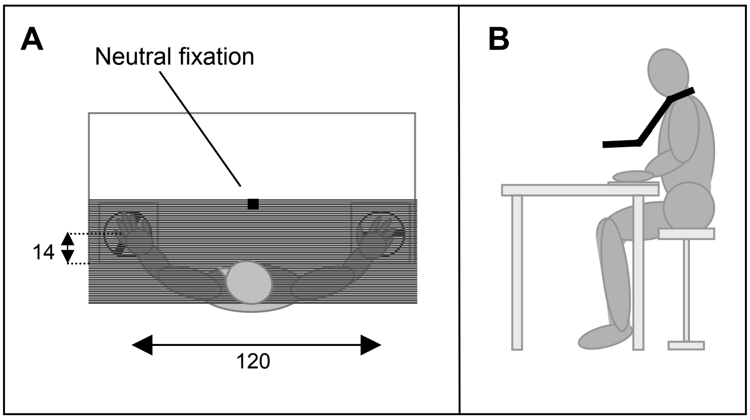
Participants

Twelve paid undergraduates of Utrecht University (six male, six female, aged 18 – 30 years) participated in the experiment, after having given their informed consent. All were right-handed as assessed by means of a standard questionnaire (Annett 1970).

Apparatus and stimuli

See Fig. 1. The participants were seated 3 – 5 cm from the middle of the long end of a table (160 x 80 cm). Two boards (28 x 28 x 0.9 cm) showing a protractor (diameter 20 cm) were fixed to the table top. The centers of the protractors were 14 cm from the table's edge, which is closer than in previous studies (20.5 cm). Each protractor contained an aluminum bar (20 x 1.1 cm) that could be rotated around the center of the protractor. The distance between the centers of the bars was 120 cm. The bar to the left of the participant served as the reference bar. This bar was presented in one of eight orientations: 18º, 42º, 66º, 84º, 108º, 132º, 156º, and 174º (0º being parallel to the long side of the table and increasing values signify a rotation in counterclockwise direction). In each trial, the bar to the right – the test bar - was to be matched to the reference bar orientation by rotating it with the right hand. The test bar was presented in a random orientation, i.e. corresponding to the orientation of the seconds-hand of a clock at that particular time. In every condition, each reference bar orientation was presented three times adding up to 24 trials per condition. The order of reference bar presentation was randomized and different for each participant.

The experiment consisted of 6 conditions: three orienting directions (the "reference hand" (i.e. the hand handling the reference bar), a central "neutral" fixation point, the "test hand" (i.e. the hand handling the test bar)) in no-vision and noninformative vision situations. Orienting meant directing head and eyes. In no-vision conditions, participants were blindfolded. In noninformative vision conditions, an opaque cloth covered the workspace (20 cm above the table) as well as the participant's limbs and shoulders (about 35 – 40 cm above the table), so that participants viewed the region of peripersonal space directly above the workspace (see Fig. 1B.). Conditions were blocked. Each participant was presented with a different sequence of conditions.



Figures 1A and B. Schematic top and side view of the experimental setup in noninformative vision conditions: an opaque cloth (transparent in the picture) covered participants' shoulders and limbs, as well as the workspace.

Procedure

Participants were instructed to use their right hand to rotate the test bar parallel to the reference bar, which they simultaneously felt with their left hand. Before the start of every trial they were instructed to orient head and eyes in the direction corresponding to the condition at hand. One experimenter monitored the direction of head and eyes. Of course, in blindfolded conditions, the direction of the eyes could not be observed. Note, however, that with the head directed at one of the fixation points, it was impossible for the participant to direct the eyes to one of the other fixation points due to the large distance between fixation points.

After having oriented head and eyes to the appropriate location, participants were allowed to touch and explore the bars freely, as long as they did not change the orientation of the reference bar, did not touch the edges of the table, and remained seated. The time per trial was restricted to 10 seconds, which proved to be more than sufficient. In between trials, participants were to place their hands right in front of them on the table, and to look straight up. The participants never received any feedback on their performance.

Data analyses

For all analyses below we computed signed average errors in degrees, assigning a positive value to deviations in the expected direction (i.e. the direction of the systematic deviations found in previous parallel-setting studies), and a negative value to deviations in the opposite direction.

Results

A 3 (orienting direction) x 2 (input condition, i.e. no vision vs. noninformative vision) within-subjects ANOVA was conducted for the mean signed errors. Significant main effects were found for orienting direction ($F(2,22) = 5.1$, $p = .016$) and input condition ($F(1,11) = 37.9$, $p < .001$). The main effect of orienting direction was expressed in different average deviations for the three orienting directions: 54.1º, 56.7º, and 59.9º for orienting to the reference hand, central fixation point and the test hand, respectively. Post-hoc testing, with Bonferroni correction lowering significance criterion α to 0.017, showed that performance with reference hand orienting was significantly better than performance with test bar orienting: $t(11) = -3.7$, $p = .004$. Differences for reference hand and test hand orienting with respect to central fixation point orienting were not significant: $t(11) = -1.4$, $p = .2$ and $t(11) = -1.7$, $p = .11$, respectively. Furthermore, the average deviations for the three orienting directions showed a significant linear trend ($F(1,11) = 13.9$, $p = .004$), implying that the facilitating effect of orienting decreases with absolute distance from the reference hand.

The main effect of input condition signified that allowing the processing of noninformative vision improved performance ($F(1,11) = 37.9$, $p < .001$): it reduced deviation size from 59.5º to 54.3º. Importantly, orienting direction and input condition showed no interaction ($F(2,22) = .19$, $p = .83$), yet an additive relation (See Fig. 2.), implying that orienting direction and noninformative vision affect haptic spatial performance independently.

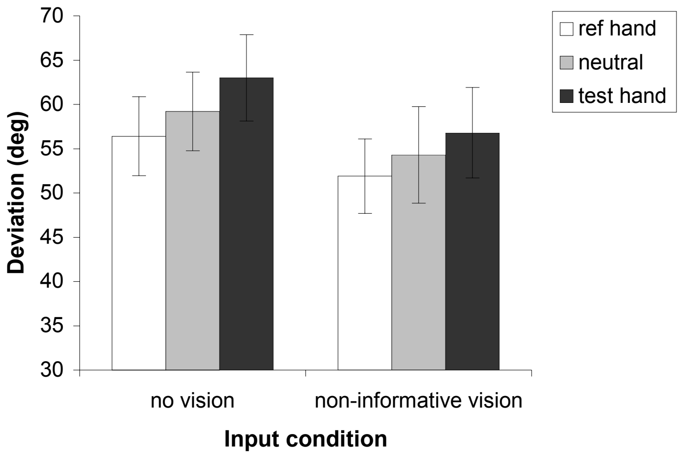


Fig. 2 Orienting direction of head and gaze affect haptic parallel-setting in both no-vision and noninformative vision conditions. Error bars represent +/- standard error of mean.

Discussion

The primary goal of the present study was to identify multimodal mechanisms involved in constructing representations of peripersonal space from haptic input. We focused on distinguishing possible effects yielded by orienting mechanisms from those of the processing of visual input that was not directly relevant for the task ('noninformative vision'). To this end, we presented participants with a bimanual parallel-setting task, in which participants were instructed to orient head and eyes towards either the reference hand, the test hand, or a neutral fixation point, in both a no-vision and a noninformative vision condition.

We found that orienting direction affected the perception of space based on haptic input: orienting towards the hand handling the reference bar yielded significantly smaller deviations than orienting towards the test hand. Moreover, the average deviations for the three orienting directions showed a significant linear trend, suggesting that the facilitating effect of orienting decreases with distance from the point of fixation to the reference hand. Furthermore, we observed that the availability of noninformative visual input facilitated parallel-setting performance, a finding that replicates Newport and colleagues (2002). Importantly, the effects of orienting direction and input condition (noninformative vision vs. no vision) proved to be independent, suggesting distinct neurocognitive mechanisms. An additional observation is that the deviations found were relatively large as compared to those in previous studies. This can be explained by relatively extreme placing of the stimuli with the bars 120 cm apart and closer to the body than in previous studies. This led to large orientation differences between the hands which has been suggested to be the main cause of deviations in haptic orientation perception (Zuidhoek et al., 2003).

An interesting question, of course, is how orienting direction and noninformative vision contribute to the representation of haptic space. Noninformative vision may improve haptic perceptions of peripersonal space by providing information about the space between and beyond the bars (although above the actual workspace), and as such serving as an allocentric reference frame. At the neural level of multimodal representation, noninformative vision then may be reflected in the increase of the number of multimodal cells activated in a parietofrontal multimodal network suggested to mediate the coding of peripersonal space and our limbs in it by integrating visual, proprioceptive, tactile and possibly also auditory inputs (Làvadas, Di Pellegrino, Farnè & Zeloni, 1998; Obayashi, Tanaka & Iriki, 2000; Newport et al. 2001; Graziano 2002; Lloyd, Shore, Spence & Calvert, 2003).

With respect to the effect of orienting direction, the current findings showed that - although the task comprised the perception of two bars - orienting towards the reference bar enhanced performance, whereas orienting towards the test bar did not. Importantly, this implies that the mere alignment of sensory systems through orienting is not sufficient to result in an improvement in (spatial) perception (cf. Kennett, Taylor-Clarke & Haggard, 2001). Rather, it seems that orienting enhances perception by facilitating additional processing, which - in the parallel-setting task - is performed exclusively on reference hand input. Two underlying mechanisms may be considered here. First, visual imagery has been suggested to play a role in improving allocentric representations of space based on haptic input (Zuidhoek et al., 2003). It may be that performing the parallel-setting task comprises imagery of the reference bar which is stimulated and/or facilitated by orienting towards it. Second, orienting may facilitate the allocation of attentional resources (Honoré et al., 1989; Driver & Grossenbacher, 1996). Then, the improvement in performance with reference hand orienting may reflect the attentional focus being primarily on the reference hand during task performance. Possibly, these two mechanisms are interlinked: imagery of the reference hand may depend on attentional resources, and in turn, attending a (visuo-tactile) image of the limb itself may be critical, since visually attending a neutral object at the location of tactile stimulation has been found not to boost perception (Kennett et al., 2001; Taylor-Clarke, Kennett & Haggard, 2002).

It is unknown how the facilitating effect of orienting on haptic perception is mediated at a neural level. However, Taylor Clarke and colleagues (2002) have argued that the effects of *vision* on tactile perception are reflected by a modulation of cell activity in the primary and secondary somatosensory cortex (SI and SII), brought about by back projections from multimodal cortical areas. Importantly, they showed that S1 processing (N80 component) is only enhanced by vision when tactile stimulation is task-relevant, suggesting top-down attentional selection. It might be that the contribution of visual imagery operates in a similar manner, i.e., via back projections from those multimodal areas concerned with visuo-tactile imagery of our moving limbs in space like the intraparietal sulcus (Obayashi et al., 2000; Lloyd et al., 2003) to S1 and S2, with those to S1 depending on task-dependent selection processes.

References

Annett, M. (1970). A classification of hand preference by association analyses. British Journal of Psychology, 61, 303-321.

Driver, J., & Grossenbacher, P.J. (1996). Multimodal constraints on tactile selective attention. In T. Inui & J.L. McClelland (Eds.) *Attention and Performance XVI* (pp 209-235). Cambridge MA: MIT Press.

Graziano, M.S. (2002). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Acadamy of Sciences of the United States of America, 96,* 10418-10421.

Honoré, J., Bourdeaud'hui, M., & Sparrow, L. (1989). Reduction of cutaneous reaction time by direction eyes towards the source of stimulation. *Neuropsychologia, 27,* 367-371.

Kappers, A.M.L. (2002). Haptic perception of parallelity in the midsagittal plane. *Acta Psychologica, 109,* 25-40.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 144,* 131-145.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology, 11,* 188-1191.

Làdavas, E., Di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience,* 10, 581-589.

Lloyd, D.M., Shore, D.I., Spence, C., & Calvert, G.A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience, 6,* 17-18.

Newport, R., Hindle, J.V., & Jackson, S.R. (2001). Links between vision and somatosensation: vision can improve the felt position of the unseen hand. *Current Biology, 11,* 975-980.

Newport, R., Rabb, B., & Jackson, S.R. (2002). Noninformative vision improves haptic spatial perception. *Current Biology, 12,* 1661-1664.

Obayashi, S., Tanaka, M., & Iriki, A. (2000). Subjective image of invisible hand coded by monkey intraparietal neurons. *Neuroreport, 11,* 3499-3505.

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Current Biology, 12,* 233-236.

Van Beers, R.J., Sittig, A.C., & Denier van der Gon, J.J. (1999). Localisation of a seen finger is based exclusively on propioception and on vision of the finger. *Experimental Brain Research, 125,* 43-49.

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

The blind

Chapter 5 | Haptic orientation perception benefits from visual experience: evidence from early blind, late blind and sighted people

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (submitted for publication)

Abstract

Early blind, late blind and blindfolded sighted participants were presented with two haptic allocentric spatial tasks: a parallel-setting task in an immediate and a 10 seconds delay condition, and a task in which a single bar orientation was verbally judged. With respect to deviation size, the data suggest that mental visual processing fulfilled a beneficial role in both tasks, showing effects of early visual experience as well as visual strategies. In the parallel-setting task, the early blind performed more variably and showed no improvement with delay, while the late blind did improve, but less than the sighted. In the verbal judgment task, both early and late blind participants displayed larger deviations than the sighted controls. With respect to the haptic oblique effect the groups did not differ, which endorses the view that it is not of visual origin. The role of visual processing mechanisms and visual experience in haptic spatial tasks is discussed.

Introduction

Our haptic sense provides us with essential information about the spatial layout of the world, especially when we lack visual input. As such, it is striking that - at least in sighted individuals - the haptic perceptions of basic spatial properties like line length (Marks & Armstrong, 1996; Lanca & Bryant, 1995), path length (Lederman, Klatzky & Barber, 1985) and orientation (e.g. Appelle & Countryman, 1986; Gentaz & Hatwell, 1998, 1999; Kappers, 1999; Zuidhoek, Visser, Bredero & Postma, 2004) in peripersonal space are liable to distortions. Interestingly, the distortions in the haptic perception of orientation appear to be systematic over multiple locations and consistent over different tasks: haptic orientation matching tasks like the parallel- and collinear-setting of a test bar to a reference bar and the pointing of a bar towards a marker, result in considerable errors that vary systematically in magnitude and direction throughout peripersonal space (Kappers & Koenderink, 1999; Kappers 1999, 2002). Recently, it has been established that these deviations result from the use of egocentric reference frames while an allocentric or extrinsic representation of the bars in space is needed to perform the task adequately (Zuidhoek, Kappers, Van der Lubbe & Postma, 2003; Kappers, 2003). Particularly hand-centered reference frames appear to bias haptic orientation perception (Zuidhoek, Kappers & Postma, 2005).

The (neurocognitive) mechanisms involved in the haptic perception of peripersonal space are by no means clear, however. Interestingly, haptic space perception may not 'just' reflect active touch processing, but rather seems to depend on a subtle interplay between haptic and visual processing. For one, it has long been suggested that orientation of touched objects is primarily represented in an imagined visual space (O'Conner & Hermelin, 1975). Importantly, a growing body of evidence indeed indicates that the representations of peripersonal space based on haptic input cannot simply be considered to comprise only processing in tactile, proprioceptive and motor areas in the brain. Recent electrophysical studies (e.g. Graziano, Hu & Gross, 1997; Graziano, 1999; Obayashi, Tanaka & Iriki, 2000; Rizzolatti, Fogassi, & Gallese, 2002), neuropsychological studies (e.g. Farnè, Pavani, Meneghello & Làdavas, 2000; Làdavas, Di Pellegrino, Farnè & Zeloni, 1998; Newport, Hindle & Jackson, 2001; Rorden, Heutink, Greenfield & Robertson, 1999) and a neuroimaging study (Lloyd, Shore, Spence & Calvert, 2003) suggest that, even in the absence of (relevant) visual input, the coding of peripersonal space and our limbs in it is mediated by a parietofrontal multimodal network concerned with the integration of proprioceptive and tactile input with (mental) visual processing. This implies that, when investigating representations of space based on haptic input, the possible influences of concurrent visual processing should always be considered as well.

Over the last couple of years evidence has been mounting that the allocentric representation of haptically perceived orientation actually benefits from the employment of visual reference frames and visuospatial imagery. For example, viewing the region of space directly above the haptic workspace has been found to improve parallel-setting performance (Newport, Rabb & Jackson, 2002; Zuidhoek et al., 2004). In addition, in the latter study, the direction of head and eyes was found to affect parallel-setting performance independently of visual input, with head and eyes directed to the reference bar resulting in better parallel-setting performance than orienting straight ahead or towards the test bar, suggesting the effects to be based on visual experience. Moreover, a haptic orientation perception task with a verbal response requiring the translation of the orientation of a single bar into a number of minutes on an imagined clock (the 'verbal judgment of orientation task'), has been found to result in very small (yet similarly systematic) deviations as compared to haptic parallel-setting (Zuidhoek et al., 2005). Interestingly, a marginally significant correlation was found between performance on this task and performance on a visuospatial imagery task (Paivio's mental clock test (1978)). This particular finding may indicate that response methods stimulating imagery of the felt orientation facilitate an allocentric representation.

An additional finding which may signify the beneficial role of mental visual processing in haptic allocentric spatial representation in a more indirect way, is that in haptic parallel-setting the retention of a reference bar orientation for 10 seconds before rotating the test bar, results in *smaller* deviations in parallel-setting performance than non-delayed performance (Zuidhoek et al., 2003). Following several visual and proprioceptive goal-directed action studies (Bridgeman, Peery & Anand, 1997; Milner, Paulignan, Dijkerman, Michel & Jeannerod, 1999; Rossetti, Gaunet & Thinus-Blanc, 1996; Rossetti & Régnier, 1995), we have interpreted this improvement to reflect a shift from an egocentric towards a more allocentric spatial representation over delay time.[1] Together, these studies suggest that there is a basic spatial processing mechanism underlying a shift from egocentric towards more

[1] Admittedly, the change in error patterns due to delay or visual reference frames in the parallel-setting task is not a qualitative one; the interpretation of a shift in reference frame use is based on the assumption that adequate performance on this task requires an allocentric representation of the bars in space, yet that egocentric reference frames form the basis of haptic spatial input. In this view, deviations in performance would result from systematic biases in egocentric referencing. Taking this approach, we assume that improvement of performance expresses increased allocentric, and/or decreased egocentric processing (Zuidhoek et al., 2003).

allocentric representations of space with retention of visual, proprioceptive and haptic spatial input. Importantly, there is evidence that this basic mechanism may depend on early visual experience: Rossetti and colleagues (1996) found that whereas delaying a pointing action in the proprioceptive domain for 8 seconds leads to a qualitatively different endpoint distribution pattern in blindfolded sighted, it does not in the early blind: while the endpoint distributions of blindfolded sighted showed a transition from alignment with the pointing movement (egocentric) in the immediate condition towards alignment with the arc-shaped target array (allocentric) with delay, those of early blinds showed end-point distributions aligned with the direction of the pointing movement in the immediate, but – although less distinct - also in the delayed conditions.

Notably, visual information processing does not always need to have beneficial effects in haptic orientation perception tasks. The exact nature of the haptic task may determine both the direction and the magnitude of the effect of vision. In line with this, in a haptic matching task for which an intrinsic or egocentric representation is believed to be sufficient (mirroring with respect to midsagittal plane) noninformative vision was found to have a slightly *negative* influence on performance, while in a parallel-setting task a positive effect of noninformative vision was found (Newport et al., 2002). Stronger detrimental effects on the haptic perception of orientation have been found with the oblique effect, which is another well known bias in orientation perception, characterized by a larger variability in the reproduction of oblique orientations than in the reproduction of horizontal and vertical orientations (e.g. Lechelt, Eliuk & Tanne, 1976; Lechelt & Verenka, 1980; Gentaz & Hatwell, 1998, 1999; Luyat, Gentaz, Corte & Guerraz, 2001). Appelle and Countryman (1986) suggested visual processing to be the cause of this effect. They found that in unilateral conditions, the oblique effect was eliminated when prior to testing no visual or verbal knowledge about the stimulus orientations was conveyed to the participants, which had been customary up till then. They concluded that the haptic oblique effect is not related to haptic sensitivity, but that it stems from mental orientation models based on visual experience and imagery (cf. Appelle & Gravetter, 1985), and is in fact a manifestation of the very similar *visual* oblique effect. A more recent study on the effect of early visual experience performance on the haptic oblique effect (Gentaz & Hatwell, 1998), however, did not support this interpretation: in this study early as well as late blind participants displayed the haptic oblique effect, and did so to the same extent.

The foregoing directly raises the question to what extent visual experience is important in performing haptic spatial tasks. From (her) many studies, Millar (1988,

1994) has inferred that the early loss of vision results in a reliance on more body-centered proprioceptive and kinesthetic information, and a related difficulty to organize spatial relationships between objects into absolute, allocentric representations. Thus, from this perspective, people who were born blind (the congenitally blind) would be predicted to be outperformed by those who were blinded later in life (the late blind) and the sighted on (haptic) tasks requiring an allocentric representation. Taking a similar account, Ernest (1987) argued that the strategies in sighted " […] are primarily visual and externally derived; in the blind they are predominantly auditory, kinesthetic, and based on internal cues. Indeed the strategies of the blind may be generalized as self-referent." Consequently, in these views, both early and late blind would be predicted to be outperformed by the sighted on tasks requiring an allocentric representation, like the haptic parallel-setting task or a single bar orientation haptic perception task with orientation being explicitly allocentrically defined.

The goal of the present study was to further establish the role of visual experience (abilities and strategies) in haptic spatial tasks. In particular, we examined the relationships between visual experience and egocentric and allocentric reference frame employment on different orientation perception tasks requiring an allocentric representation. We had early blind, late blind and blindfolded sighted participants perform two tasks that are thought to differ in the extent to which they stimulate egocentric and allocentric reference frame employment: the parallel-setting task (Kappers, 2003; Zuidhoek et al., 2003; Newport et al., 2002) and the verbal judgment task (Zuidhoek et al., 2005).

Experiment 1: Parallel-setting task

Our first task was a haptic parallel-setting task (two bar stimuli, motor response), Performed in 0 and 10 seconds delay conditions. As discussed above, Zuidhoek et al. (2003) showed that in the 0 seconds delay condition blindfolded sighted individuals rely to a great extent on an egocentric reference framework, resulting in relatively large distortions of haptic orientation processing. With a 10 second delay performance by they improved, suggesting a shift to a more allocentric representation. Here we focused specifically on the role of visual experience in the shift from egocentric to allocentric reference frames in this haptic orientation matching task (cf. Rossetti et al., 1996).

Method

Participants

Appendix A shows the list of participants. Thirteen early blind, seventeen late blind and sixteen sighted people participated in both experiments. The blind were recruited with announcements in magazines for the visually impaired. The sighted participants had blind partners or relatives, or worked (paid or on voluntary basis) in institutions for the blind. None of the participants had neurological or motor deficits. The early blind group consisted of congenitally blind and early blind individuals that had become blind before the age of three. Those that were not blind from birth had no memory of vision whatsoever. All participants in the late blind group had rich vivid visual memories, and reported to have had used vision as a primary spatial modality. The blindness of the participants had different etiologies (see Appendix A). Some late blind participants were born visually impaired and had gradually become blind during life. Others had lost their sight due to accidents. A minority of the blind participants had diffuse light sensations, but denied being able to use this in any form of spatial behavior. Sighted control participants where blindfolded.

Early blind, late blind and sighted control participants were matched for sex ($\chi^2(2) = 1.1$, $p = .57$), and approximately matched for age and education. Importantly, verbal IQ as assessed with two subscales (Vocabulary and Similarities) of the Dutch version of the WAIS-III (Wechsler, 1997) showed no significant difference between the three groups ($F(2, 43)= 1.4$, $p= .3$). Almost all participants were right-handed as assessed with Annett's handedness questionnaire (Annett, 1970); three participants were ambidexter or left-handed (see Appendix A, Etiology and other characteristics).

All participants gave their informed consent to inclusion in this study and received payment for their participation. They were naive to all aspects of the tasks, i.e., they had never seen or felt the set-up, were unaware of the experimental purposes, and were never given any feedback.

General Procedure

All participants were enrolled in an elaborate study on spatial cognition in the blind comprising several more tasks to be reported elsewhere. Each participant performed haptic, verbal and imagery tasks, on one day of testing. About half of the participants performed haptic tasks in the morning and verbal and imagery tasks in the afternoon, after lunch. For the other half, it was the other way around. The haptic parallel-setting task was always performed before the verbal judgment of orientation task. Experimental sessions were short (max. 30 minutes) to avoid weariness and fatigue during the experiments. In addition to a lunch break (1 hour) between the morning and afternoon session and two coffee breaks (10 minutes), participants were allowed breaks whenever they needed them.

Design

The experiment had a mixed design with delay and orientation as within- and group as between-subjects factor. It comprised two conditions, i.e. immediate and delayed motor matching of haptically perceived orientation (0s and 10s delay, respectively). Haptic exploration time (1s) and response time (1.4s) were held constant. These time restrictions for exploration, delay and response were based on the findings of Zuidhoek et al. (2003), which showed that with an exploration time of 1 second the delay effect was slightly more pronounced than with a 5 second exploration time, without affecting the variability of the data (Experiment 1). With respect to response time, that study also demonstrated 1.4 seconds to be a large enough time window to produce parallel-setting responses that participants find satisfactory. Conditions were blocked. Half of the participants started with the immediate condition, the other half with the 10-seconds delay condition. Stimulus presentation within a condition was randomized and different for participants.

Apparatus and stimuli

See Figure 1. The participants were seated 3 – 5 cm from the middle of the long end of a table with an iron table top. The stimuli were two aluminum bars with a length of 20 cm and a diameter of 1.1 cm presented on the two protractors (diameter 20 cm) indicated by the circles in Figure 1. The centers of these protractors were 20.5 cm from the table's edge. The aluminum bars could be rotated around the center of the protractor around a small pin attached to the middle of the bar, which fitted exactly into a hole in the center of the protractor. At both ends the bars were tapered off, allowing the experimenter an accurate reading of their orientation (uncertainty of about 0.5º). Small magnets fixed to the bars were used to increase the resistance to movement. The bars were both used as reference and test bar. In each trial, the test bar was to be matched to the reference bar orientation by rotating it with the corresponding hand, i.e., the bar to the left from the body was rotated/explored with the left hand, and those presented to the right were handled with the right. The reference bar was presented in one of six orientations to provide variation: 0º, 30º, 60º, 90º, 120º, and 150º (0º being parallel to the long side of the table and increasing values signify a rotation in counterclockwise direction). The test bar was presented in a random orientation, i.e.

corresponding to the orientation of the seconds-hand of a clock at that particular time. In both conditions, each reference bar orientation was presented three times at both bar locations, adding up to 36 trials per condition. The order of reference bar presentation was randomized and different for each participant. An Apple Macintosh computer was used to provide time restriction signals.

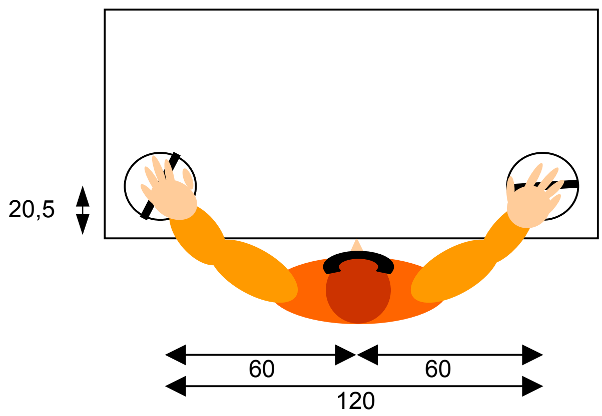


Figure 1. Top view of the experimental set up used in the parallel-setting task.

Procedure

Before the actual experiment, the participants were presented with an extensive pre-experimental session to make sure they had a correct understanding of parallelity, understood the basics of the task at hand and to give the experimenter a general impression of their individual haptic sense of parallelism. They were asked to sit down at the stimulus presentation table, which was covered by cloths concealing fifteen bars, at this point. Sighted participants were blindfolded. Participants were told that they were sitting at a table on which were several bars. Their first task was to rotate all the bars until they were parallel to the bar right in front of them (the position marked X in Figure 1). They were asked if they were familiar with the term 'parallel'. All participants reported that they were. A couple of measures were taken to make sure that their understanding of parallelity was correct. A Dutch synonym of parallel was given ('evenwijdig') as well as the following definition of parallelism: "Bars are parallel when they do never meet or cross, when elongated infinitely." As examples of parallel lines, railroad tracks were mentioned, as well as the opposite sides of a rectangle. In addition, participants were asked to come up with an example themselves. Furthermore they were given two pens and were asked to lay them parallel to one another right in front of them on the table. All participants expressed a normal and correct understanding of parallelity. To give the experimenter a general indication of their sense of parallelity, they were then asked to rotate all fifteen bars parallel to the bar closest to them and right in front of them as accurately as possible, using their right hand only while remaining seated on the stool with their navels in front of the middle of the long end of the table. They were free in choice of strategy, and were allowed to take as long as they wanted within 10 minutes, which proved more than sufficient for all participants.

After this pre-experimental “parallelity training/assessment session”, participants were told that at this point all bars were removed except for two. The experimenter took the hands of a participant and guided them to the remaining bars. Then, the instructions for the coming condition (non-delay or delay) were given. The participants were instructed that they repeatedly were to feel a reference orientation, and that after this they had to rotate the test bar in such a way that they thought it was parallel to the just-felt reference bar orientation, either with or without a delay. The timing of the sequence of required actions was carried out by a computer: a sampled male voice uttered the numbers "one", "two", "three" and in the 10-seconds delay condition also "four" in a timed sequence to indicate which action was desired from the participant. In the non-delay trials (i.e. delay time is 0s) "one" signified the start of the exploration period of the reference bar. "Two" signified both the end of the exploration period and the start of the setting of the test bar. "Three" signified the end of the setting of the test bar. In the delay trials, "one" signified the start of the exploration period of the reference bar. "Two" signified the end of the exploration period and the start of the 10-seconds delay period. At "three" the participant was required to start the parallel-setting, and "four" was the signal to terminate the parallel-setting. After a participant had confirmed that he/she understood this instruction, 5 practice trials were performed to ensure that the instructions were understood correctly, and to get used to the timed sequence in which the actions had to be performed. In each trial, the experimenter positioned the reference bar in a predetermined orientation and the test bar in a random orientation. Next, he took the hand that had to explore the reference bar in that particular trial while saying (the Dutch equivalent of) "here is the reference bar" and left it to float about 5 cm above the reference bar. He then took the participant's other hand, saying "here is the test bar" and left it to float about 5 cm above the test bar. After this, the experimenter started the timed sequence.

Participants had to stick to the time restrictions when they explored the reference bar with one hand, waited, or rotated the test bar with the other. In the exploration and response phase, the participants were free in their choice of strategy as long as they did not change the orientation of the reference bar, did not touch the edges of the table and remained seated. After exploration of the reference bar, the reference hand had to be returned to the body without touching the edge of the table. After the participant had finished the trial, the experimenter noted down the orientation of the test bar and positioned the bars for the next trial.

The participant was instructed to do the parallel-setting as accurately as possible, and to finish at the latest when he/she heard the last signal (either "three" in non-delay conditions or "four" in delay conditions). Occasionally 1.4 seconds turned out to be too narrow a time window to perform the parallel-setting action. These trials (approximately 5 – 10 % of the trials) were discarded and presented again at a later time during the session. The time to complete a condition was about 20 minutes for the non-delay condition, and about 25 for the delay condition.

Data analysis

In previous studies, the errors were found to be systematic, i.e. clockwise with test bars to the right of the reference bar, and counterclockwise with test bars to the left of the reference bar (e.g. Kappers & Koenderink, 1999; Kappers, 1999, 2003; Zuidhoek et al., 2003, Zuidhoek et al., 2004). To be able to easily differentiate between errors in this systematic direction and errors in the other direction, and to be able to pool test bar left and test bar right trials, the most recent of these studies use mean signed errors expressing size and systematics, with a positive value in degrees signifying the bar to the right to be rotated clockwise with respect to the left bar, and a negative value expressing a counterclockwise error. However, in the present study, a relatively large amount of large counterclockwise errors in the *unexpected* direction was found in contrast to the previous studies, especially in the early blind group. The error patterns suggested that (many of) these large errors in the unexpected direction may very well be interpreted as (even larger) errors in the *expected* direction. For example, an error of -89º should probably be interpreted as an error of +91º for participants that display deviation patterns in which large deviations of 60º through 90º degrees are common. Thus, to just run a signed error analysis in the current study would show misleading results, since especially the sign of large errors has large impact on the mean size of the deviations found. Therefore, in the present study, we turned to circular data manipulation methods, i.e. to apply vector algebra (Batschelet, 1981) to compute mean deviations for our mixed ANOVA's (see Results, Deviation size analyses). We also examined the effects of the independent variables on the variability, expressed by the length of the mean vector, which was given by its x and y values (see Results, Variability analyses).

As we were interested in the effects of both visual and haptic experience, as well as possible interaction effects, we planned comparisons for all group combinations when addressing the theoretical issues raised in the introduction. In analyses of secondary interest or of explorative character, the three level between-subjects factor of experimental group was default. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction.

Results

Deviation size analyses

A 2 (delay) x 6 (orientation) x 3 (group) mixed ANOVA showed significant main effects for delay ($F(1,43) = 11.9$, $p = .001$), and orientation ($F(5,215) = 5.0$, $p < .000$, $\varepsilon = .60$) on deviation size. The main effect of delay signified an improvement with delayed performance as compared to immediate parallel-setting, reducing mean signed error size from 37.3° to 29.6°. The main effect of orientation was expressed in different mean deviation sizes for different orientations: 34.6°, 35.7°, 32.1°, 24.8°, 36.0°, 37.6°, for 0°, 30°, 60°, 90°, 120° and 150°, respectively. The means suggest relatively spared performance for 90° reference orientations. Fifteen paired t-tests confirmed this: although the differences between performance on 60° and 30° and 60° and 150° may have contributed in causing the main effect of orientation ($t(45) = 2.1$, $p = .04$; $t(45) = 2.2$, $p = .03$, respectively), the only true significant differences and trends found with Bonferroni correction lowering α to .0033, concerned differences between performance on 90° and the other reference bar orientations (all p-values < .005).

No significant main effect of group was found ($F(2,43) = 1.9$, $p = .165$). Furthermore, no differences were found between the groups with respect to orientation effects. Importantly, a significant group x delay interaction was found (See Figure 2). Further examination of this interaction revealed that the groups differed with respect to the effect of delay ($F(2,43) = 4.2$, $p = .022$): whereas delay did not affect performance in the early blind (39.7° and 40.1° for non-delay and delay conditions, respectively; $F(1,12) = .003$), it improved performance in the late blind (37.0°, vs. 29.4°, $F(1,16) = 40.9$, $p < .001$) and sighted control groups (35.2° vs. 19.3°, $F(1,15) = 27.0$, $p < .001$)). Furthermore, this interaction effect signified that performance differed for the groups in delay conditions ($F(2,43) = 4.2$, $p =$

.022), while it did not in the non-delay condition ($F(2,43) = .2$). Comparing late blind and sighted performance with a 2 (delay) x 6 (orientation) x 2 (group) mixed ANOVA showed that the sighted improve significantly more with delay that the late blind ($F(1,31) = 6.6$, $p = .016$).

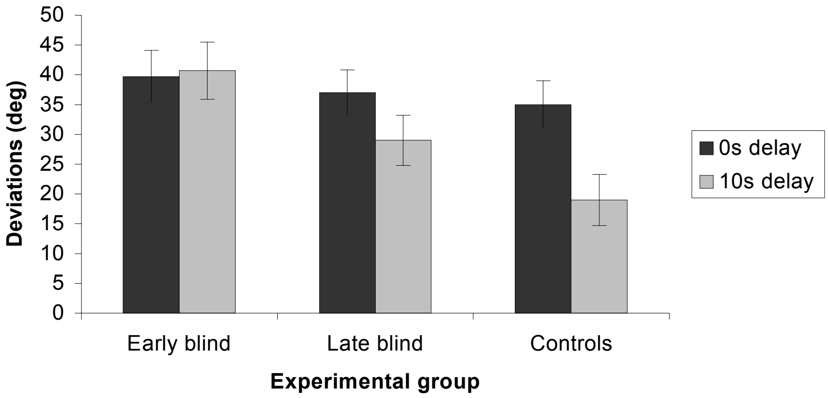


Figure 2. The interaction effect of group x delay on deviation size in the parallel-setting task. Error bars show +/- 1.0 standard errors of mean.

In addition, a delay x orientation interaction was found ($F(5,215) = 2.7$, $p = .044$, $\varepsilon = .60$), suggesting that the effect of delay depends on orientation. The means suggest that delay performance was better for all orientations. For 0º delay reduced deviation size from 37.6 to 31.6; for 30º from 38.7 to 32.7; for 60º: 34.0 to 30.2; for 90º: 28.5 to 21.0; for 120º: 40.0 to 32.0; and for 150º from 45.2 to 30.0. Six paired t-tests with Bonferroni correction lowering α to .0083 showed that, delay significantly improved performance for 90º ($t(45) = 3.3$, $p = .002$), 120º ($t(45) = 3.6$, $p = .001$) and 150º ($t(45) = 5.5$, $p < .000$), and not for 30º ($t(45) = 1.6$) and 60º $t(45) = 1.1$). For 0º, a trend could be reported: $t(45) = 2.7$, $p = .009$.

Variability analyses

A 2 (delay) x 6 (orientation) x 3 (group) mixed ANOVA showed significant main effects for group (($F(2,43) = 5.8$, $p = .006$), delay ($F(1,43) = 8.4$, $p = .006$), and orientation ($F(5,215) = 3.3$, $p = .012$, $\varepsilon = .79$) on the variability of performance, which is expressed by the length of the mean vector. The main effect of group signified differences between the groups with respect to mean variability: .76 (early blind), .88 (late blind), .85 (sighted). Examination of this effect showed a significantly larger variability (expressed in a smaller mean vector) for early blind participants than for late blind ($F(1,28) = 7.9$, $p = .009$) and sighted ($F(1,27) = 4.4$, $p = .047$). The main effect of delay signified less variability in delayed performance as compared to immediate parallel-setting, expressed by mean vector lengths of .81 to .84, respectively. The main effect of orientation was expressed in differences in the variability for different orientations: vector lengths .84, .85, .82, .87, .80 and .80 for 0º, 30º, 60º, 90º, 120º and 150º, respectively. Fifteen post-hoc t-tests with Bonferroni correction lowering α to .0033 did not result in significant differences between the six different orientation levels. Furthermore a group x orientation interaction was found ($F(10,215) = 2.2$, $p = .016$). Closer examination suggested that it was predominantly caused by an effect of orientation in the sighted group ($F(5,75) = 2.9$, $p = .048$, $\varepsilon = .59$, where no significant orientation effect was found for the early and late blind groups. The means suggest that performance on 90º was less variable than performance on the other orientations with mean vector lengths of .86, .87, .84, .90, .84, .79 for 0º, 30º, 60º, 90º, 120º and 150º, respectively. Fifteen post-hoc t-tests with Bonferroni correction lowering significance level α to .0033 revealed only one significant difference: between 90º and 120º ($t(45) = 5.1$, $p < .001$).

Discussion of Experiment 1

The present experiment showed some important commonalities and differences between early blind, late blind and sighted individuals on the haptic parallel-setting task. Let us first focus on the commonalities in the performance of the three groups. The results revealed that in immediate haptic parallel-setting, early blind, late blind and sighted individuals produce errors that are comparable with respect to size and direction, suggesting similar reference frame employment. Interestingly, performance on 90º was relatively spared independently of (early) visual experience, indicating that with the present task the perception of 90º orientations elicits relatively more allocentric reference frame involvement than oblique and horizontal orientations in all three groups. This particular finding suggests that ego- and allocentric reference frame employment is flexible in both the blind and sighted and may signify a special role of 90º orientations (i.e., orientations parallel to the participants midsagittal plane) for generating representations of orientation based on haptic input.

The present experiment revealed three important differences between the early blind group, late blind and sighted groups. First, the early blind's performance was more variable than that of late blind and sighted individuals, indicating that visual experience provides structure to haptic spatial input. This finding suggests that early blind individuals are less consistent in the generation of an allocentric representation of haptically perceived orientations. Somewhat surprisingly, delay reduced variability indicating that performance of the three groups becomes more reliable when more time is provided, while one may have expected the retention of a bar's orientation to result in less reliable performance. Second, while deviation size in immediate performance was comparable for the groups, differences emerged when the parallel-setting action was delayed: whereas delay did not affect early blind performance, it improved late blind and sighted performance (cf. Zuidhoek et al., 2003). As an improvement with delay has been interpreted as a shift from predominantly egocentric to more allocentric reference frame involvement over time (Zuidhoek et al., 2003), the current finding suggests that a specific mechanism set up by early visual input is responsible for this shift in frame use (Rossetti et al., 1996). Third, within the visually experienced groups, the sighted control group improved more with delay than did the late blind group. While the two former findings suggest that early visual experience results in differences in the ability to generate allocentric representations (Millar, 1988, 1994), the latter indicates that with the loss of vision the drive or the ability to use this visual mechanism reduces, and/or that becoming blind results in the employment of different, i.e. less visual strategies (Millar, 1988, 1994; Ernest, 1987) to retain haptic (orientation) information.

Experiment 2: Verbal judgment of orientation task

In this second task, we focused on the role of visual experience in a task designed to trigger a more allocentric representation of haptically perceived orientation, even in non-delay situations (cf. Zuidhoek et al., 2005). The experimental groups assigned a number of minutes on an imagined clock (verbal response) to the haptic perception of a single bar orientation, which was explicitly defined with respect to the stimulus table. By explicitly defining orientation allocentrically (i.e. with respect to the stimulus presentation table) and stimulating (visual) imagery of the bar's orientation the task was expected to increase allocentric reference frame involvement. In addition, asking for a verbal instead of a motor response minimizes the involvement of egocentric response-related biases (i.e. distortions that may derive either or both from perceiving and manipulating the response bar, as is the case with a motor response).

Indeed, a previous study on the verbal judgment of haptic orientation input revealed that, as mentioned, the deviations in the verbal judgment task are much smaller than those reported in haptic parallel-setting tasks, even when we consider that parallel-setting comprises two bars (Zuidhoek et al., 2005): whereas the maximum deviation in the verbal judgment study was about 1.2 minutes (or 7.2º) on average for extreme hand-midsagittal plane misalignments, haptic parallel-setting with similarly extreme misalignments have reported average deviations as large as 55º or more (Kappers 1999; Zuidhoek et al., 2004). Although small, the deviations in the verbal judgment task show the same characteristics as those resulting from the parallel-setting task, and point to hand-centered reference frames to be the origin of the deviations in both tasks: the larger the hand-midsagittal plane misalignment, the larger the bias in perception. As the deviations in the verbal judgment task have been found to be very small even with large hand-midsagittal plane misalignments, one may argue that there is less room for an effect of delay. Indeed, in our previous study, only a minor delay effect (a small improvement for right hand perceptions only) was obtained (Zuidhoek et al., 2005). Therefore, we decided to not include a delay condition in the present verbal judgment task.

In addition, it is of clear interest to explore the haptic oblique effect in the verbal judgment task (cf. Zuidhoek et al., 2005). It should provide information on the performance of the early blind, the late blind and the sighted on the oblique effect in a task expected to trigger a more allocentric representation of orientation than the previous studies, which used motor reproduction responses. In this respect, it may be valuable for the aforementioned controversy between previous studies on the role of visual processing in the haptic oblique effect (Appelle & Countryman, 1986; Appelle & Gravetter, 1985; Gentaz & Hatwell, 1998).

Method

Participants and General procedure

Participants and General procedure are the same as in experiment 1.

Design

The experiment had a mixed design with position and orientation as within-, and group as between-subjects factor. It comprised the immediate verbal judgment of haptically perceived orientation (cf. Zuidhoek et al., 2005). The time restrictions were the same as in the non-delayed parallel-setting task in the current study, comprising a haptic exploration period of 1s, a delay of 0s, and verbal response period of 1.4s. Previously, these particular time restrictions were found to result in reliable and quite accurate performance in blindfolded sighted individuals (Zuidhoek et al., 2005).

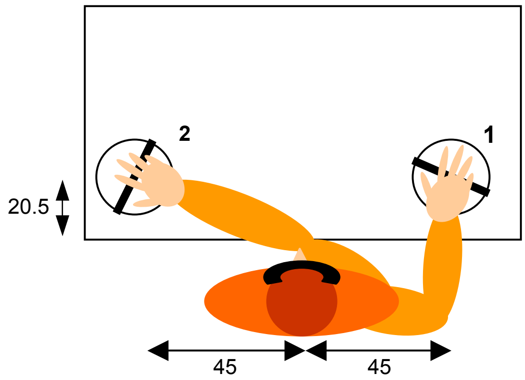


Figure 3. Top view of the experimental set up used in the verbal judgment of orientation task.

Apparatus and stimuli

The experimental set up was the same as in experiment 1. Two stimulus positions were used. The placing of the bars was slightly different, however (see Figure 3). The bar stimuli appeared under one of eight possible orientations, in random order. To limit the experiment's duration, we chose to have the stimuli explored unimanually by the right hand only, since previous work has pointed that performance is equally good for both hands (Zuidhoek et al., 2005). The orientations were chosen in such a way that they corresponded to whole minutes. In addition, we made sure they did not correspond to multiples of 5 minutes to avoid response biases affecting the data. The following minutes were presented: 1, 4, 8, 12, 16, 19, 23, 27, corresponding to the following orientations of 84º, 66º, 42º, 18º, 174º, 156º, 132º, 108º (where 0º is parallel to the long side of the table; increasing orientation values signify a rotation in counterclockwise direction).

The total number of combinations was 16 (2 (stimulus locations) x 8 (stimulus orientations)). All combinations were presented three times, adding up to a total of 48 trials. The order of presentation was random and different for each participant.

Procedure

The blind or blindfolded participants were told that they were sitting at the stimulus presentation table and that they were about to repeatedly feel the orientation of a bar on different locations on the table with their right hand. They were instructed to keep their exploring limb in a natural position and to think of the felt bar as the minutes hand of a clock, and to assign a number of minutes to its orientation. The orientation was allocentrically defined, i.e., it was defined with respect to the stimulus presentation table. More specifically, they were told that all ‘clocks’ on the table were positioned in such a way that when the minutes hand signified 15 or 45 minutes, it was parallel to the side of the table they were sitting at. To be sure that they understood this, the participants were asked to place a pen on a table in the orientation corresponding to 15 and 45 minutes. Performance of all participants expressed normal understanding. They were instructed to respond as accurately as possible in whole minutes within a response range of 0 to 60 minutes immediately after having felt the bar.

Before the start of a trial, the experimenter positioned the bar in a predetermined orientation. Next, he took the right hand, while saying (the Dutch equivalent of) "here is the bar" and left it to float about 5 cm above the bar. After this, the experimenter started the timed sequence on the computer. A sampled male voice uttered the numbers "one", "two", "three" which indicated which action was desired from the participant at a particular point in time. "One" signified the start of the 1-second exploration period of the bar. "Two" signified the end of the exploration period and also the start of the period in which the verbal response had to be given. "Three" signified that the response period (1.4s) was over.

Participants had to obey the time restrictions when exploring the bar or verbally responding. In addition, they were not allowed to touch the edges of the table during the trials and had to remain seated the way they were. In between trials they were allowed to touch the table to check their positioning with respect to the table, which happened only occasionally. Trials in which these restrictions were not met, as checked by the experimenter, were presented again at a later time during the session (approximately 10% of the trials). Participants were free in choice of strategy when exploring the bar. In practice, participants would just press the hand on the bar. Occasionally, the hand press was followed by a quick hand movement over the bar. After exploration of the bar, the reference hand had to be returned to the body. After the participant had finished the trial by giving his verbal response, the experimenter noted it down and both continued with the next trial.

Data analyses

Analyses were performed on signed errors to examine the differences between the groups with respect to systematic errors. A positive value signified an overestimation of the number of minutes on the haptically perceived clock, expressing the perception of the orientation of bars as if rotated clockwise from their 'true' orientations; a negative value signified an underestimation, expressing the perception of the orientation of bars as if rotated counterclockwise from their true orientations. Note that deviations of exactly 15 minutes can, in principle, be interpreted as a large overestimation as well as a large underestimation. Therefore errors of 15 minutes (only 2 of 2208 data points) were left out the signed error analyses.

With respect to the haptic oblique effect it has to be noted that our stimuli did not contain purely horizontal (0°), vertical (90°) or "ideal" oblique (45°, 135°) orientations, as stimulus orientations corresponding to multiples of five minutes (0°, 90°) could have led to response biases, and 45° and 135° do not correspond to whole minutes (7.5 min and 22.5 minutes, respectively). However, the orientations we did use deviated only a small amount from the "ideal" horizontal, vertical and oblique orientations. To examine whether the oblique effect holds for verbal judgments of haptically obtained orientation information, the four orientations closest to the horizontal (i.e. 174° and 18°), vertical (84° and 108°) and those four closest to the ideal oblique orientations (42°, 66°, 132° and 156°) were taken together to form groups of horizontal-vertical and oblique orientations, respectively, corresponding to the factor orientation type. For the haptic oblique effect analyses, mean *standard deviations* (sd, in minutes) were computed, to assess the variability for these orientation groups.

As we were interested in the effects of both visual and haptic experience, as well as possible interaction effects, we planned comparisons for all group combinations when addressing the theoretical issues raised in the introduction. In analyses of secondary interest or of explorative character, the three level between-subjects factor of experimental group was default. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction.

Results

Perceptual biases

A 2 (position) x 8 (orientation) x 3 (group) mixed ANOVA was performed on the mean signed errors. It revealed significant main effects for position ($F(1,43) = 18.7$,

$p < .001$), and orientation ($F(3.8, 162.0) = 4.7$, $p < .002$, $\varepsilon = .54$). The main effect of position signified a difference between performance for both positions: on position 1, the mean performance reflected an underestimation of orientation of -.77 minutes (corresponding to 4.6º), and a mean overestimation of orientation on position 2 of .81 minutes (corresponding to 4.9º). The main effect of orientation was expressed in differently signed mean deviation sizes for different orientations: .26, .58, .50, .1, -.32, -.53, -.62 and .16 for 1, 4, 8, 12, 16, 19, 23 and 27 minutes, respectively. Fifteen paired t-tests with Bonferroni correction lowering α to .0033 suggested that the interaction is particularly caused by performance on a bar orientation of 23 minutes, which seemed to differ significantly from performance on 8 minutes ($t(45) = 3.3$, $p = .002$), and showed trends towards differing from performance on 1 ($t(45) = 2.8$, $p = .008$), 4 ($t(45) = 2.8$, $p = .008$) and 12 minutes ($t(45) = 3.0$, $p = .005$). All other t-values < 2.6, p-values > .01.

Figure 4 depicts performance of all three experimental groups with respect to deviations and their dependence on spatial position. With deviations averaged over the two positions being close to 0 for all groups, no significant main effect of group was found ($F(2,43) = .52$). However, a trend was found for a group x position interaction ($F(2,43) = 2.8$, $p = .07$), which may signify larger and more systematic errors for the blind (see figure 4): early blind, late blind and sighted controls produced the following deviations (in minutes) in verbal judgments on positions 1 and 2, respectively: early blind, -1.3, 1.3; late blind, -1.0, .6; controls, .02, .48. To investigate whether the absolute mean signed error sizes over both positions were different for the groups (1.3, .8, .24, for the early blind, the late blind and the sighted, respectively), additional univariate mixed ANOVA's with group as 2-level between-subjects were performed, which showed that the blind (early + late blind) made significantly larger errors than the sighted $F(1,44) = 4.5$, $p = .04$. Comparing the visually experienced (late blind + sighted) to the visually inexperienced, resulted in a trend ($F(1,44) = 3.5$, $p = .068$). No differences were found between the groups with respect to the effect of orientation.

Interestingly, the mean deviation sizes for different bar orientations mentioned above suggest relatively spared performance for the bar orientations the orientations closest to 90º and 0º as compared to the more oblique orientations, i.e., performance on the bar orientations corresponding to 27, 1, 12, and 16 minutes seems to deviate less from 0 than performance on the minutes corresponding to more oblique orientations: .21 minutes and .56 respectively, when direction of the mean errors is ignored. As this may theoretically be important with respect to the oblique effect, we decided to investigate this: a mixed ANOVA with group (3) as between-subjects factor was carried out for orientation type (2 levels). Indeed, a main effect of orientation type was found: F(1,43) = 6.8, p = .013. No effects of group were found.

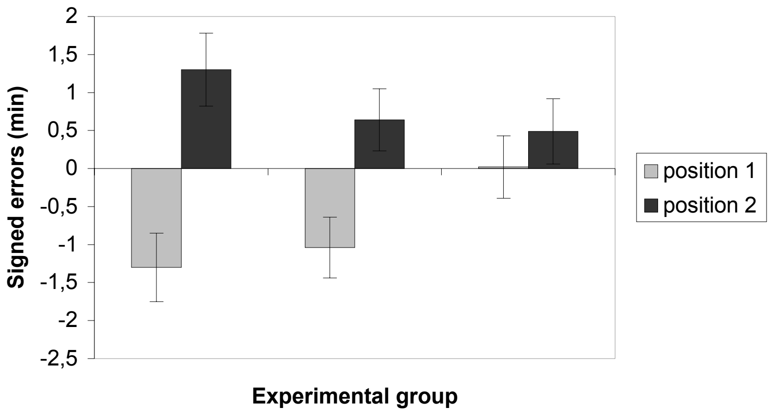


Figure 4. Performance of early blind, late blind and sighted participants on positions 1 and 2 in the verbal judgment task. Error bars show +/- 1.0 standard errors of mean.

Haptic oblique effect

A 2 (position) x 2 (orientation type) x 3 (group) mixed ANOVA was performed on mean standard deviations. It revealed a significant main effects for orientation type (F(1,43) = 7.1, p = .011) as well as position (F(1,43) = 4.2, p = .046). The effect of orientation type signified a smaller mean standard deviation for bar orientations close to 0º and 90º, than for the more oblique ones: 2.0 minutes vs. 2.2 minutes. The effect of position reflected mean standard deviation to be smaller on position 1 than on position 2: 2.0 vs. 2.2 minutes, respectively.

No main or interaction effects for group were found, not using the present, nor with similar mixed ANOVA's after regroupings, with group as 2-level between-subjects factors. In addition, no effect of position x orientation type was found (F(1,43) = .1), suggesting that the haptic oblique effect is independent of the location of the perceived bar.

Discussion of experiment 2

The results showed that the haptic perception of single bar orientation is systematically biased in blind as well as sighted individuals. The directions and the sizes of the mean errors on both positions were consistent with those of a previous study, which suggested these deviations to result from hand-centered reference frames (Zuidhoek et al., 2005). Importantly, the deviations appeared to be more pronounced in the blind. The late blind seemed to perform more like the early blind than the sighted which is in contrast with experiment 1, in which late blind performance resembled that of sighted (less variable and improvement with delay). Both findings seem to underline, however, that becoming blind reduces the (ability or drive to) use of visual strategies (cf. Ernest, 1987). Interestingly, when verbally judging single bar orientations, our participants seemed to perform better on those close to 0º and 90º over oblique ones irrespective of their visual or haptic experience. This was reflected in the variability in performance as expressed in the haptic oblique effect, which replicates Zuidhoek et al. (2005), as well as in the veridicality of the perception. The present findings are in line with that of Gentaz and Hatwell (1998) who showed that visual experience did not affect the haptic oblique effect with a motor reproduction task.

Interestingly, the systematic bias in perception and the haptic oblique effect seem to result from different neurocognitive mechanisms, since they are affected differently by location in space and experimental group. Whereas the systematic bias in perception and its variability (standard deviation) both depended on location of the bar in space, the haptic oblique effect (the difference in variability for horizontal and vertical orientations as compared to oblique orientations) did not (cf. Zuidhoek et al., 2005). Furthermore, while being blind resulted in larger systematic errors in the haptic perception of a single bar orientation, blindness did *not* affect the haptic oblique effect.

General discussion

The main goal of the present study was to investigate the role of visual experience in the haptic perception of orientation in peripersonal space. To this end, early blind late blind, and sighted participants were presented with two tasks requiring allocentric representations in order to be performed successfully. Differences in performance of the groups on these tasks were used to shed light on the mechanisms involved in haptic orientation perception, and to evaluate the relevancy of some of the leading ideas on the effect of blindness on spatial representation for haptic spatial perception in peripersonal space. In the first experiment, a haptic matching task, a test bar had to be rotated until it was parallel to a reference bar in immediate and 10 seconds delay conditions. In a second experiment, instead of a motor response a verbal response was required: participants had to assign a number of minutes on an imagined clock to the orientation of a single bar, with orientation explicitly defined to an allocentric reference frame, namely the stimulus table.

In general, the results of the present study suggest that mental visual processing mechanisms fulfill a beneficial role in the generation of allocentric representations of haptically perceived space. Moreover, the effects of visual experience we found in the present study indicate that visual experience may exert different effects in different haptic spatial tasks requiring an allocentric representation of bar orientation in space. In the parallel-setting task, the early blind displayed more variable performance than the visually experienced groups, and did not improve with delay while the visually experienced did. The sighted were found to improve more than the late blind participants. In the verbal judgment task, performance of the late blind resembled that of the early blind: both groups were outperformed by the sighted. Together, these results suggest that early visual experience provides structure (i.e. makes performance more reliable and consistent) and is necessary for a shift from ego- to more allocentric representations over delay time (cf. Rossetti et al., 1996). In addition, having lost vision later in life seems to reduce the ability or tendency to employ visual strategies (cf. Ernest, 1987).

The foregoing shows that the effect of (early) visual experience in contributing to allocentrically representing space depends on task characteristics. One may speculate on the nature of critical task characteristics that determine the influence of visual experience. Intuitively, a crucial task characteristic for effects of early visual experience to be found, may be the extent to which the visually experienced actually feel the need to make use of their visual experience, which may critically depend on respond method and seems to differ for late blind and sighted regarding their performance differences on the present tasks. An immediate motor response may cause participants of all experimental groups to act on their egocentrically biased haptic perception of the bars' orientations, i.e. they may act on what they haptically perceive without feeling the need to address other mechanisms to represent the bars. In contrast, a delay may stimulate or force the visually experienced participants to turn to other, arguably visual mechanisms (such as visual imagery) to retain the haptic orientation information. In turn, this may result in a recoding of the haptic information in more allocentric reference frames. In addition, explicitly defining bar orientation with respect to an allocentric reference frame (i.e. the stimulus table) in the verbal judgment task, may result in the mental employment of this reference frame to interpret the orientation of the bar. Seen in this light, it seems that differences between the early blind, the late blind and the sighted on allocentric haptic perception tasks may particularly emerge in tasks that stimulate or force participants to abandon representations at the haptic or motor level.

Having established that visual mechanisms play a role in haptic spatial perception, the obvious next question concerns the nature of these mechanisms. A likely mechanism would be visual imagery. The literature points to different underlying causes of why the imagery of the congenitally blind would be inferior to that of the visually experienced. According to Thinus-Blanc and Gaunet (1997), "[…] the consequence of an early lack of vision would be that (a) the amount of information stored in the form of mental images is diminished (or lacking) and (b) complex computations that rely on such types of representations are more difficult". This view may explain the structuring effect of vision and the advantage of the visually experienced on the verbal judgment task, yet can not explain the shift with delay in the parallel-setting task as it does not comprise differences related to time manipulation. Another approach is that of Cornoldi and Vecchi (2003), who concluded on the basis of their several studies on visuospatial working memory that congenitally blind individuals specifically experience problems with the generation, maintenance and manipulation of *multiple* mental images. This may explain the early blind's poorer performance on the parallel-setting task as compared with the verbal judgment task (two images vs. one), yet not why it only occurs in the delayed condition. In addition, it does not explain the differences in performance between the groups on the verbal judgment task (single image).

In addition to performance differences following from quantitative aspects of mental imagery (*amount* of images stored, *multiple* image generation), *qualitative* differences between visual and non-visual imagery may play a major role: in the spatial representation of haptic input, the forming of specifically *allocentric* and not egocentric representations of spatial information is helped by visual experience (Millar, 1988, 1994). A similar relationship between vision and the quality of spatial representation has been made with respect to concurrent *visual input*: Newport and colleagues (2002) have found that the facilitating effect of noninformative visual input is only found in haptic matching tasks requiring an *allocentric* representation (parallel-setting), and not in a similar matching task in which an egocentric representation was sufficient (mirroring with respect to midsagittal plane) in which noninformative vision was found to have a slightly *negative* influence on performance. In line with the foregoing, this would indicate that visual processing is qualitatively different from haptic processing with respect to the reference frames in which spatial input is coded. Our guess is that the same qualitative differences hold for *mental* visual processing and haptic processing. Seen in this light, visual imagery is qualitatively different from haptic imagery: having had visual experience results in images stored in memory that are more allocentric than only having had haptic experience, which makes it easier for visually experienced to adopt an allocentric reference frame to code space.

With respect to the haptic oblique effect as found with the verbal response in the verbal judgment task, no effect of visual experience was found. This replicates the findings by Gentaz and Hatwell (1998), who used a motor reproduction response in stead of a verbal response. This difference in dependence on visual experience between the systematic perceptual deviation and the oblique effect, suggests that these distortions in haptic orientation perception result from different neurocognitive mechanisms. In line with this, the oblique effect in the present study was found not to depend on spatial positioning of the stimuli while the systematic perceptual deviation - as displayed in both present tasks - did. Interestingly, however, a similar general, vision- and location-independent preference for orientations of 0º and 90º was also found in the location-based deviation in perception: with 90º, performance was better (smaller deviations) than on the other orientations in parallel-setting, and orientations close to 90º and 0º orientations were judged more accurately than the more oblique orientations in the verbal judgment task. Note, however, that the preference for 0º (parallel to the stimulus table's edge) in the verbal judgment task may result from the explicit definition of the bar's orientation with respect to the stimulus table in this task. This general preference of some orientations over others observed in both variability (oblique effect) and deviation size may reflect a general preference in the haptic system for the coding of orientations that are aligned with body and head axes and gravitational force (Luyat et al., 2001), independently of response mode, location in space and visual experience.

To conclude, the present findings indicate that with respect to the haptic perception of orientation, the current perspectives on haptic spatial representation, and blindness and spatial representation need refinement and elaboration. For one, the role of visual experience on haptic orientation processing depends on the aspect under examination. While visual experience reduced the size or variability of the systematic deviations in haptic orientation perception, it did not affect the haptic oblique effect, which suggests the distortions to depend on distinct neurocognitive mechanisms. The present findings indicate that the beneficial role of visual experience on haptic orientation perception may result from differences in strategy or ability due to early visual experience (Millar, 1988, 1994), the presence of stored visual images due to visual experience (Thinus Blanc & Gaunet, 1997), and the tendency or ability to use visual imagery (cf. Ernest, 1987) which appears to be diminished in the late blind as compared to the sighted. In the view proposed here, different haptic tasks engage different relative contributions of egocentric and allocentric reference frames as is expressed in the deviation patterns of a task (cf. Zuidhoek et al., 2003, Zuidhoek et al., 2005; Kappers, 2003). Importantly, the effects of (mental) visual processing are task-dependent. In tasks in which visual imagery is not encouraged, the effect of visual experience may be restricted to reducing variability in performance. The beneficial role of visual experience with respect to deviation size, may only be beneficial in tasks requiring allocentric representation (Newport et al., 2002). For such tasks, the effects of vision further depend on other task characteristics like temporal manipulations (delay), response mode (motor, verbal) and the extent to which (mental) reference frames are provided (explicitly allocentrically defined haptic input, noninformative vision). Taken together, the current findings imply that the ability to recode haptic spatial input to visuospatial images can be an important tool to improve allocentric representations required in certain haptic spatial tasks.

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References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61,* 303-321.

Appelle, S., Gravetter, F. (1985). Effects of modality-specific experience on visual and haptic judgment of orientation. *Perception, 14,* 763-773.

Appelle, S., & Countryman, M. (1986). Eliminating the haptic oblique effect: Influence of scanning incongruity and prior knowledge of the standards. *Perception, 15,* 325-329.

Batschelet, E. (1981). *Circular statistics in biology*. London, England: Academic Press Inc.

Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics, 59,* 456-469.

Cornoldi, C., & Vecchi, T. (2003). *Visuo-spatial working memory and individual differences*. Hove, England: Psychology Press.

Ernest, C.H. (1987). Imagery and memory in the blind: A review. In M.A. McDaniel & M. Presley (Eds.), *Imagery and related mnemonic processes: Theories, individual differences and applications* (pp. 218-337). New York: Springer-Verlag.

Farne, A., Pavani, F., Meneghello, F., & Ladavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain, 123,* 2350-2360.

Gentaz, E., & Hatwell, Y. (1998). The haptic oblique effect in the perception of rod orientation by blind adults. *Perception & Psychophysics, 60,* 157-167.

Gentaz, E., & Hatwell, Y. (1999). Role of memorization conditions in the haptic processing of orientations and the 'oblique effect'. *British Journal of Psychology, 90,* 373-388.

Graziano, M.S.A., Xin Tian Hu, & Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology, 77,* 2268 - 2292.

Graziano, M.S.A. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc Natl Acad Sci U S A, 96,* 10418-10421.

Kappers, A.M.L. (1999). Large systematic deviations in the haptic perception of parellelity. *Perception, 28,* 1001-1012.

Kappers, A.M.L. (2002). Haptic perception of parallelity in the midsagittal plane. *Acta Psychologica, 109,* 25-40.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 114,* 131-145.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Làvadas, E., Pellegrino, G. di, Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience, 10,* 581-589.

Lanca, M., & Bryant, D.J. (1995). Effect of orientation in haptic reproduction of line length. *Percept Mot Skills, 80,* 1291-1298.

Lechelt, E.C., Eliuk, J., & Tanne, G. (1976). Perception orientational asymmetries: A comparison of visual and haptic space. *Perception & Psychophysics, 20,* 463-469.

Lechelt, E.C., & Verenka, A. (1980). Spatial anisotropy in intramodal and cross-modal judgments of stimulus orientation: The stability of the oblique effect. *Perception, 9,* 581-589.

Lederman, S.J., Klatzky, R.L., & Barber, P.O. (1985). Spatial and movement-based heuristics for encoding pattern information through touch. *Journal of Experimental Psychology: General, 114,* 33-49.

Lloyd, D.M., Shore, D.I., Spence, C., & Calvert, G.A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience, 6,* 17-18.

Luyat, M., Gentaz, E., Corte, T.R., & Guerraz, M. (2001). Reference frames and haptic perception: body and head tilt effects on the oblique effect. *Perception and Psychophysics, 63,* 541-554.

Marks, L.E., & Armstrong, L. (1996). Haptic and visual representations of space. In T. Inui & J.L. McClelland (Eds.) *Attention and performance 16: Information integration in perception and communication* (pp. 263-287). Cambridge, MA, USA: Mit Press.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England: Clarendon Press/Oxford University Press.

Milner, A.D., Paulignan, Y., Dijkerman, H.C., Michel, F., & Jeannerod, M. (1999) A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Proc R Soc Lond B Biol Sci, 266,* 2225-2229.

Newport, R., Rabb, B., & Jackson, S.R. (2002). Noninformative vision improves haptic spatial perception. *Current Biology, 12,* 1661-1664.

Obayashi, S., Tanaka, M., & Iriki, A. (2000). Subjective image of invisible hand coded by monkey intraparietal neurons. *Neuroreport, 11,* 3499-3505

O'Connor, N., & Hermelin, B. (1975). Modality-specific spatial coordinates. *Perception & Psychophysics, 17,* 213-216.

Paivio, A. (1978). Comparisons of mental clocks. *Journal of Experimental Psychology: Human Perception and Performance, 4,* 61-71.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Curr. Opin. Neurobiol., 12,* 149-154.

Rorden, C., Heutink, J., Greenfield, E., & Robertson, I.H. (1999) When a rubber hand 'feels' what the real hand cannot. *Neuroreport, 10,* 135-138.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Rossetti, Y., & Régnier, C. (1995). Representations in action: pointing to a target with various representations. In B.G. Bard, R.J. Bootsma, & Y. Guiard (Eds.), *Studies in Perception and Action III* (pp. 233-236). Mahwah, NJ, Laurence Erlbaum Associates Inc.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-44.

Wechsler, D. (1997). *Wechsler Adult Intelligence Scale, Third Edition.* San Antonio, TX: The Psychological Corporation.

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). Multiple integration mechanisms in haptic space perception. *Experimental Brain Research, 157,* 265 - 268.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2005). Effects of hand orientation and delay on the verbal judgment of haptically perceived orientation. *Perception, 34,* 741-755.

Appendix A: Sample description of participants

Early blind

Subject number	*Occupation*	*Education level*	*Sex*	*Age*	*Etiology and further characteristics*	*Age of onset (years)*
1	Sports masseuse	Secondary school	F	41	Leber's amarosis, Ambidexter	0
2	Policy worker	University	M	41	Retino blastoma	0
3	Computer programmer	Higher education	M	33	Macula degeneration	0
4	Office assistant	Vocational Education	F	49	Rubella (mother)	0
5	Retired operator	Secondary school	M	58	Glaucoma, Ambidexter	2
6	Office assistant	Secondary school	F	34	Retrolental fibroplasias	0
7	Operator	Secondary school	M	38	Rubella (mother)	2-3
8	Translator	Higher education	F	30	Retrolental fibroplasias	0
9	Retired	Vocational Education	M	64	Retino blastoma	2-3
10	Teacher	Higher education	M	46	Leber's amarosis	0
11	Systems designer	Higher education	M	46	Retino blastoma	0-1
12	Consultant	Secondary school	F	55	Retino blastoma	0-1
13	Sound technician	Higher education	M	49	Retrolental fibroplasias	0

Late blind

Subject number	*Occupation*	*Education level*	*Sex*	*Age*	*Etiology and further characteristics*	*Age of onset (years)*
1	Physiotherapist	Higher education	M	52	Accident	10
2	IT-employee	Higher education	M	57	Born partially blind in one eye, other eye glaucoma	25
3	Social worker	Vocational Education	M	57	Usher's syndrome and an accident	25
4	Piano tuner	Vocational Education	M	40	Accident, Left-handed	19
5	Volunteer	Higher education	M	54	Macular degeneration	10
6	Office assistant	Secondary school	M	64	Congenital glaucoma	7
7	Operator	Secondary school	F	59		9
8	Music teacher	Higher education	M	64	Retinitis pigmentosa	40
9	Correspondence clerk	Vocational Education	M	60	Congenital glaucoma	49
10	Civil servant	Higher education	M	38	Brain tumour	4
11	Employment-finding for the blind	Higher education	M	59	Leber opticus artrosa and glaucoma	32
12	Social worker	Vocational Education	M	53	Aniridi and glaucoma	20
13	Operator	Vocational Education	F	58	Retinitis pigmentosa	14
14	Therapist	Secondary school	F	52	Born blind in one eye Glaucoma and inflammation of the cornea of the other eye	30
15	School teacher	Higher education	F	53	Congenital glaucoma	22
16	Psychologist	University	F	51	Congenital glaucoma	40
17	Social worker	Higher education	F	39	Unknown	35

Sighted controls

Subject number	*Occupation*	*Education level*	*Sex*	*Age*
1	Editor	Higher education	F	32
2	Editor	University	F	30
3	Retired	University	M	58
4	Research	University	M	37
5	Retired	Vocational Education	F	58
6	Ergotherapist	Higher education	F	36
7	Ergotherapist	Higher education	F	46
8	Journalist	Higher education	M	56
9	Musician	Higher education	M	53
10	Volunteer	Vocational Education	F	60
11	Personnel coordinator	Higher education	F	54
12	Administration	Higher education	M	67
13	Housewife	Secondary school	F	63
14	Ortho-pedagogue	University	F	40
15	Service manager	Higher education	M	48
16	Editor	University	M	51

Chapter 6 | Differences between early blind, late blind and blindfolded sighted people in implicit haptic spatial configuration learning and resulting memory traces

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Abstract

The present study focused on the roles of visual and haptic experience in implicit haptic spatial learning and resulting memory traces. During three trials, early blind, late blind and blindfolded sighted implicitly learned a spatial configuration of ten shapes by haptically matching these to cutouts in a board as fast as possible. Both blind groups were much faster than the sighted on all three trials. All three groups improved considerably from trial to trial, yet the sighted improved more than the blind, particularly from the first to the second trial. Subsequent memory assessment showed that the explicitness of the response is determining for the effects of visual and haptic experience on task performance. While superiority of the blind remained in the speeded implicit matching task after rotation of the stimulus frame, coordinate and categorical memory assessment with a non-speeded motor response showed no significant differences between the groups. Moreover, when assessed with an explicit verbal response, categorical spatial memory appeared strongest in the late blind group. Together, these findings suggest that haptic experience predominantly facilitates performance on implicit haptic spatial tasks, while visual experience becomes increasingly important as tasks require more explicit spatial knowledge.

Introduction

The visual and haptic input channels provide us with crucial information concerning the identity and location of objects in peripersonal space. Whereas the sighted depend particularly on vision to represent (peripersonal) space, the blind are bound to use the haptic system. As a consequence, one may expect that – when vision is not available - the blind are better, faster and more efficient in identifying and handling objects in peripersonal space than the sighted, as well as in learning and representing their locations. Strikingly, however, most studies seem to suggest that *visual* experience - either in combination with haptic experience or not - rather than haptic experience alone, facilitates haptic object identification and spatial representation in peripersonal space. Here, we wish to argue that this visual advantage may particularly be evident in tasks that are *explicit* (i.e., requiring conscious processing and declarative knowledge), and that varying tasks on the implicit-explicit dimension can have large impact on the performance differences between the early blind, late blind and sighted on a given haptic spatial task.

Identification accuracy

With respect to haptic identification *accuracy* of familiar 3-D objects or depictions of these, either no differences between early blind and visually experienced (i.e. late blind and sighted) groups are reported (Morrongiello, Humphrey, Timney, Choi, & Rocca, 1994; Heller, 1989b, Experiment 1), or differences that favor only the visually experienced, i.e. the late blind (Heller, 1989b, Experiment 2) or both the late blind and the blindfolded sighted (Shimizu, Saida & Shimura, 1993). Several explanations have been put forward to account for such differences. Differences between the late blind and the sighted are likely to arise from the lack of haptic experience in the sighted. The beneficial effects of visual experience on haptic identification of particularly (familiar) 3-D stimuli (Shimizu et al., 1993) may result from similar (James, Humphrey, Gati, Servos, Menon & Goodale, 2002; Newell, Ernst, Tjan & Bulthoff, 2001) or common representation of haptic and visual form (Reales & Ballesteros, 1999). In addition, for the inferior performance of the early blind on 2-D identification tasks (e.g. Shimizu et al., 1993, Heller, 1989b, Experiment 2), several theoretical explanations have been put forward, such as differences in haptic exploration (Magi & Kennedy, 1980), problems with making decisions (Heller, 1989b), and/or dependence on egocentric coding (Millar, 1981).

Identification speed

Although no advantage of haptic experience alone for haptic identification *accuracy* has been reported, there is an indication that it may *speed up* the identification process, at least in some circumstances: Heller (1989b, Experiment 1) found that congenitally and late blind participants were much faster than the sighted on the matching of simple braille-sized 2-D shapes, while no differences in matching accuracy could be reported. The precise origin of this specific advantage of haptic experience is unclear. It may be due to the size of the objects, as braille reading experience may facilitate the recognition of patterns on the fingertip. In support of this, Morrongiello and colleagues (1994) did not find identification speed differences between sighted and early blind children (aged 3-8 years) for familiar 3-D stimuli. Another possibility is that the influences of haptic and visual experience depend on the nature of the depictions: in contrast to the aforementioned studies (Shimizu et al., 1993; Heller, 1989b, Experiment 2; Morrongiello et al., 1994) the stimuli in Heller's study (1989b, experiment 1) were simple and abstract (yet for the greater part familiar) shapes. It may be that visual imagery facilitates the accuracy of the haptic identification of (depictions of) more complex stimuli (Heller, 1989a, but see Morrongiello et al., 1994), whereas haptic experience increases the speed of the identification process of simple, more abstract shapes.

Identification: implicit vs. explicit factors

Another critical factor, on which we focus in the present study, may be the degree to which a task requires explicit processing: a matching response (Heller, 1989b, Experiment 1) may entail less explicit identification than naming (Shimizu et al., 1993; Heller, 1989b, Experiment 2; Morrongiello et al., 1994). While the former requires "just" a same/different judgment, the latter requires true and full identification. In other words, identification as assessed with matching and naming may entail processing at different levels, with matching triggering more implicit, and naming triggering more explicit processing. Considering the aforementioned findings, it may be that visual processing becomes increasingly important when more explicit measures of identification are required, while more implicit measures may favor haptic experience. This interpretation would be in line with the intuitive superiority of the blind with respect to the speed with which objects can be purposefully handled in spatial tasks.

Space, explicit learning

Also with respect to *spatial* representation of multiple objects, visual experience rather than haptic experience has been found to improve task performance.

Importantly, however, the respective roles of visual and haptic experience have been subject of study only under conditions in which participants were given unlimited time to *explicitly learn* the objects and their locations by heart before the actual experiments began (Ungar, Blades & Spencer, 1995; Hollins & Kelley, 1988). These studies have demonstrated an advantage for the visually experienced in the localization of objects, yet only after object configuration *rotation*. This advantage was found to result from qualitative differences in spatial coding of haptic spatial information, with the visually impaired, and the early blind in particular, relying predominantly on egocentric and movement memory to code spatial location in peripersonal space, in stead of external frames of reference. This is in line with the ideas of Millar (1979, 1981, 1988, 1994), who proposed that three types of coding are used in peripersonal space - egocentric, allocentric, and movement coding -, and has shown repeatedly that visual experience affects the extent to which these three types of coding are adopted.

Space, implicit learning: quantitative advantages for the blind?

Importantly, to our knowledge, the roles of visual and haptic experience in the *implicit* spatial learning through haptically acting with multiple objects and the resulting memory characteristics have not been addressed yet. We wish to speculate that more implicit spatial learning tasks may show *quantitative* differences favoring the blind. More specifically, differences in (implicit) haptic identification and general handling speed may result in differences in the implicit learning of and memory for objects in peripersonal space. For one, haptic dexterity and speeded (implicit) identification may create more room for memorization processes at implicit but also more explicit levels. In addition, the blind may display faster, more automated learning and storing of the objects and their locations than the sighted, since not storing this information would result in repeatedly having to haptically scan the environment for a desired object, which is a much more elaborate and time consuming process than visually scanning.

Space, implicit learning: smaller qualitative differences between the blind and the sighted?

In addition, one may argue that varying tasks along the implicit-explicit dimension during learning can cause *qualitative* differences (in terms of reference frame employment) between the blind and the sighted in spatial representation as well. According to Milner and Goodale (1995), egocentric coding is employed in fast implicit tasks and used for immediate goal-directed movements, while allocentric coding is used in explicit tasks underlying conscious perception and spatial memory. Thus, whereas explicit learning may comprise more allocentric reference frame employment, implicit learning may trigger more egocentric reference frame involvement. Therefore, one may argue that tasks that require multiple fast actions predominantly trigger egocentric reference frame involvement. In addition, it may be that such tasks actively hamper the generation of an allocentric (i.e., explicit) representation, as the maintenance of haptically acquired spatial information in working memory has been found to be effortful (Gentaz, & Hatwell, 1999), and spatial movements may occupy the (visuo-)spatial sketch pad (e.g. Logie, 1995; Noordzij, Van der Lubbe, Neggers & Postma, 2004). Consequently, in contrast to tasks in which the spatial material is explicitly learned (Hollins & Kelley, 1988; Ungar et al., 1995), it may be that demanding tasks requiring multiple fast movements to learn the locations of multiple objects show no or minimal advantage for the sighted, even after rotation.

Space: implicit vs. explicit responses

In addition to the possible effects of varying tasks along the implicit-explicit dimension by manipulating learning conditions, it has been found that also the explicitness of the *response* affects the relative employment of egocentric and allocentric reference frames in tasks. Whereas implicit immediate goal-directed action responses have been found to trigger (multiple) egocentric reference frames (Paillard, 1991, Milner & Goodale, 1995), explicit responses like matching, judging and comparing vary in their recruitment of egocentric and allocentric frames (Creem & Profitt 1998), depending on the specific response modality. *Verbal* judgment responses predominantly trigger predominantly allocentric reference frames (Sterken, Postma, De Haan & Dingemans, 1999; Zuidhoek, Kappers & Postma, 2005). In contrast, *motor matching* responses have been found to be considerably influenced by egocentric reference frames associated with the motor response (Kappers, 2003; Zuidhoek, Kappers, Van der Lubbe & Postma, 2003; Zuidhoek, Visser, Bredero & Postma, 2004).

Space, blindness and responses from memory: qualitative differences

Importantly, under memory conditions, the abovementioned egocentric influences appear to be reduced in the sighted and (less) in the late blind, yet to be undiminished in the early blind (Zuidhoek, Kappers, Noordzij, Van der Lubbe & Postma, 2004; Zuidhoek, Noordzij, Kappers & Postma, submitted). In line with this, delayed pointing in the early blind has been suggested to reflect predominantly egocentric spatial coding, in contrast to that of sighted (Rossetti, Gaunet, & Thinus-Blanc, 1996). It may be that in *object configuration* memory after implicit learning these qualitative differences are also present, with egocentric coding being more prominently used by the blind than by the sighted. However, considering the foregoing, it is likely that the results depend largely on the explicitness of the response.

In sum, looking at haptic spatial performance from an explicit-implicit perspective may shed a new and valuable light on spatial performance by the blind and the sighted. The aim of the present study was to examine the roles of visual and haptic experience in implicit spatial learning of object configurations and the resulting memory representations. Differences in memory representations between the early blind, late blind and sighted were addressed by employing several response methods that vary in explicitness, focusing on recall of object locations and performance after mental rotation of an object configuration in peripersonal space. The object array used was that of the portable tactual performance test (pTPT), which is part of the Halstead-Reitan Test Battery (Reitan & Wolfson, 1993).

Early blind, late blind and blindfolded sighted individuals learned ten objects (familiar shapes) and their locations during a speeded matching task, which was repeated twice. During these three trials participants were to fit the shapes into matching cutouts in a board as fast as possible, providing information on matching speed and implicit learning. We expected haptic experience to be more important than visual experience to perform this task, since it seems to require: (a) fast handling of objects which requires haptic dexterity; (b) many movements likely to interfere with spatial working memory processing which may particularly hamper allocentric reference frame generation; (c) only implicit identification (matching and not naming).

Furthermore, to examine several characteristics of the resulting spatial memory traces on different processing levels, we varied the degree to which they would be expected to address implicit and explicit spatial representations. For one, we addressed the possible differences between the groups after rotation of the object configuration, as did previous studies (Hollins & Kelley, 1988; Ungar et al., 1995) which showed an advantage for visually experienced individuals. In the present study, however, participants were to execute the same speeded matching task they had used in the first three implicit learning trials, which we expected to trigger mainly implicit, egocentric spatial representations, also in the visually experienced. Since these representations do not match the allocentric nature of the task, we anticipated no or only minimal advantages for the visually experienced groups after rotation.

Two further trials assessed spatial memory characteristics after implicit learning of the object locations, using free recall conditions. One was a (relatively implicit) non-speeded motor response, the other an (explicit) verbal response. In the motor response trial, participants had to place the shapes on a (non-rotated) board of equal size without cutouts, as accurately as possible. As such, this trial can be expected to assess both explicit spatial memory and implicit motor representations. To investigate the involvement of both, differences in performance with respect to the *spatial grain* of the motor responses were examined. It has been suggested that implicit egocentric coding is highly accurate ('coordinate coding'), and explicit allocentric coding is of more categorical nature (i.e., less metrically accurate, yet comprising relative and rough spatial relations) (Milner & Goodale, 1995). Thus, relatively more or better egocentric coding by the blind (e.g. Millar, 1981, 1988, 1994) could be expressed in more accurate, metric placement for this group (cf. Jones, 1972). Indeed, along the same line, allocentric coding, used more often by the sighted and – maybe to a lesser extent – by the late blind (cf. Millar, 1981, 1988, 1994), may result in better categorical coding of object location for these groups (cf. Milner & Goodale, 1995).

The verbal response, a description of the shapes and their location, was expected to reflect the explicit, declarative spatial knowledge of the object configuration, without possible response-related implicit influences of the motor response. In addition, the accuracy of verbal descriptions of the *shapes* may provide insight in the level to these were identified. Furthermore, as proposed by Brambring (1982), the characteristics of verbal descriptions of the spatial relations in locomotor space may reflect the spatial coding strategies used. He found that the route descriptions by the blind and the sighted differ: whereas the sighted gave environment-oriented (or allocentric) descriptions, the blind tended to use more person-oriented (or egocentric) descriptions. Although no data are available on verbal descriptions of haptically explored *small* scale environments, and the roles of haptic and visual experience, similar rules may apply.

Method

Participants

Appendix A (*Chapter 5*) shows the list of participants. Thirteen early blind, seventeen late blind and sixteen sighted people participated in both experiments. The blind were recruited with announcements in magazines for the visually impaired. The sighted participants had blind partners or relatives, or worked (paid or on voluntary basis) in institutions for the blind. None of the participants had neurological or motor deficits. The early blind group consisted of congenitally blind and early blind individuals that had become blind before the age of three. Those that were not blind from birth had no memory of vision whatsoever. All participants in the late blind group had rich vivid visual memories, and reported to have had used vision as a primary spatial modality. The blindness of the participants had different etiologies. Some late blind participants were born visually impaired and had gradually become blind during life. Others had lost their sight due to accidents. A minority of the blind participants had diffuse light sensations, but denied being able to use this in any form of spatial behavior. Sighted control participants where blindfolded.

Early blind, late blind and sighted control participants were matched for sex ($\chi^2(2) = 1.1$, $p = .57$), and approximately matched for age and education. Importantly, verbal IQ as assessed with two subscales (Vocabulary and Similarities) of the Dutch version of the WAIS-III (Wechsler, 1997) showed no significant difference between the three groups ($F(2, 43)= 1.4$, $p= .3$). Almost all participants were right-handed as assessed with Annett's handedness questionnaire (Annett, 1970); three participants were ambidexter or left-handed.

All participants gave their informed consent to inclusion in this study and received payment for their participation. They were naive to all aspects of the tasks, i.e., they had never seen or felt the set-up, were unaware of the experimental purposes, and were never given any feedback.

General Procedure

All participants were enrolled in an elaborate study on spatial cognition in the blind comprising several more tasks to be reported elsewhere. Participants individually performed haptic, verbal and imagery tasks, on one day of testing. About half of the participants performed haptic tasks in the morning and verbal and imagery tasks in the afternoon, after lunch. For the other half, it was the other way around. Experimental sessions were short (max. 30 minutes) to avoid weariness and fatigue during the experiments. In addition to a lunch break (1 hour) between the morning and afternoon session and two coffee breaks (10 minutes), participants were allowed breaks whenever they needed them.

Apparatus and stimuli

The portable tactual performance test (Reitan & Wolfson, 1993) is originally a measure for haptic shape recognition and incidental memory for haptic spatial relations. To serve the present purposes, the material was used differently. See Figure 1 for a schematic drawing of the stimuli and their locations. The stimuli consisted of a 45.5 x 30.2 x 2.1 cm wooden board containing ten shape cutouts and ten different geometrical shapes. The shapes included square, oval, star, diamond, hexagon, rectangle, circle, semicircle, triangle, cross. All shapes were 2.1 cm thick, but varied in their proportions. The smallest shape was 7.5 x 7.5 cm (square), the largest 16.7 x 7 cm. Each cutout could contain only one shape. The board was placed on a table right in front of the seated subject, with the longer sides parallel to the table's edge. In one trial, this board was replaced by a board of equal size without cutouts. A piece of paper showing the outlines of the shapes in their proper locations was attached to this board. During testing the boards were taped to the table to avoid shifting. The ten shapes were placed in four random piles - two piles of three shapes, and two of two shapes – placed either to the right or to the left of the board, depending on hand preference.

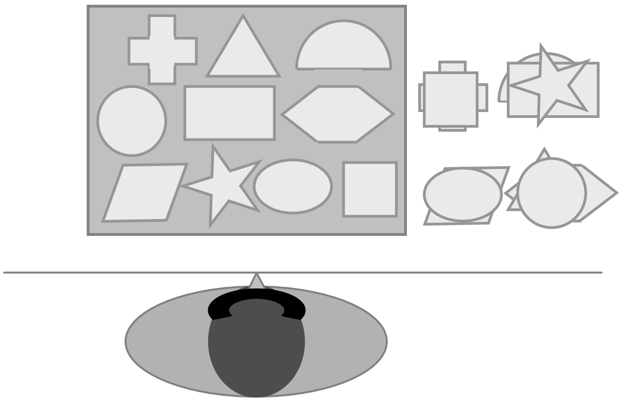

Figure1. Top view of the board and objects of the portable Tactual Performance Test (pTPT), as presented to right-handed participants in trials 1-3.

Procedure

Sighted participants and those with residual diffuse light sensations were blindfolded before the experimenter brought out the board and shapes. The participants were not allowed to explore the board or the shapes before actual testing, and it was not before the start of a trial that they were informed about their task in only that particular trial. In the first three trials, they were asked to fit the shapes into the proper cutouts as fast as possible. They were allowed to use both hands and were free in choice of strategy. The experimenter started the stopwatch when participants first touched the board or (one of the) shapes; the stopwatch was stopped right after the participant had correctly placed the last piece. Before the fourth trial, the board was replaced by a wooden board of equal size and position, yet without the cutouts. Now, participants were to place the shapes on their proper locations as accurately as possible (trial 4). They were allowed to take as much time as they needed; time was not recorded. After participants had completed this task, the locations of the shapes were recorded by outlining them with a pencil on the piece of paper covering the board which also showed the correct outlines. In the fifth trial, this board was replaced by the original board, but now it was rotated 90º counterclockwise. Participants were verbally notified of this and had to hold the short ends of the board while the experimenter was rotating it in order to clarify what they had been notified of. Next they were asked to again fit the shapes into the proper cutouts as fast as possible. Once more, time was recorded. After this, both the board and shapes were removed. Now participants were asked to name or describe the objects and describe how the different shapes were situated on the (non-rotated) board, as accurately as possible, and in such a way that one could place the shapes in their right location using their descriptions only (trial 6). Their descriptions were recorded using sound recording equipment.

Although other sequences of trials 4 through 6 are conceivable, we chose to have the non-speeded motor response (trial 4) before the rotation trial (trial 5) as we anticipated that rotation of the board may disrupt coordinate (movement, egocentric) coding, which we planned to assess with the non-speeded motor response. Because the verbal response was expected to trigger explicit spatial reasoning we chose it to be the final trial, in which case it would not affect performance on the other trials.

Data analyses

General

As we were interested in the effects of both visual and haptic experience as well as possible interaction effects, we used (general linear model) ANOVAs with the 3 groups as between subjects factor, as a default, and planned to compare performance of the blind (EB + LB) with that of the sighted, that of the early blind to that of the visually experienced (LB + BS), and that of the late blind to that of the other groups (EB + BS), as well. Those comparisons that did not result in one or more significant effects (or trends) have not been mentioned in the results section. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction.

Haptic matching and object configuration learning: trials 1, 2 and 3

The time (in s) to complete trials 1 through 3 provides information about the haptic matching capacity and implicit learning of an object configuration.

Rotation: trials 3 and 5.

To examine the effects of rotating the board on speeded haptic matching performance, the differences between the groups in completion time for trial 3 and trial 5 were analyzed.

Coordinate and categorical accuracy of free placement of shapes: trial 4

Both coordinate and categorical accuracy of free placement of the shapes were measured to provide information about the spatial grain of object location memory after three trials of implicit learning. The accuracy of coordinate or metric placement provides information about the extent to which egocentric and movement coding was used to represent space. Our measure of metric accuracy indicated how far an object was placed from its original position (the distance between the geometrical centers of the objects, in cm).

The measure of accuracy of categorical placement was a measure of categorical distance, which indicated how far, on average, the objects were *categorically* removed from their original position. Categorical positions were chosen in such a way that they could be easily verbally coded in terms of top, center, bottom and left, center, right. For this reason, star and ellipse were placed in the same categorical position, i.e. the bottom-center position. If an object was placed closer to its original location than to other object locations, the object was assigned 0. If it was placed closest to another object's position, it was assigned a number corresponding to the sum of horizontal and vertical categorical distance to it, or in other words, the number of steps in horizontal and vertical direction needed to get from this categorical position to the original categorical position. Differences between the groups with respect to categorical accuracy, may be indicative for differences in the amount of *allocentric* coding of object locations.

Verbal descriptions of objects and their spatial locations (free recall): trial 6
A number of measures was examined. First we investigated whether visual or haptic (or both) experience affected the number of objects remembered and the way the objects were named and described. To examine possible differences between the descriptions of the objects, we discerned between the number of objects correctly named (e.g. calling the cross a "cross" or a "plus sign"), correctly described (e.g. calling the semicircle a "shape, round at one side and flat at the other") and ambiguous, unclear or incorrect descriptions ("a thing with multiple protruding parts"). The absolute numbers of correctly named objects, objects described correctly, and objects incorrectly described, were used to examine possible differences between the groups with respect to explicit haptic identification.

Second, we investigated whether spatial language differed for the three experimental groups, which may reflect coding strategy differences between the blind and the sighted (cf. Brambring, 1982). Following Ungar and colleagues (1995) who observed different strategies employed to encode spatial configuration of objects, we examined the number of spatial descriptions in which the object's position a) was pointed out by referring to the board ("the cross was to the top left of the board"); b) was described with respect to another object ("the triangle was right of the cross"); c) was described with respect to a part of the participant's body ("the circle was over here" or "the circle was to my left "). In order to get a measure of the characteristics of the descriptions irrespective of possible differences in object descriptions, also descriptions involving incorrect or unclear descriptions were included. Furthermore, we recorded the number of deviant ways to describe the positions of the objects (using the clock face and wind quarters), number of times visual language was used (calling the semicircle "a setting sun") and the number of times extra (correct) information was given about the shape of the board, number of rows and columns, or the placement (orientation) of the objects on the board ("the long side of the semicircle was parallel to the long end of the board").

Third, the number of objects verbally placed in their correct categorical position (using any of the above mentioned referral types) were counted, providing a measure for differences with respect to the correctness of the representation of the relations between the different objects within the configuration.

Results

Haptic matching speed and object configuration learning: trials 1, 2 and 3

Figure 2 shows the average performance of the three experimental groups over the four time trials. A 3 (trial) x 3 (group) mixed repeated measures ANOVA was conducted to examine the learning over the first three trials, as expressed in completion times. Main effects for group ($F(2,43) = 14.8$, $p < .001$) and trial ($F(2,86) = 31.4$, $p < .001$) were found, as well as a trend towards a group x trial interaction ($F(4,86) = 2.2$, $p = .07$). The main effect of group was expressed in different mean completion times for the groups: EB took 79 s on average to perform the task, LB 75 s, and BS 138 s, suggesting (as does Figure 2) that performance differences were in favor of the blind over the sighted. The main effect of trial was expressed in different means for trials 1, 2, 3 which were 125 s, 90 s , 76 s, respectively. Contrast analyses showed that this main trial effect expressed significant learning from trial 1 to trial 2 ($F(1,43) = 26.8$, $p < .001$), and from trial 2 to trial 3 ($F(1,43) = 6.5$, $p = .015$).

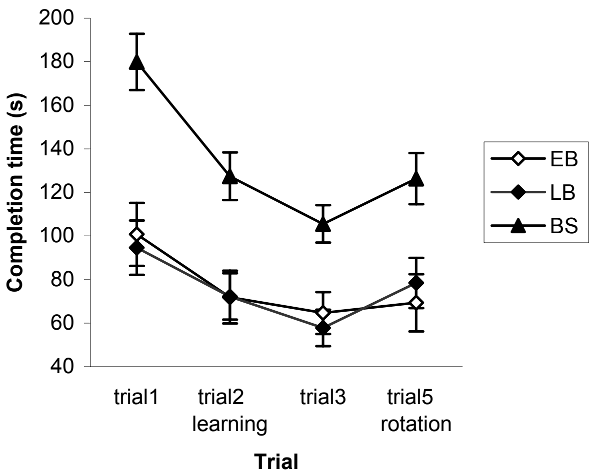

Figure 2. Completion times on the time trials for the early blind (EB), late blind (LB) and blindfolded sighted (BS) participants, in seconds. Performance over trials 1 to 3 reflect implicit learning; trial 5 expresses performance after rotation of the stimulus frame.

A two 3 (trial) x 2 (group) mixed ANOVA's comparing the blind (EB + LB) with the BS showed a strong main effect of group ($F(1,44) = 30.1$, $p < .000$), indicating a clear advantage for the blind. In addition, an (unsurprising) main trial effect ($F(2,88) = 37.5$), as well as a significant trial x group interaction were found: $F(2,88) = 4.4$, $p = .015$. Contrast analyses showed that this effect was mainly due to differences in learning from trial 1 to trial 2. Here, the sighted improved performance by 53 s, while the blind improved only 25 s ($F(1,44) = 3.9$, $p = .054$); the learning differences between the groups over trials 2 to 3 were far from significant ($F(1,44) = .8$). Visual inspection of Figure 2. seems to suggests that the learning differences between the blind and the sighted from trial 1 to trial 2 are primarily due to differences between the sighted and the late blind.

Effects of Rotation on completion time: trials 3 and 5

A 2 (trials) x 3 (group) mixed ANOVA showed main effects of trial ($F(1,43) = 8.0$, $p = .007$) and group ($F(2,43) = 8.8$, $p = .001$), yet no group by trial interaction $F(2,43) = .9$). The main effect of trial was a decline in performance from trial 3 to trial 5: mean completion times went up from 76 s to 91 s. The main effect of group was a difference in mean completion times between the groups over both trials: 67 s, 68 s and 116 s, for EB, LB and BS, respectively, suggesting that the blind outperform the sighted on trials 3 and 5.

Accuracy of coordinate and categorical coding: trial 4

Table 1 shows group means. ANOVA's comparing the scores of the three groups showed no difference between the groups for metric ('coordinate') distance ($F(2,43) = .850$, $p = .44$) nor for average categorical distance ($F(2,43) = 2.0$, $p = .153$) of objects. Comparing the LB with the (CB + BS) on categorical distance showed a trend ($F(1,44) = 3.9$, $p = .056$, suggesting a possible LB superiority with respect to categorical accuracy of the object placement.

Table 1. Means (SE) of metric and categorical distance scores for the experimental groups on trial 4, the non-speeded motor response.

	Metric	*Categorical*
EB	9.9 (1.6)	.9 (.2)
LB	8.3 (1.0)	.6 (.1)
BS	10.2 (.9)	.9 (.1)
Average	9.4 (.6)	.8 (.1)

Verbal descriptions of objects and their spatial locations (free recall): trial 6

Object descriptions. See Table 2 for group means. We found no differences between the three groups with respect to the total number of objects described (F(2,43) = 1.4). In addition, no differences between the groups were found for the number of correctly named objects, correctly described, and incorrectly described objects (all p-values < .15). This suggests that there were no differences between the group with respect to recalling and identifying the objects by touch, and naming and describing them.

Table 2. Mean numbers (SE) of objects recalled and the quality of the object descriptions given by the experimental groups, as reflected in the means numbers of objects named correctly, described correctly, and described incorrectly/ambiguously.

	Total	Correctly Named	Correctly *described*	Incorrectly described
EB	8.3 (.5)	6.5 (.5)	.5 (.3)	1.2 (.3)
LB	9.1 (.2)	7.2 (.5)	.5 (.2)	1.4 (.2)
BS	8.8 (.3)	7.2 (.4)	.3 (.1)	1.3 (.3)
Average	8.7 (.2)	7.0 (.3)	.4 (.1)	1.3 (.1)

Spatial descriptions. Table 3 shows group means. No significant difference was found for the three groups with respect to the total number of spatial descriptions (F(2,43) = 1.0, p = .37). A significant main effect was found for the number of descriptions with respect to other objects (F(2,43) = 3.4, p = .043). It appeared that the blind (CB + LB) used more descriptions with respect to other objects than the BS

(F(1,43) = 5.7, p = .021). No significant main effect was found for number of descriptions with respect to the board (F(2,43) = 1.9, p = .16). However, comparing the blind (EB + LB) to the BS on the number of board descriptions resulted in a trend (F(1,44) = 3.7, p = .06), which indicates that the sighted may refer more to the board when describing an object's position than do the blind. No differences or trends could be reported for the number of descriptions with respect to (parts of the) participant's body, or other reference classes (wind quarters, clock face), which were used only incidentally (means: .35, .09 and .09, respectively). In line with this, no differences were found with respect to (the low) frequency of "visual" language or verbal expressions conveying additional spatial information (means: .35 and .46, respectively).

Table 3. Mean numbers (SE) of total amount of spatial descriptions, referrals to other objects, to the board and to other, and the number of objects correctly verbally positioned.

	Total	Object descriptions	*Board* descriptions	Other	Correctly positioned
EB	9.0 (.8)	4.1 (.8)	4.2 (.5)	0.7 (.5)	4.9 (.9)
LB	10.2	5.1 (.6)	4.6 (.6)	0.5 (.2)	6.3 (.6)
BS	9.0 (.8)	2.6 (.7)	5.8 (.7)	0.6 (.3)	3.8 (.7)
Average	9.4 (.4)	4.0 (.4)	5.0 (.4)	0.6 (.2)	5.0 (.4)

Verbal positioning. See Table 3 for group means. An ANOVA pointed out that the number of objects verbally placed in the correct categorical position was different for the three groups, (F(2,43) = 3.7, p = .034), which was expressed in different means: 4.9, 6.2 and 3.8, for EB, LB and BS, respectively. Contrasting the blind (EB + LB) to the BS indicated that the blind verbally assigned relatively more correctly named or described objects to the correct categorical locations than did the sighted. (F(1,44) = 5.3, p = .026). This effect appeared to result from a difference between the LB and the BS (F(1,31) = 8.3, p = .007), and not from one between the EB to the BS (F(1,28) = 1.2, p = .29). In line with this, contrasting the LB with the (EB + BS) was also significant (F(1,44) = 5.9, p = .019), suggesting that particularly having both haptic and visual experience was an advantage over having just haptic or visual experience, when verbally describing the objects' locations in the current task.

General discussion

The goal of the present study was to investigate roles of visual and haptic experience in implicit haptic object configuration learning in peripersonal space and the resulting spatial memory traces. To address multiple levels of memory and different memory characteristics, we varied the response on the implicit-explicit dimension.

The completion times of the groups for the first three trials suggested that primarily haptic experience is important for the speeded handling and motor matching of simple familiar 3-D shapes to their 2-D projections: the blind were much faster than the sighted. This is in concordance with findings by Heller on the speeded haptic matching of comparable, yet smaller, 2-D shapes (1989b). The verbal response as a measure of identification accuracy (trial 6) did not result in differences between the groups (both absolute numbers and proportions) with respect to naming and correctly describing the objects, which is in line with reports on haptic identification of 3-D familiar objects (Morrongiello et al., 1994, Shimizu et al., 1993). This may suggest that the consistent difference between the blind and the sighted found in the haptic matching speed, does not depend on differences between the groups with respect to the level or accuracy of haptic identification, but rather haptic dexterity and/or haptic identification speed differences.

With respect to implicit learning, it appeared that the groups all showed considerable improvement over the three trials. Although the blind displayed faster object to location matching, they did not display faster *learning* than the sighted. In fact, we found that the sighted improved more than the blind, particularly from the first to the second trial. This may be an effect of mental visual processing, but since the learning difference seems to result mainly from differences between the sighted and the *late* blind, it is more likely to reflect a fast yet small reduction of a disadvantage of the lack of haptic experience. Haptic experience may have allowed the blind to handle the objects faster and/or to identify them faster. As it is unlikely that the disadvantage of the sighted with respect to haptic dexterity is made up for in only one trial of haptic exploration and perception, it seems to reflect a reduction of the sighted group's problem in identifying the haptic stimuli or matching the objects to the cutouts marking their locations. Then, the constant and quite substantial difference between the blind and the sighted in completion time during all four time trials seems to reflect haptic dexterity differences. It is good to keep in mind, however, that haptic dexterity and identification speed are likely to be related and that their relationship may have contributed to the constant completion time differences between the groups.

With respect to the rotation of the board, no significant differences between the groups were found with regard to the size of completion time increase, which indicates that they were hindered to the same extent by the rotation: the blind were faster during implicit learning and remained so after rotation. Thus, in contrast to studies in which the spatial material was explicitly learned (Ungar et al., 1995; Hollins & Kelley, 1988), no advantage of visual experience was found in the present study. Our finding suggests that the roles of visual and haptic experience on the performance on mental rotation tasks depends on the specific natures of the task: in any case, it seems that visual experience does *not* facilitate performance on such a task if it comprises both implicit learning and an implicit response.

With the non-speeded free placement of the objects on the board without the cutouts in trial 4, we anticipated to trigger both more explicit object location memory representations and implicit egocentric and movement representations associated with the motor response. The results did not reveal differences in coordinate memory representations between the groups: the blind did not show smaller absolute metric distances between object placement and original object location. With respect to the accuracy of categorical memory for object location, a trend was found which suggests that the late blind may outperform both the sighted and the early blind with respect to the categorical coding of object location, as assessed with an implicit response.

Importantly, when assessed with an *explicit* response, visual experience unambiguously does affect spatial performance. We found that the explicit spatial knowledge of the object configuration benefits from visual experience, yet only when combined with sufficient haptic experience: the spatial verbal description (trial 6) resulted in an advantage for particularly the late blind. This indicates that, in the present task, haptic experience was a prerequisite to make use of visual experience in the explicit categorical coding the location of haptically explored objects. Interestingly, this may suggest that in speeded haptic spatial memory tasks, haptic dexterity (and maybe related speeded implicit identification) creates more room for *explicit*, possibly allocentric spatial memorization processes, which can only be utilized with visual experience.

With respect to spatial coding strategies, the descriptions of the spatial location of the objects resulted in an interesting difference between the blind and the sighted groups. It was found that, while the sighted may use more board referrals than the blind to point out the locations of objects (allocentric, extrinsic, cf. Ungar et al., 1995), the blind refer more to other objects on the board (allocentric, intrinsic) than the sighted. Although both types of descriptions can be called allocentric, one could argue that the nature of the descriptions is different, and may be indicative of differences in which the spatial information is coded in the blind and the sighted. However, in the literature, a clear and unambiguous frame to infer representations from descriptions seems to be lacking, but it may be that referring to the surrounding frame (i.e., the board) is the expression of a map-like, bird-view representation, and that referring to other objects to point out an object's location reflects a spatial representation in terms of a route (cf. Brambring, 1982). In line with this, Noordzij, Zuidhoek & Postma (submitted) have shown that when generating a spatial representation of a large scale environment from verbal descriptions, the blind perform better on distance comparison tasks after listening to a route description than a bird-view description.

With respect to freely recalling, describing and naming the *objects*, no differences were found between the experimental groups. This indicates that – although haptic experience seems to speed up performance, and visual experience may help explicit spatial coding - haptic dexterity nor visual experience facilitates haptic identification or recall of abstract familiar shapes as measured with a verbal response.

In sum, where previous studies found an advantage of visual experience in haptic spatial representation after explicit spatial learning, the present study showed that under speeded, more implicit learning conditions, haptic experience fulfills an important role in haptic spatial learning as well as spatial memory. Importantly, the facilitating role of visual experience became increasingly important when the level of explicitness of the task was increased. Together, the present findings suggest that the effects of visual and haptic experience on haptic spatial performance depend on the implicitness/explicitness of the representation(s) triggered by specific task characteristics. It seems that both the nature of the learning process and the type of the response affect the level of the representation addressed.

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References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61,* 303-321.

Brambring, M. (1982). Language and Geographical orientation for the blind. In R.J. Jarvella & W. Klein (Eds.) *Speech, Place and Action* (pp. 203-218). Chichester: John Wiley & Sons Ltd.

Creem, S.H., & Proffitt, D.R. (1998). Two memories for geographical slant: Separation and interdependence of action and awareness. *Psychonomic Bulletin & Review , 5,* 22-36.

Gentaz, E., & Hatwell, Y. (1999). Role of memorization conditions in the haptic processing of orientations and the 'oblique effect'. *British Journal of Psychology, 90,* 373-388.

Heller, M.A. (1989a). Tactile memory in sighted and blind observers: the influence of orientation and rate of presentation. *Perception, 18,* 121-133.

Heller, M.A. (1989b). Picture and pattern perception in the sighted and the blind: the advantage of the late blind. *Perception, 18,* 379-389.

Hollins, M., & Kelley, E.K. (1988). Spatial updating in blind and sighted people. *Perception and Psychophysics, 43,* 380-388.

James, T.W., Humphrey, G.K., Gati, J.S., Servos, P., Menon, K.S., & Goodale, M.A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia, 40,* 1706-1714.

Jones, B. (1972). The development of cutaneous and kinaesthetic locatlization in blind and sighted children. Developmental Psychology, *6,* 349-352.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 144,* 131-145.

Logie, R.H. (1995).*Visual-spatial working memory*. Hove, UK: Lawrence Erlbaum Associates, Inc.

Magee, L.E., & Kennedy, J.M. (1980). Exploring pictures tactually. *Nature, 278,* 287-288.

Millar, S. (1979). The utilization of external and movement cues in simple spatial tasks by blind and sighted children. *Perception, 8,* 11-20.

Millar, S. (1981). Self reference and movement cues in coding location by blind and sighted children. Perception, *10,* 255-264.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England, UK: Clarendon Press/Oxford University Press.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* Oxford, England UK: Oxford University Press,

Morrongielo B.A., Humphrey, K., Timney, B., Choi, J., & Rocca, P.T. (1994). Tactual object exploration and recognition in blind and sighted children. *Perception, 23,* 833-848.

Newell, F.N., Ernst, M.O., Tjan, B.S., & Bulthoff, H.H. (2001). Viewpoint dependence in visual and haptic object recognition. *Psychological Science, 12,* 37-42.

Noordzij, M.L., Van der Lubbe, R.H.J., Neggers, S.F.W., & Postma, A. (2004) Spatial tapping interferes with the processing of linguistic spatial relations. *Canadian Journal of Experimental Psychology, 58,* 259-271.

Noordzij, M.L., Zuidhoek, S., & Postma, A. (submitted). The influence of visual experience on the ability to form spatial mental models based on route and survey descriptions.

Paillard, J. (1991). Motor and representational framing of space. In J. Paillard (Ed.) *Brain and space* (pp. 163-182). Oxford, England UK: Oxford University Press.

Reales, J.M. & Ballesteros, S. (1999) Implicit and explicit memory for visual and haptic objects: cross-modal priming depends on structural descriptions. *Journal of Experimental Psychology: Learning, Memory and Cognition, 25,* 644-663.

Reitan, R.M., & Wolfson, D. (1993). *The Halstead-Reitan Neuropsychological Test Battery: Theory and clinical interpretation.* Tucson, AZ: Neuropsychology Press.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Shimizu, Y., Saida, S., & Shimura, H. (1993). Tactile pattern recognition by graphic display: Importance of 3-D information for haptic perception of familiar objects. *Perception & Psychophysics, 53,* 43-48.

Sterken, Y., Postma, A., de Haan, E.H.F., & Dingemans, A. (1999). Egocentric and exocentric spatial judgements of visual displacement. *Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology, 52A,* 1047-1055.

Ungar, S., Blades, M., & Spencer, C. (1995). Mental rotation of a tactile layout by young visually impaired children. *Perception, 24,* 891-900.

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). Multisensory integration mechanisms in haptic space perception. *Experimental Brain Research, 157,* 265-268.

Zuidhoek, S., Kappers, A.M.L., Noordzij, M.L., Van der Lubbe, R.H.J., & Postma, A. (2004). Frames of reference in a haptic parallelity task: temporal dynamics and the possible role of vision. In S. Ballesteros, & M.A. Heller (Eds.), *Touch, blindness and neuroscience*. Madrid, Spain: UNED Press.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2005). Effects of hand orientation and delay on the verbal judgment of haptically perceived orientation. *Perception, 34,* 741-755.

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (submitted). Haptic orientation perception benefits from visual experience: evidence from early blind, late blind and sighted people.

The sexes

Chapter 7 | Haptic orientation perception: sex differences and lateralization of functions

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (submitted for publication)

Abstract

The present study examined sex differences in haptic orientation representation using three tasks: a bimanual parallel-setting task comprising haptic orientation perception and motor matching action, and two unimanual tasks focusing on the perception and action elements separately. A verbal judgment task focused on haptic orientation perception: participants were to assign a number of minutes to a felt orientation. An orientation production task required the rotation of a bar to match a verbally presented number of minutes. Although both male and female performance was systematically biased we found that males are more accurate in parallel-setting and verbal judgment of orientation, suggesting differences in haptic orientation *perception*, in particular. Increasing allocentric reference frame involvement by delaying the action in the parallel-setting task did not affect the sex difference found. In addition to a male advantage over tasks, performance on both unimanual tasks suggests sex differences in lateralization of haptic orientation processing; a dependence on hand orientation was found only for right hand performance in males.

Introduction

Despite their importance for human behavior in peripersonal space, sex differences in haptic spatial abilities have been examined surprisingly sparsely. Consequently, although Kappers (2003) has shown clear sex differences in haptic parallelity perception and although there are some indications of effects resulting from lateralization of attention (Laeng, Buchtel & Butter, 1996) and spatial abilities (Ernest, 1998; Findlay, Ashton & McFarland, 1994), a systematic overview of sex differences in haptic spatial abilities is lacking. In contrast, sex differences in *visuo*spatial abilities, generally favoring males, have been well documented (see for overviews Maccoby & Jacklin, 1974; Harris, 1981; Kolb & Whishaw, 1995, Voyer, Voyer & Bryden, 1995), which had led to the identification of only a limited number of key differences between the sexes in cognitive spatial ability and strategy which may underlie the large body of behavioral sex differences. Considering their seemingly modality independent nature these may also apply to haptics.

Three key sex differences in visuospatial ability and/or strategy favoring males have been identified: mental rotation ability (Linn & Peterson, 1985; Moffat, Hampson & Hatzipantelis, 1998; Galea & Kimura, 1993; Geary, 1995), superior understanding of Euclidean space and a related tendency to employ more absolute world-centered or allocentric and geometrical information (Geary, 1996; Matthews, 1986; Webley & Whalley, 1987; Galea & Kimura, 1993; McGuiness & Sparks, 1983), and the ability to predict and anticipate on the trajectory and relative speed of moving objects (Kaiser, Proffitt, Whelan & Hecht, 1992; Law, Pellgrino & Hunt, 1993). In contrast, only one key difference seems to favor females: the ability and/or larger tendency to remember the relative locations of objects (Silverman & Eals, 1992; Eals & Silverman, 1994; Barnfield, 1999; James & Kimura, 1997) and a related superiority in reporting landmarks (Ward, Newcombe & Overton, 1986; Montello, Lovelace, Golledge & Self, 1999).

Although the abovementioned spatial ability and strategy differences may very well apply to haptic spatial perception, haptic and visual perception differ in possibly crucial respects. For one, haptic spatial perception comprises totally different input channels: two moving hands. In contrast to vision, these input channels can move around in space independently. In addition, information coming from the right and the left hands terminates fully in the left and right hemispheres, respectively, which have been found to differ with respect to spatial abilities (categorical/relative and coordinate/Euclidean/manipulospatial, for the left and right hemispheres, respectively (Kosslyn, Koenig, Barrett, Cave, Tang & Gabrieli, 1989; Jager & Postma, 1999; Corballis, 1980; LeDoux, Wilson & Gazzaniga, 1977)), attentional allocation (right hemisphere)(e.g. Kinsbourne, 1987) and verbal abilities (left hemisphere) (e.g. Kinsbourne & Cook, 1971). Thus, haptic input is likely to result in different hemispace effects and hand by hemispace interactions than vision, in particular when a hand crosses to the opposite hemispace. In turn, these may differ for the sexes, as men have been suggested to have a larger lateralization of functions than women (Kimura, 1983, 1992; Lewis & Christiansen, 1989) In line with this, measuring tactile rod bisection, Laeng and colleagues (1996) found a number of significant interactions between hand, hemispace and sex, in addition to some trends for sex differences favoring males.

In addition, the nature of the input (visual, haptic) may greatly affect the reference frames employed, which - considering the aforementioned ability and preference differences between the sexes - may give rise to sex differences. For one, it has been argued that visual input is more apt when allocentric spatial codes are desired for task performance, (Millar, 1988, 1994; Thinus-Blanc & Gaunet, 1997), since vision is faster and allows (more) simultaneous input, and consequently integration of different locations in near as well as far space. In contrast, in haptic perception, particularly egocentric reference frames seem to play a crucial role (the hands, the midsagittal plane (Zuidhoek, Kappers & Postma, 2005), the body (Heller, Calcaterra, Green & Barnette, 1999) and a subjective gravitational frame (Luyat, Gentaz, Corte & Guerraz, 2001)). Moreover, hand-centered reference frames have been argued to (often grossly) bias absolute representations of orientation in peripersonal, particularly in haptic tasks requiring an allocentric reference frame while no such frame is physically available (Zuidhoek et al., 2003; Kappers, 2003; Zuidhoek, Visser, Bredero & Postma, 2004).

Consequently, one may argue that sex differences resulting from males' allocentric preferences may be minimal or absent, since physical allocentric reference frames in haptic tasks are often not, or to a lesser extent, available. In line with this, the males' advantage on the visual water level task (Robert, Pelletier, St-Onge, & Bertiaume, 1994) has been found to vanish when the task is presented haptically (Bertiaume, Robert, St-Onge, & Pelletier, 1993; Robert et al., 1994; Heller et al., 1999). A similar disappearance of sex differences due to a reduction of allocentric reference frame availability has been observed for the visual modality: males' advantage in visual orientation matching (participants had to pick one of thirteen orientations for each orientation presented) has been found to disappear when visual allocentric reference cues within the test environment were no longer useful (Collear & Nelson, 2002). In contrast, Kappers (2003) has found clear sex differences in a so-called haptic parallel-setting task, a task requiring allocentric representation in which also no physical allocentric information was provided:

participants were to rotate a number of bars parallel to a bar with a certain reference orientation in the horizontal plane, using their haptic sense. Although all participants showed (large, up to 60°) systematic egocentric deviations, men's deviations were smaller, suggesting that they were more able than women to overcome egocentric biases by employing a *mental* allocentric reference frame (since no physical one was provided).

Importantly, the task used by Kappers assessed integrated haptic performance, i.e., it did not distinguish between haptic perception and action. As the former tasks (haptic water level task and visual orientation perception) ask for a forced choice response in stead of a motor response, one may argue that the discrepancy between these and the parallel-setting task lies in a difference between males and females with respect to the motor response type favoring males, which may go back to their more proficient use of projectiles (Ecuyer-Dab & Robert, 2004; Kaiser et al., 1992). Thus, it may be that the male advantage in the parallel-setting task results from specific sex differences in haptic action, and not from the underlying perception per se. In addition, it may well be that it is not the egocentric biases per se, but rather the *integration* of haptic input coming from different hands or different regions of space, is what makes the sex difference on the parallel-setting task. This suggests that whether a task assesses "purely" haptic performance (haptic perception and motor response integrated in one task), or just haptic perception or haptic action alone, may well affect the extent to which this task reveals sex differences.

In sum, the foregoing suggests that a number of factors are particularly promising to zoom in on, when examining sex differences in haptic spatial performance. First, reference frame use. In general, the amount of allocentric reference frames provided in a task may affect the extent to which sex differences are found. With respect to the parallel-setting task, the dealing with biasing egocentric input may be crucially different for the sexes, due to a possible larger tendency or ability of males to generate a mental allocentric frame to overcome these biases. Second, the lateralization of spatial processing (hand use), and its relation to hemispace of stimulus presentation (possible attentional effects, hemispace by hand interactions). Third, the distinction between tasks that focus on haptic perception, haptic action, or tasks that integrate both. Hence, the goal of the present study was a systematic exploration of these issues. We focused on performance on haptic orientation perception tasks, which has been studied quite extensively to examine reference frame employment throughout peripersonal space using different responses (motor and verbal). In order to determine whether sex differences result from haptic perception, haptic action, or specifically from "pure" haptic tasks requiring both, we had males and females perform one bimanual and two unimanual tasks in the horizontal plane; whereas the former focused on the integration of perception and action, the latter two focused on haptic perception and haptic production, respectively.

The first task was a bimanual parallel-setting task (haptic perception and motor response). We expected to replicate the male advantage as reported by Kappers (2003). In this task we chose the natural situation of both hands on their own side of the body. Interestingly, another previous parallel-setting task has provided information on the temporal dynamics of egocentric and allocentric reference frame involvement in haptic spatial perception: delaying the parallel-setting action by 10 seconds resulted in a decrease of the perceptual deviation. This improvement has been interpreted to result from a shift from egocentric to more allocentric reference frames over the delay period (Zuidhoek et al., 2003; cf. e.g., Rossetti & Régnier, 1995; Rossetti, Gaunet & Thinus-Blanc, 1996, Milner & Goodale, 1995), due to stimulation of allocentric reference frame involvement (visual imagery, cognitive processing during delay (Zuidhoek et al., 2003)). In the present study, we also had participants perform the parallel-setting task in 0 and 10 seconds delay conditions in order to examine whether stimulation of mental allocentric reference frame employment would affect sex differences on the parallel-setting task.

With this first task, however, we were unable to differentiate between hand and hemispace effects. The two unimanual tasks did give us this opportunity, by having two bars - one in the left and the other in the right hemispace - be perceived/handled by either hand. Left hand performance may generally lead to smaller deviations than right hand performance, due to right hemisphere advantages in Euclidean processing and manipulospatial abilities, as well as attentional allocation. Due to the stronger lateralization in males, these differences should be particularly clear in males. They also allowed us to look at sex differences in haptic perception and haptic action, separately.

The first unimanual task, focusing on haptic perception, was a so-called verbal judgment task (cf. Zuidhoek et al., 2005; Hermens, Kappers & Gielen, in press)), which requires the assignment of a number of minutes on an imagined clock to a unimanually perceived orientation using a verbal response. Our second unimanual task was very similar to the verbal judgment task, but instead of examining perception, it focused on haptic action: participants were asked to rotate a bar to match a verbally provided number of minutes on an imagined clock (cf. Hermens, Kappers & Gielen, in press). Importantly, the previous recent studies showed that performance is remarkably accurate on both these tasks (with a maximum average deviation of 7°) as compared to parallel-setting, suggesting that both these tasks seem to stimulate mental allocentric reference frame employment. This may be due to (1) explicit allocentric definition of bar orientation (with respect to stimulus table); (2) (visuo)spatial imagery of a clock face; (3) the cognitive, explicit nature of the task (Zuidhoek et al., 2005). This stimulation of mental allocentric reference frame employment may increase the presumed sex differences in the same way as the actual presence of physical allocentric reference frames seems to do in the water level task and the visual perception of line orientation. In addition, the verbal judgment task in particular has revealed a clear relationship between hand orientation (i.e., hand-midsagittal plane misalignment) and error size and direction (Zuidhoek et al., 2005)). It should be noted that this relationship may result in hand by hemispace interactions in the present study, independently of those hand hemispace interactions resulting from attentional effects.

General methods

Participants

Twenty male and twenty female undergraduates of Utrecht University, aged 18 – 25 years of age, participated in the present study. Eleven of the males and thirteen of the females were science students. The remaining participants were social science students. They were naïve with respect to the experimental purposes, had never seen the experimental setup, were not told about the orientations and stimulus locations used, and were never given any feedback on their performances. All were right-handed as assessed with Annett's handedness scale (1970).

General procedure

The experiments were performed in two sessions which were on different days. Session one consisted of the gathering of personalia, Annett's handedness scale (1970) and haptic parallel-setting in non-delay and delay conditions, which was balanced over participants within a group. Session two consisted of the verbal judgment task and the production of orientation task. At the end of session one and session two short additional tasks (a mental visuospatial imagery task, and a visual spatial task, respectively) were included, to be reported elsewhere. In total, sessions 1 and 2 took about 65 minutes and 80 minutes, respectively, including a short break to avoid weariness.

General data analyses

In the present study, the basis of the analyses in all three experiments is to first visually inspect the expected systematic error patterns, and then perform mixed ANOVA's with sex as between subject factor to investigate differences in error size. Where necessary, the degrees of freedom were corrected by using Greenhouse-Geisser ε-correction. In the present study, orientation was only varied to provide variation in stimulus presentation. Since we were not particularly interested in orientation effects and orientation interaction effects with factors other than sex, these were only superficially examined for the sake of transparency.

Experiment 1: Parallel-setting task

Design

The experiment had a mixed design with hemispace/exploring hand (2 levels: right and left), delay (2 levels: 0s and 10s) and orientation (6 levels: 0º, 30º, 60º, 90º, 120º, 150º) as within-subjects factors and sex (2 levels: male and female) as between-subjects factor.

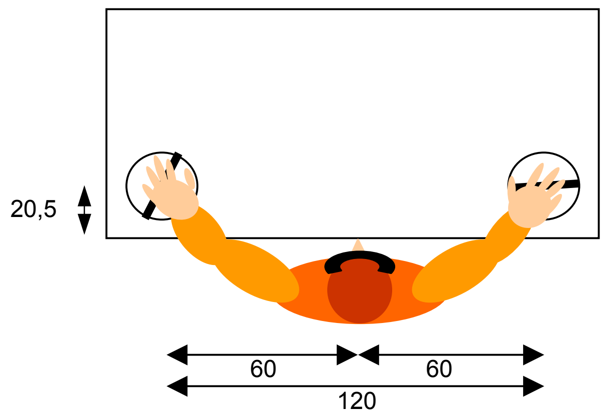


Figure 1. Top view of the experimental setup used in the parallel-setting task.

Apparatus and stimuli

Participants were seated on a stool (adjustable in height), 3 – 5 cm from the middle of long-side of the stimulus presentation table, as depicted in Figure 1. This table had an iron table top, covered by a plastic layer showing protractors (diameter 20 cm). The haptic stimuli were two aluminum bars (length 20 cm, diameter 1.1 cm) presented within the protractors shown in Figure 1. The centers of the protractors were 20.5 cm from the table's edge. A small pin attached to the center of a bar fitted into a hole at the center of a protractor, which allowed the bars to be rotated around the centers of the protractors. Small magnets attached to the bars increased their resistance to movement. The bars were tapered off at both ends, allowing the experimenter an accurate read out of their orientations (uncertainty of about 0.5 degrees).

Both bars were used as reference and test bar. In each trial the test bar had to be rotated parallel to the reference bar. The bar to the left of the participant was always explored/rotated by the left hand; the bar to the right was always handled by the right hand. The reference bar was presented under one of six orientations to provide variation (0º, 30º, 60º, 90º, 120º, 150º, where 0º is parallel to the long side of the table, and increasing values signify rotation in counterclockwise direction). The test bar was always presented in a random orientation, i.e. corresponding to the orientation of a clock's seconds-hand at that particular time. Each reference bar orientation was presented three times on both stimulus locations in both conditions, which adds up to 36 trials per condition. The order of reference bar orientation presentations was randomized and different for every participants. An Apple Macintosh computer was used to provide auditory time restriction signals.

Procedure

Before a participant was blindfolded and taken to the experimental setup, the experimenter ensured that he/she had a correct understanding of parallelity. First a Dutch synonym for parallelity was provided ("evenwijdig"). Then a definition of parallelity was given: "bars are parallel when they do never meet or cross, when elongated infinitely." As examples of parallel lines, railroad tracks were mentioned, as well as the opposite sides of a rectangle. In addition, participants were given two pens and were asked to lay them parallel to one another right in front of them on the table. All participants expressed a normal and correct understanding of parallelity.

After participants had been blindfolded and taken to the stimulus presentation table, they were seated on the stool and received the following instructions. They were told that they would repeatedly feel a reference orientation with one hand, and would have to rotate a second bar parallel to the just-felt orientation, either immediately or with a delay. A timed sequence of a sampled male voice uttering the numbers "one", "two", "three" and in the 10-seconds delay condition also "four" indicated which action was desired from the participant. In the non-delay trials (i.e. delay time is 0 s) "one" signified the start of the 2-seconds exploration period of the reference bar. "Two" signified both the end of the exploration period and the start of the rotating of the test bar. "Three" signified the end of the 2-second response period. In the delay trials, "one" signified the start of the 2-second exploration period of the reference bar. "Two" signified the end of the exploration period and the start of the 10-seconds delay period. At "three" the participant was required to start the rotating, and "four" was the signal to terminate the rotating and the end of the 2-second response period. In the exploration and response phase, the participants were free in their choice of strategy as long as they did not change the orientation of the reference bar, did not touch the edges of the table and remained seated. After exploration of the reference bar, the reference hand had to be returned to the body without touching the edge of the table.

After a participant had confirmed that he/she understood the instructions, 5 practice trials were performed to ensure that the instructions were understood correctly, and to get used to the timed sequence in which the actions had to be performed. Before each trial, the experimenter positioned the reference bar in a predetermined orientation and the test bar in a random orientation. Next, he took the hand that had to explore the reference bar in that particular trial while saying (the Dutch equivalent of) "here is the reference bar" and left it to float about 5 cm above the reference bar. He then took the participant's other hand, saying "here is the test bar" and left it to float about 5 cm above the test bar. After this, the experimenter started the timed sequence.

Data analyses

In previous studies, the errors were found to be systematic, i.e. clockwise with test bars to the right of the reference bar, and counterclockwise with test bars to the left of the reference bar (e.g. Kappers & Koenderink, 1999; Kappers, 1999, 2003; Zuidhoek et al., 2003, Zuidhoek et al., 2004). To be able to easily differentiate between errors in this systematic direction and errors in the other direction, and to be able to compare the mean sizes of the deviations resulting from right and left hand reference bar explorations, we used mean signed errors expressing size and systematics, with a positive value in degrees signifying a systematic error (i.e. an error in the expected direction), and a negative value signifying an error in the opposite direction. However, in contrast to earlier studies (Zuidhoek et al., 2003; Zuidhoek et al., 2004; but see Zuidhoek, Noordzij, Kappers & Postma, submitted), the data patterns of some participants in the present study suggest that some of the large errors in the unexpected direction may very well be interpreted as (even larger) errors in the *expected* direction. For example, an error of -89° (a large error in the unexpected direction) should probably be interpreted as an error of +91º (a large error in the expected direction) for participants that display deviation patterns in which large deviations of 50º through 90º degrees are common. Therefore, we turned to circular data manipulation methods comprising vector algebra in the present study (Batschelet, 1981) in order to compute the mean deviations for our analyses.

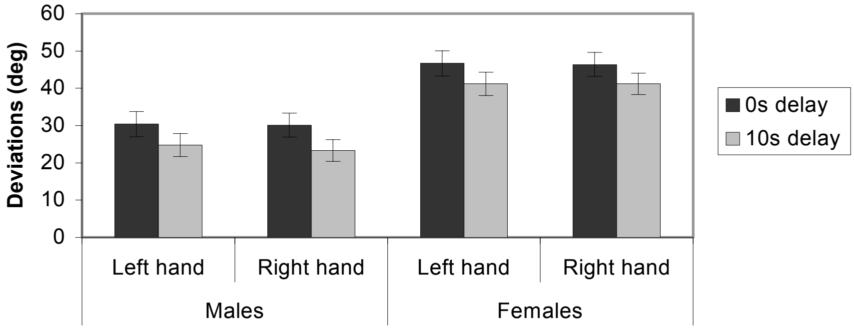


Figure 2. The main effects of group and delay on deviation size in the parallel-setting task. Error bars show +/- 1.0 standard errors of mean.

Results

The 2 (delay) x 2 (reference bar positions/hands) x 6 (orientations) x 2 (sex) mixed ANOVA showed significant main effects for sex ($F(1,38) = 16.9$, $p < .001$), delay ($F(1,38) = 14.4$, $p = .001$) and orientation ($F(5,190) = 3.9$, $p = .021$, $\varepsilon = .43$). The main effect of sex signified a male advantage expressed in smaller systematic deviations as compared to female performance: 27.1° and 43.8° for males and females, respectively. The main effect of delay was an improvement of performance with 10 seconds delay (32.6°) as compared to immediate parallel-setting performance (38.4°). The main effect of orientation was expressed in different means for different orientations: 33.9°, 37.7°, 36.0°, 30.5°, 35.0°, 39.8°, for 0°, 30°, 60°, 90°, 120° and 150°, respectively. The means suggest relatively spared performance for 90° and possibly 0° reference orientations.

Table 1. The reference hand/hemispace by orientation interaction in parallel-setting performance: mean deviations (SE) in degrees.

Reference orientation (deg)	Reference hand/hemispace	
	Right	Left
0	34.0 (2.6)	33.9 (3.1)
30	37.6 (2.9)	37.8 (1.8)
60	28.8 (2.1)	43.3 (3.6)
90	29.6 (3.7)	31.4 (3.3)
120	42.0 (3.0)	27.9 (1.7)
150	39.3 (2.1)	40.3 (2.5)

Importantly, none of the within-subjects factors interacted with sex. Figure 2 shows the lack of interactions between sex, delay and position. The only interaction effect found, was one of position by orientation. This interaction is shown in Table 1. The interaction appears to be due to differences between positions 1 and 2 in mean deviation sizes with reference bar orientations 60° and 120°. Participants seem to perform badly with 60° reference bar orientation when this orientation is explored by the left hand (position 2) and perform relatively well when this orientation is explored by the right hand (position 1). In contrast, participants seem to perform badly with 120° when explored by the right hand (position 1), and relatively well when explored by the left hand.

Discussion of Experiment 1

The most important finding of this first experiment is that males performed better on the haptic parallel-setting task, as reported earlier (Kappers, 2003). We found no differences between the sexes with respect to the systematics of the errors: both sexes show systematic deviations in the direction found in previous studies, i.e. clockwise deviations with test bars to the right of the reference bar, and counterclockwise with test bars to the left of the reference bar (e.g. Kappers & Koenderink, 1999; Kappers, 1999, 2003; Zuidhoek et al., 2003, Zuidhoek et al., 2004). In addition, we replicated the beneficial effect of delaying the parallel-setting action once again (Zuidhoek et al., 2003; Zuidhoek, Noordzij, Kappers, Van der Lubbe & Postma, 2004; Zuidhoek et al., submitted). Importantly, no sex by delay interaction was found, suggesting that the amount of improvement with delay does not differ for the sexes. This indicates that the extent to which mental allocentric reference frame employment is stimulated does not affect the male advantage to correct for egocentric biases. Also, no (sex) differences were found with respect to hand use or the hemispace in which the reference bar/test bar was, suggesting no effects of lateralization of spatial functions/attention on performance in the present task. One may argue, however, that possible effects may have been masked by the bimanual nature of the task.

In line with previous studies, we found an effect of orientation: participants seem to prefer 90° (which is orthogonal to the edge of the stimulus table) over the other orientations (e.g. Zuidhoek et al., 2003). In addition, performance on orientations seemed to differ for the different hemispaces. The results show that participants perform badly with 60° reference bar orientation when this orientation is explored by the left hand (or on position 2) and perform relatively well when this orientation is explored by the right hand (position 1). In contrast, participants seem to perform badly with 120° when explored by the right hand (position 1), and relatively well when explored by the left hand. Considering that previous research has suggested that the perception of a bar depends on the angle between the bar and the exploring hand, and that the angle between one hand and 60° is comparable to that between the other hand and 120° suggests that these results are not surprising. Rather, these results suggest that similar angles between the hand and the bar lead to similar deviation sizes, which is in line with the idea that hand-centered reference frames are involved in the perception of haptic orientation (Zuidhoek et al., 2005).

Experiment 2: Verbal judgment of orientation task

Design

The experiment had a mixed design with hemispace (2 levels: right and left), exploring hand (2 levels: right and left) and orientation (8 levels: 1, 4, 8, 12, 16, 19, 23, 27 minutes) as within-subjects factors and sex (2 levels: male and female) as between-subjects factor.

Apparatus and stimuli

The experimental setup was similar to that of Experiment 1. The same stimulus presentation table and bars were used. The placing of the two bars was slightly different, however, in order to enable both hands to reach both bar stimuli (see

Figure 3). The bars were presented under one of eight possible orientations mainly to provide variation, in random order, on either of the two positions, and were explored by either hand. The orientations were chosen in such a way that they corresponded to whole minutes. In addition, they did not correspond to multiples of 5 minutes to avoid response biases affecting the data. The following minutes were presented: 1, 4, 8, 12, 16, 19, 23, 27, corresponding to the following orientations: 84º, 66º, 42º, 18º, 174º, 156º, 132º, 108º (where 0º is parallel to the long side of the table; increasing values signify rotation in counterclockwise direction).

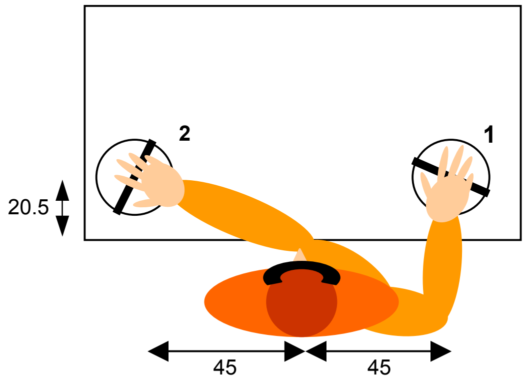


Figure 3. Top view of the experimental setup used in the verbal judgment and production of orientation tasks.

The total number of combinations was 32 (2 (stimulus location) x 2 (hand) x 8 (stimulus orientation)). All combinations were presented three times, adding up to a total of 96 trials. The order of presentation was random and different for each participant. An Apple Macintosh computer was used to provide auditory time restriction signals.

Procedure

The blindfolded participants were seated on a stool at the stimulus presentation table. They were told that they were about to repeatedly feel the orientation of a bar on different locations on the table with either their right or their left hand. They were instructed to keep their exploring limb in a natural position and to think of the felt bar as the minutes hand of a clock, and to assign a number of minutes to its orientation. Orientation was explicitly defined allocentrically, i.e., it was defined with respect to the stimulus presentation table. More specifically, participants were told that all 'clocks' on the table were positioned in such a way that when the minutes hand corresponded to15 or 45 minutes, it was parallel to the side of the table they were sitting at. Next, they were asked to place a pen on a table in the orientation corresponding to 15 and 45 minutes. All participants expressed normal understanding.

Before the start of every trial, the experimenter positioned a bar in a predetermined orientation. Next, he took a hand, left it to float about 5 cm above the bar and said (the Dutch equivalent of) "here is the bar". After this, the experimenter started the timed sequence on the computer. A sampled male voice uttered the numbers "one", "two" and "three" which indicated which action was desired from the participant. "One" signified the start of the 2-second exploration period of the bar. "Two" signified the end of the exploration period and also the start of the period in which the verbal response had to be given. "Three" indicated that the response period (2s) was over. Participants were instructed to obey the time restrictions and to respond in whole minutes within a range of 0 to 60 minutes as accurately as possible.

During the trials, participants were not allowed to touch the edges of the table and were to remain seated the way they were. They were allowed to touch the table to check their positioning with respect to the table only in between trials, which happened only occasionally. Trials in which the restrictions were not met, were presented again at a later time during the session (approximately 2% of the trials). Participants were free in choice of strategy when exploring the bar. In practice, participants would press the hand on the bar. Sometimes, the hand press was followed by a hand movement over the bar. After exploration of the bar, the reference hand had to be returned to the body. After the participant had finished the trial by giving his verbal response, the experimenter noted it down and both continued with the next trial.

Results

Error systematics

Figure 4 shows the mean signed errors (in minutes) resulting from verbal judgment performance by men and women for both hands in the right and the left hemispace. The systematics of the errors seem to be in line with findings of previous studies: while the orientation of a bar in the right hemispace is underestimated, i.e. assigned a lower number of minutes than it actually represents, the orientation of a bar in the

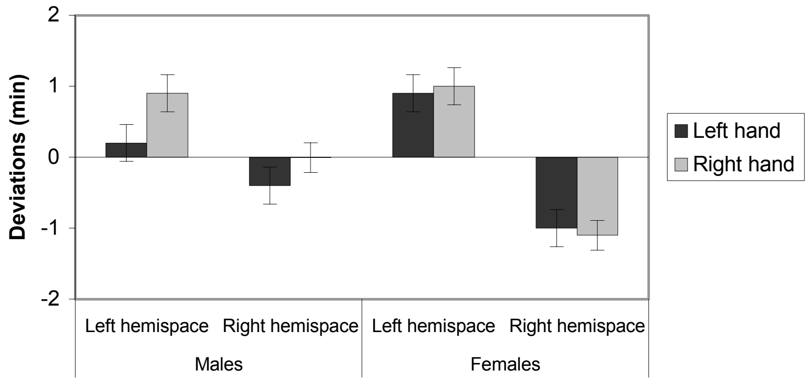


Figure 4. Mean signed errors (in minutes) resulting from the verbal judgment task by men and women for both hands in the right and the left hemispace. Error bars show +/- 1.0 standard errors of mean.

left hemispace is overestimated (Zuidhoek et al., 2005; Zuidhoek et al., submitted). Interestingly, however, it seems that the relationship between hand orientation and error size found in a previous study (Zuidhoek et al., 2005), is only clearly present in males: while crossing the hands - which leads to a larger hand-midsagittal plane misalignment (see Figure 3) - results in larger errors in males, it does not in females.

Importantly, Figure 4 seems to suggest that men perform better than women on this particular task: on average, they show smaller errors in both hemispaces and with both hands. However, as explained in the Data analyses section, the differences in sign for the mean errors resulting from underestimation in the right hemispace and overestimation in the left led to average errors close to zero for both men and women. In other words, using differently signed mean signed errors in an ANOVA may obscure a main sex effect. Therefore, we now turn to analyses in which the mean deviation sizes can be compared independently of differences in sign related to hemispatial position. The data were recoded to values as displayed in Figure 5., i.e., we changed the sign of right hemispace performances. In addition, the unit of the dependent variable was changed from minutes to degrees (º) to facilitate comparison of the results of Experiment 2 with Experiments 1 and 3. As one minute on a clock face corresponds to 6º, this was done by multiplying deviations in minutes by 6.

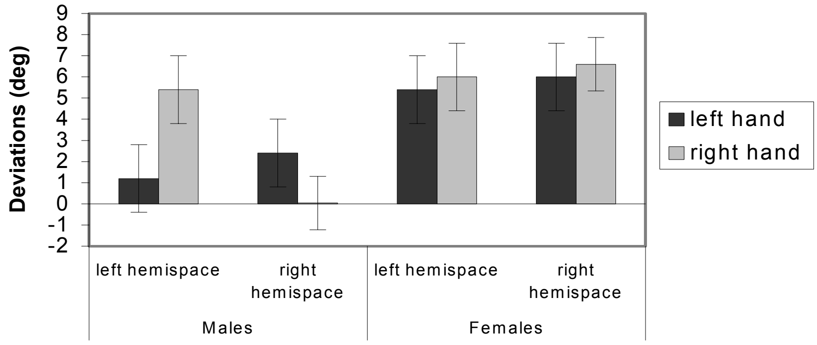


Figure 5. Recoded mean signed errors (in *degrees*) resulting from the verbal judgment task by men and women for both hands in the right and the left hemispace. Mean signed errors resulting from performance in the right hemispace are recoded to left hemispace performances by changing their sign. Error bars show +/- 1.0 standard errors of mean.

Deviation sizes

A 2 (hemispace) x 2 (hand) x 8 (orientation) x 2 (sex) mixed ANOVA showed a main effect of sex ($F(1,38) = 7.5$, $p = .009$), which signified males' superior performance: average deviations of 2.1º and 6.0º, for men and women, respectively. A trend for a main effect of hand was found ($F(1,38) = 3.0$, $p = .09$), suggesting that left hand performance may have been be slightly better than right hand performance: 3.6º and 4.6º, respectively.

Importantly, a sex x hand x hemispace interaction was found ($F(1,38) = 5.2$, $p = .028$). This interaction was further broken down for the two groups separately, showing a hand x hemispace interaction for men ($F(1,19) = 6.5$, $p = .02$), but not for women ($F(1,19) = .1$). This male interaction effect signified that position had an effect on perceptions with the right hand ($F(1,19) = 10.4$, $p = .004$), but not on perceptions with the left ($F(1,19) = .2$): while performance with the right hand was particularly good in the right (0.0º), it was bad in the left hemispace (5.4º).

A main effect of orientation ($F(7,266) = 9.2$, $p < .001$) reflected differences in performance on the different orientations, as shown in Table 2 (Average values). In addition, an interaction was found for orientation x hemispace ($F(7,266) = 11.0$, $p < .001$, $\varepsilon = .62$), which is also shown in Table 2. These values suggest that, in general, participants are better at judging orientations close to 0 or 30 minutes (the 'vertical'), than judging orientations close to 15 minutes (the 'horizontal'). Visual inspection of this table suggests that the interaction effect is mainly due to the differences in performance on the stimulus locations for 4, 8, 19 and 23 minutes, which may be denominated the 'oblique' orientations.

Table 2. The hemispace by orientation interaction in verbal judgment performance: mean deviations (SE) in degrees.

Presented orientation (min)	Right hemispace (deg)	Left hemispace (deg)	Average (deg)
1	-.8 (1.1)	2.4 (1.4)	.8 (.9)
4	-1.7 (1.2)	6.3 (1.6)	2.4 (.9)
8	.9 (1.4)	9.2(1.3)	5.0 (.9)
12	6.3 (1.4)	4.8 (1.4)	5.6 (.9)
16	5.1 (.8)	6.5 (1.3)	5.8 (1.0)
19	7.7 (1.1)	4.4 (1.6)	6.1 (1.0)
23	8.0 (1.1)	1.8 (1.4)	4.9 (1.0)
27	3.7 (1.8)	.4 (1.4)	2.1 (1.1)

Discussion Experiment 2

This verbal judgment task resulted in small systematic deviations, which replicates a previous study in the horizontal plane (Zuidhoek et al., 2005; but see Hermens et al. (in press) which showed similarly small errors for the fronto-parallel plane, but not systematically in the same direction for all observers). The most important finding is that – again - men outperformed women. This male advantage resulted from left hand performance in particular, and remarkably right hand performance in the right hemispace. Interestingly, crossing the right hand to the left hemispace resulted in performance level dropping to that of females.

Males' left hand advantage may be explained by their stronger lateralization of (spatial) functions, with the right hemisphere involved in coordinate, more absolute spatial abilities and the understanding of Euclidean space. Stronger lateralization may also explain why right hand performance was different over the hemispaces in males, while for females, performance by both hands was comparable for both hemispaces. It seems that the right hand (which projects to the brain's left hemisphere) is particularly affected by hand orientation in males only, resulting in a large difference between (good) performance with the right hand in a natural orientation (i.e., small hand-midsagittal plane misalignment) in the right hemispace and bad performance with the right hand in an unusual orientation (i.e., large hand-midsagittal plane misalignment) in the left. The findings suggest that in males, the brain's left hemisphere is less able than the right in transforming egocentric/hand-centered spatial coding to a more allocentric representation. In females the ego- and allocentric processing areas seem to be less (or not at all) lateralized: orientation information seems to be processed to similar extent by both hemispheres, resulting in hand orientation independent, yet hemispace dependent judgments (see Figure 4).

An additional finding was that stimulus orientation affected performance: it seems that – in general - particularly vertical orientations (orthogonal to the edge of the table) are judged accurately. This is in line with the findings of the parallel-setting task in the current study, as well as with previous studies (Zuidhoek et al., 2003, Zuidhoek et al., 2005). In addition, particularly 4, 8, 19 and 23 minute stimuli – which may be assigned the term 'oblique orientations' affected performance differently in the hemispaces. These effects may be explained by the fact that the oblique orientations depend on their positioning with respect to the perceiver (hands/body-midline): an orientation of e.g. 8 minutes (42°) in left hemispace, is comparable to an orientation of 22 minutes (138°) in the right, whereas orientations of 0° and 90° are independent of positioning with respect to the body. Inspection of Table 2 suggests that comparable stimulus orientations indeed result in similar performances.

Experiment 3: Haptic production of orientation

Design

Design was similar to Experiment 2.

Apparatus and stimuli

The experimental setup was the same as in Experiment 2 (Verbal judgment task) and is depicted in Figure 3. The participants were verbally presented with one of eight possible numbers of minutes. The following minutes were presented: 1, 4, 8, 12, 16, 19, 23, 27 in random order. These minute values corresponded to the following orientations on the protractors: 84º, 66º, 42º, 18º, 174º, 156º, 132º, 108º (where 0º is parallel to the long side of the table; increasing values signify rotation in counterclockwise direction). Participants were to produce the orientation corresponding to these numbers of minutes with either hand on either of the two positions, resulting in the same number of combinations (32) as in Experiment 2. Stimulus presentation and randomization was the same as in Experiment 2. Auditory time restriction signals, however, were provided by means of a chess clock.

Procedure

Procedure was similar to that of Experiment 2, but now participants had to rotate a bar to match the number of minutes mentioned by the experimenter, as accurately as possible. They were told that they had limited time to produce the orientation, and that they would have to stop the rotation of the bar when hearing a click which was produced by a chess clock.

Before the start of every trial, the experimenter positioned the bar in question in a random orientation, i.e., corresponding to the orientation of the seconds hand of a clock at that particular time. Next, he took a hand, left it to float about 5 cm above the bar and said (the Dutch equivalent of) "here is the bar". After this, the experimenter uttered the number of minutes that was to be produced in that particular trial. Directly afterwards, he pressed a button on the chess clock, which produced a clicking sound after 2 seconds, signifying the end of the response phase. Participants were free in choice of strategy when rotating the bar. In practice, participants would drop their hands on the bar, and rotate it by pressing the palm on the bar while rotating the hand by means of rotating the wrist. Sometimes, after the hand had been dropped, the hand grasped the bar using the palm and fingers before rotating. After the participant had finished the trial, the experimenter noted down the orientation of the bar in degrees and both continued with the next trial.

Results

Error systematics

Figure 6 shows the mean signed errors (in degrees) for both hands in the right and the left hemispace. As anticipated, it reveals systematics in the signs of mean errors with respect to hemispace. Interestingly, they seem to be the opposite from those resulting from the verbal judgment task in the present study: while the orientation of a bar in the right hemispace is *over*estimated, i.e. rotated to match a higher number of minutes than it actually represents, the orientation of a bar in the left hemispace is underestimated.

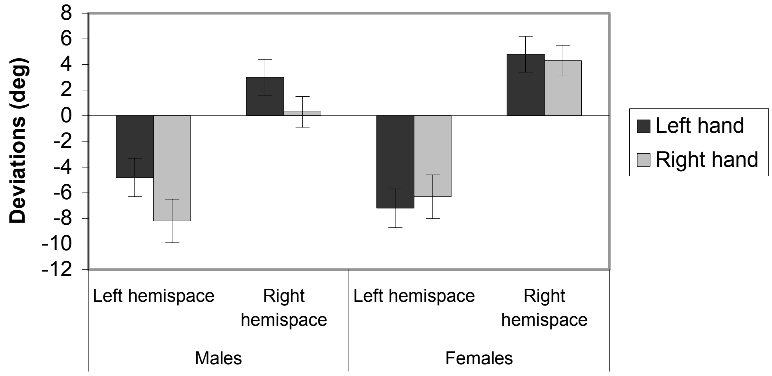


Figure 6. Mean signed errors (in degrees) resulting from the orientation production task by men and women for both hands in the right and the left hemispace. Error bars show +/- 1.0 standard errors of mean.

As explained in Experiment 2, the differences in sign for the mean errors in the different hemispaces may lead to average errors close to zero for both men and women. Therefore, we now turn to analyses in which the mean deviation sizes can be compared independently of differences in sign related to hemispatial position. The data were recoded to values as displayed in Figure 7, i.e., as in Experiment 2, we changed the sign of right hemispace performances.

Deviation size

A 2 (hemispace) x 2 (hand) x 8 (orientation) x 2 (sex) mixed ANOVA showed main effects for hemispace ($F(1,38) = 5.5$, $p = .025$) and orientation ($F(7,266) = 16.0$, $p < .001$, $\varepsilon = .67$). No significant main effect of sex was found ($F(1,38) = 1.8$, $p = .19$). The main effect of hemispace reflected an advantage of right hemispace performance: mean deviations of -3.1° and -6.6° for right and left hemispace performance, respectively. In addition, a hemispace x hand interaction ($F(1,38) = 5.3$, $p = .027$) and a sex x hemispace x hand interaction ($F(1,38) = 7.5$, $p = .01$) were found. The hemispace x hand interaction signified a significant effect of hemispace specifically for right hand performances ($F(1,38) = 8.7$, $p = .005$; mean deviations -2.3° and –7.2° for right and left hemispace performance, respectively), and not for left hand performances ($F(1,38) = 1.7$, $p = .19$). The sex x hemispace x hand interaction reflected that this hemispace effect for the right hand was predominantly a result of male performance: For males, the right hand showed a significant hemispace effect ($F(1,19) = 16.2$, $p = .001$; mean deviations -.03° and –

8.2°, for right and left hemisphere performance, respectively), while for females it did not: (F(1,19) = .1).

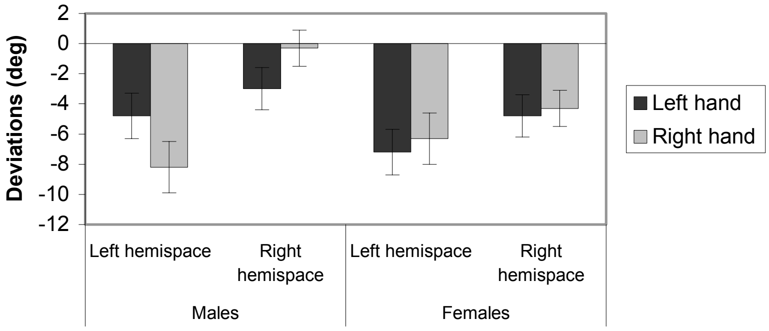


Figure 7. Recoded mean signed errors (in degrees) resulting from the orientation production task by men and women for both hands in the right and the left hemispace. Mean signed errors resulting from performance in the right hemispace are recoded to left hemispace performances by changing their sign. Error bars show +/- 1.0 standard errors of mean.

In addition to the main effect of orientation, a hemispace x orientation interaction ($F(7,266) = 26.2$, $p < .001$, $\varepsilon = .54$), and a hand x hemispace x orientation interaction were found ($F(7,266) = 2.9$, $p = .006$). The effect of orientation suggests differences in performance on the different orientations. The average values, reflecting the main effect of orientation as shown in Table 3, suggest that, in general, it is easier to produce orientations close to 0 or 30 minutes (the 'vertical'), than producing orientations close to 15 minutes (the 'horizontal'). The interaction effect of hemispace by orientation indicates that the effect of hemispace was not the same for each orientation. This effect was further modulated by hand use.

Table 3. The hemispace by hand by orientation interaction and the orientation main effect (overall averages) in orientation production performance. Tables show mean deviation (SE) in degrees.

	Left hand performance		Right hand		
Stimulus (min)	Right hemispace	Left hemispace	Right hemispace	Left hemispace	Average Overall
1	.2 (1.2)	-.1 (1.4)	-1.2 (1.0)	-1.1 (1.1)	-.6 (.7)
4	2.6 (1.7)	-5.5 (1.6)	1.5 (1.4)	-8.6 (1.4)	-2.5 (.8)
8	-1.1 (1.9)	-11.9 (1.4)	1.2 (1.9)	-9.6 (1.5)	-5.4 (.8)
12	.6 (2.2)	-15.5 (2.2)	4.8 (2.0)	-19.0 (2.2)	-7.3 (1.0)
16	-8.1 (1.6)	-7.9 (1.3)	-5.8 (1.5)	-7.9 (1.2)	-7.4 (.8)
19	-16.4 (1.9)	.9 (1.9)	-12.6 (1.5)	-3.6 (2.3)	-7.9 (.9)
23	-5.8 (1.7)	-7.2 (2.2)	-2.7 (1.5)	-7.6 (2.2)	-5.8 (1.1)
27	-3.1 (1.0)	-.9 (1.7)	-3.5 (1.5)	-.4 (1.9)	-2.0 (.9)

Discussion Experiment 3

In line with an orientation production study in the fronto-parallel plane (Hermens et al., in press), the production of an orientation matching a specific number of minutes resulted in small errors. In contrast to that study, however, the errors in the present experiment were systematically signed, with the nature of the sign depending on the hemispace in which the orientation is produced. Strikingly, the systematic errors found in the current production of orientation task were opposite to those found in the verbal judgment task (Experiment 2, see Figure 4): while (on average) the orientation of a bar in the right hemispace was rotated in such a way that it matched a higher number of minutes than it actually represents, the orientation of a bar rotated in the left hemispace was found to match a lower number of minutes (see Figure 6). Together these findings suggest that, in the horizontal plane, the deviation in the production of orientation is a result of the deviation in perception: a counterclockwise deviation in the perception of a bar orientation results in a clockwise production error, whereas a clockwise deviation in perception leads to a counterclockwise production error.

Importantly, although no main effect of sex was found, analyses of the different factors on the size of the errors showed that the general effect of hemispace (right hemispace performance was better than left hemispace performance) was modulated by hand use and sex (see Figure 7). Specifically, this effect of hemispace on performance was a result of male right hand performance in particular. Similar to the findings of the verbal judgment task in the current study, it seems that for males, right hand performance was different over the hemispaces, while their left hand performance was not modulated by hemispace. For females, performance by both hands was comparable for both hemispaces. A possible interpretation, analogous to what was suggested for verbal judgment performance, is that, for males, the right hand (which projects to the brain's left hemisphere) is particularly affected by hand orientation, resulting in a large difference between (good) performance with the right hand in a natural orientation (small hand-midsagittal plane misalignment) in the right hemispace and relatively bad performance with the right hand in an unusual orientation (large hand-midsagittal plane misalignment) in the left hemispace. The findings further corroborate the claim that in males performance with the right hand (projecting to the brain's left hemisphere) is particularly egocentric, while in females the ego- and allocentric processing is less lateralized.

Additional findings concerned the main effect of orientation and the interaction effects of orientation by hemispace and of orientation by hemispace by hand. Table 3 suggests that - similar to verbal judgment performance - it is easier to produce orientations close to 0 or 30 minutes (the 'vertical'), than producing orientations close to 15 minutes (the 'horizontal'). Again, the orientation effect was modulated by hemispace. The means suggest that - analogous to the findings of the verbal judgment task - comparable stimulus orientations (for example 8 minutes in the left hemispace and 23 minutes in the right) result in similar performances, yet that performances on these particular orientations differ for the hands with respect to error size.

General Discussion

The present study examined sex differences in three different haptic orientation perception tasks, focusing on haptic spatial perception, action and integration of the two. For each of these tasks, differences in reference frame employment and lateralization of spatial abilities and attention (hand and hemispace effects) were considered.

Our first task, a bimanual haptic parallel-setting task, comprising both perception and action showed a clear advantage for male performance, which replicates the findings of a previous study (Kappers, 2003). This advantage was not modulated by a 10-seconds delay between perception of the reference bar and the action of rotating the test bar: the sexes showed similar improvement with delay (cf. Zuidhoek et al., 2003). Since the improvement is believed to reflect a shift from egocentric to more allocentric reference frame employment during the delay period, this particular finding suggests that the stimulation of mental allocentric reference frame employment does not increase or otherwise affect the advantage of males in haptic orientation matching. Interestingly, the hand/hemispace manipulation did not affect performance in this particular task, nor did it result in sex differences, indicating that possible sex differences in performance related to lateralization of spatial ability and/or attention are not reflected in performance on a bimanual task with symmetric placement of the bars with respect to the midsagittal plane. This suggests that if such differences play a role in this task, they affect reference bar exploration (perception) and test bar rotation (action) to similar extent.

Our second task was a verbal judgment of haptically perceived orientation task, which focused on hemispace and hand effects in haptic *perception*; participants were to assign a number of minutes to a unimanually explored orientation. Both sexes showed small, yet systematically signed deviations with respect to hemispace, similar to those that have been reported earlier in the horizontal plane (Zuidhoek et al., 2005). Importantly, also in this task a male advantage was found: again, males' deviations were smaller in general. In addition to this main effect, it was found that for males the size of the error was modulated by the right hand over the hemispaces, while for females hand nor hemispace affected error size. Only with their right hands, men performed particularly well on same hemispace judgments, and badly on judgments of haptically explored bars in the left hemispace.

Interestingly, a similar sex, hand, hemispace effect was found in our third task which focused on sex differences in haptic action: participants had to rotate a bar to match a number of minutes on an imagined clock face. Although no significant main effect of sex was found in this particular task, a specific modulation of right hand performance over both hemispaces was found for male performance also in this task: whereas for females hand nor hemispace affected error size, male right hand performance was near perfect for same hemispace rotations, and relatively bad for rotations performed in the opposite hemispace. In addition, like in the verbal judgment task, participants produced small and systematically signed deviations. Importantly, however, although similar in size, the deviations of production were opposite in sign to those in verbal judgment, resulting in a complementary deviation pattern.

These findings have some important general implications for the processes underlying haptic orientation performance. First, the complementary nature of the error patterns of the two tasks suggests that similar processes determine perception and action. More specifically, the deviations in perception seem to underlie those in production; the deviation in production seems to be a result of compensating for a deviation in perception. Second, orientation production being quite accurate (cf. Hermens et al., in press), indicates that the act of rotating is not grossly biased by egocentric reference frames per se. Seen in this light, the large deviations resulting from parallel-setting stem from large deviations in only perception of the two bars, and not the act of rotating per se. Apparently, differences in deviation size for different haptic orientation tasks result from task characteristics other than response type per se, like the extent to which mental allocentric reference frame employment is stimulated by e.g. visual imagery, defining orientation allocentrically, stimulating cognitive processes. Third, performances in the horizontal and the fronto-parallel planes may partly employ different reference frames: although verbal judgment and orientation production performance in the fronto-parallel plane has also resulted in small errors, the *direction* of the error did not systematically depend on hemispace (Hermens et al., in press), as it did in the present study. Possibly, performance in the fronto-parallel plane involves (a larger contribution of) a subjective gravitational frame (Luyat et al., 2001).

Also the sex differences found have some important implications. For one, males seem to outperform females on tasks that address haptic orientation perception and a combination of perception and action. This is in line with several studies in the visual domain that suggest that males have superior understanding of Euclidean space and a related tendency to employ more absolute world-centered, allocentric and geometrical information (Geary, 1996; Matthews, 1986; Webley & Whalley, 1987; Galea & Kimura, 1993; McGuiness & Sparks, 1983). Furthermore, we found that the stimulation of mental allocentric reference frame employment results in smaller deviations in the parallel-setting task (by means of delay), and in small deviations in the verbal judgment and production tasks. Interestingly, this did not result in an increase of the male advantage: not within the parallel-setting task (no sex by delay interaction), nor in the other tasks. The absence of a main of sex effect in the production task may even reflect a decrease rather than an increase of the male advantage. Together, the findings seem to suggest that the male advantage does not depend on the extent of mental allocentric reference frame stimulation, but rather from a general superior ability to overcome egocentric biases in haptic performance.

Importantly, the effects of hand and hemispace on only male performance in the verbal judgment and orientation production tasks, suggest lateralization differences in haptic orientation perception between men and women. More specifically, the findings seem to suggest that right hand performance in males is more susceptible to hand orientation effects than left hand performance. In contrast, female performance does not seem to depend on hand orientation. This may indicate that the male's left hemisphere codes space more in hand-centered coordinates then does the male's right and both female hemispheres. Interestingly, male (right hand) performance seems to be more in line with the overall performance in our previous verbal judgment study, comprising both males and females (Zuidhoek et al., 2005). Reflecting no effect of hand orientation on performance in the present study, female performance may even suggest midsagittal plane related deviations rather than hand related deviations. This discrepancy may be due to differences in the temporal restrictions between this and the previous study: whereas trials in the previous study took 2.4 seconds, those in the present task took 4 seconds. Speculatively, after representing the orientation of a bar in hand-centered reference frames, this biased representation is converted to an - arguably more allocentric - midsagittal plane-centered representation, which removes (some) of the biasing hand-centered information in terms of error size, but preserves differences between the hemispaces in terms of direction. Possibly, males' right hand performance needs more time to complete allocentric haptic spatial processing. In line with this, delaying verbal judgment by 10 seconds in our previous verbal judgment study resulted in a small but significant improvement only for right hand performance (Zuidhoek et al., 2005). This right hand disadvantage may be explained by a spatial (and temporal) integrative function of the right partietal cortex for both sides of the body (Knecht et al., 1996).

In sum, the present study revealed new insights in sex differences in haptic spatial performance, as well as haptic spatial performance in general. The findings indicate that males are more accurate than females when haptically perceiving the orientation of bars in the horizontal plane, irrespective of whether the task triggers egocentric (parallel-setting) or allocentric reference frames involvement (verbal response). Specific sex differences concerning hand and hemispace found in both the verbal judgment and motor production of orientation may suggest that males' orientation perception is more lateralized than that of females, with hand-centered coding residing in the left hemisphere, and coding with respect to the midsagittal plane - which is arguably more allocentric - in the right. Other similarities for performance on the verbal judgment task and the orientation production task indicate that deviations in perception underlie those in production, and that the sheer motor response of rotating a bar does not result in large deviations. Together, these findings indicate that large deviations in haptic orientation performance are caused by biases in perception and not action, and that they predominantly depend on task characteristics other than response mode, like the extent to which mental allocentric reference frames use is stimulated.

References

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61,* 303-321.

Barnfield, A.M.C. (1999). Development of sex differences in spatial memory. *Perceptual and motor skills, 89,* 339-350.

Batschelet, E. (1981). *Circular statistics in biology.* London, England: Academic Press Inc.

Berthiaume, F., Robert, M., St-Onge, R., & Pelletier, J. (1993). Absence of a gender difference in a haptic version of the water-level task. *Bulletin of the Psychonomic Society, 31,* 57-60.

Collear, M.L., & Nelson, J.D. (2002). Large visuospatial sex difference in line judgment: possible role of attentional factors. *Brain and Cognition, 49,* 1-12.

Corballis. M.C. (1980). Laterality and myth. *Americal Psychologist, 35,* 284-295.

Eals, M., & Silverman, I. (1994). The hunter-gatherer theory of spatial sex differences: proximate factors mediating the female advantage in recall of object arrays. *Ethology and Sociobiology, 15,* 95-105.

Ecuyer-Dab, I., & Robert, M. (2004). Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition, 91,* 221-257.

Ernest, C.H. (1998). Spatial ability and lateralization in the haptic modality. *Brain and Cognition, 36,* 1-20.

Findlay, R., Ashton, R., & McFarland, K. (1994). Hemispheric differences in image generation and use in the haptic modality. *Brain and Cognition, 25,* 67-78.

Galea, L.A.M., & Kimura, D. (1993). Sex differences in route-learning. *Personality and individual differences, 14,* 53-65.

Geary, D.C. (1995). Sexual selection and sex differences in spatial cognition. *Learning and Individual differences, 7,* 289-301.

Geary, D.C. (1996). Response: a biosocial framework for studying cognitive sex differences. *Learning and Individual differences, 8,* 55-60.

Harris, L.J. (1981). Sex-related variations in spatial skill. In L.S. Liben, A.H. Patterson, & N. Newcombe (Eds.), *Spatial representation and behavior across the life span.* New York: Academic Press.

Heller, M.A., Calcaterra, J.A., Green, S., & Barnette, S.L. (1999). Perception in the horizontal and vertical in tangible displays: minimal gender differences. *Perception 28,* 387-394.

Hermens, F., Kappers, A.M.L., & Gielen, S. (in press). The structure of fronto-parallel haptic space is task dependent. *Perception & Psycholphysics.*

Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. *Neuropsychologia, 41,* 504-515.

James, T.W., & Kimura, D. (1997). Sex differences in remembering the locations of objects in an array: location shifts versus location-exchanges. *Evolution and human behavior, 18,* 155-163.

Kaiser, M.K., Proffitt, D.R., Whelan, S.M., & Hecht, H. (1992). Influence of animation on dynamic judgments. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 669-690.

Kappers, A.M.L. (1999). Large systematic deviations in the haptic perception of parellelity. *Perception, 28,* 1001-1012.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 114,* 131-145.

Kappers, A.M.L., & Koenderink, J.J. (1999). Haptic perception of spatial relations. *Perception, 28,* 781-795.

Kimura, D. (1983). Sex differences in cerebral organization for speech and praxic functions. *Candian Journal of Psychology, 37,* 19-35.

Kimura, D. (1992). Sex differences in the brain. *Scientific American, 267,* 118-225.

Kinsbourne, M. (1987). Mechanisms ofunilateral neglect. In M. Jeannerod (Ed.) *Neurophysiological and Neuropsychological Aspects of Spatial Neglect.* Amsterdam: North Holland.

Kinsbourne, M., & Cook, J. Generalized and lateralized effects of concurrent verbalization on a unimanual skill. *Quarterly Journal of Experimental Psychology, 23,* 341-345.

Knecht, S., Kunesch, E., & Schnitzler, A. (1996). Parallel and serial processing of haptic information in man: Effects of parietal lesions on sensorimotor hand function. *Neuropsychologia, 34,* 669-687.

Kolb, B., & Whishaw, I.Q. (1995). Fundamentals of human neuropsychology. New York: Freeman.

Kosslyn, S.M., Koenig, O., Barrett, A., Cave, C., Tang, J., & Gabrielig, J.D.E. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate spatial relations. *Journal of Experimental Psychology: Perception and Performance, 15,* 723-735.

Laeng, B., Buchtel H.A., & Butter C.M. (1996). Tactile rod bisection: Hemispheric activation and sex differences. *Neuropsychologia, 34,* 1115-1121.

Law, D.J., Pellegrino, J.W., & Hunt, E.B. (1993). Comparing the tortoise and the hare: gender differences and experience in dynamic spatial reasoning tasks. *Psychological Science, 4,* 35-40.

LeDoux, J.E., Wilson, D.H., & Gazzaniga, M.S. (1977). Manipulospatial aspects of cerebral lateralization: Clues to the origin of lateralization. *Neuropsychologia, 15,* 743-749.

Lewis, R.S., & Christiansen, L. (1989). Intrahemispheric sex differences in the functional representation of language and praxic functions in normal individuals. *Brain and Cognition, 9,* 238-243.

Linn, M.C., & Peterson, A.C. (1985). Emergence and characterization of sex differences in spatial abilities: A meta-analysis. *Child Development, 56,* 1479-1498.

Luyat, M., Gentaz, E., Corte, T.R., & Guerraz, M. (2001). Reference frames and haptic perception: body and head tilt effects on the oblique effect. *Perception and Psychophysics, 63,* 541-554.

Maccoby, E.E., & Jacklin, C.N. (1974). *Psychology of sex differences.* Stanford, CA: Stanford University Press.

Matthews, M.H. (1986). The influence of gender on the environmental cognition of young boys and girls. *Journal of Genetic Psychology, 147,* 295-302.

McGuiness, D., & Sparks, J. (1983). Cognitive style and cognitive maps: sex differences in representation of a familiar terrain. *Journal of Mental Imagery, 7,* 91-100.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England: Clarendon Press/Oxford University Press.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* Oxford, England UK: Oxford University Press.

Moffat, S.D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a virtual maze: sex differences and correlations with psychometric measures of spatial ability in humans. *Evolution and Human Behavior,* 19, 73-87.

Montello, D.R., Lovelace, K.L., Golledge, R.G., & Self, C.M. (1999). Sex-related differences and similarities in geographic and environmental spatial abilities. *Annals of the Associations of American Geographers, 89,* 515-534.

Robert, M., Pelletier, J., St-Onge, R., & Bertiaume, F. (1994). Women's deficiency in water-level representation: Present in visual conditions, yet absent in haptic contexts. *Acta Psychologica, 87,* 19-32.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Rossetti, Y., & Régnier, C. (1995). Representations in action: pointing to a target with various representations. In B.G. Bard, R.J. Bootsma, & Y. Guiard (Eds.) *Studies in Perception and Action III* (pp. 233-236). Mahwah, NJ: Laurence Erlbaum Associates Inc.

Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: evolutionary theory and data. In J.H. Barkow, L. Cosmides, & J. Tooby (Eds.) *The adapted mind: evolutionary psychology and the generation of culture* (pp. 533-549). Oxford: Oxford University Press.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-44.

Voyer, D., Voyer, S., & Bryden, M.P. (1995). Magnitude of sex differences in spatial abilities: a meta-analyses and consideration of critical variables. *Psychological Bulletin, 117,* 250-270.

Ward, S.L., Newcombe, N., & Overton, W.F. (1986). Turn left at the church, or three miles north: a study of direction giving and sex differences. *Environment and Behavior, 18,* 192- 213.

Webley, P., & Whalley, A. (1987). Sex differences in home range and cognitive maps in eight-year old children. *Journal of Environmental Psychology, 1,* 293-302.

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). Multiple integration mechanisms in haptic space perception. *Experimental Brain Research, 157,* 265 - 268.

Zuidhoek, S., Kappers, A.M.L., Noordzij, M.L., Van der Lubbe, R.H.J., & Postma, A. (2004). Frames of reference in a haptic parallelity task: temporal dynamics and the possible role of vision. In S. Ballesteros, & M.A. Heller (Eds.) *Touch, blindness and neuroscience*. Madrid, Spain: UNED Press.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2005). Effects of hand orientation and delay on the verbal judgment of haptically perceived orientation. *Perception, 34,* 741-755.

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (submitted). Haptic orientation perception benefits from visual experience: evidence from early blind, late blind and sighted people.

Conclusions

Chapter 8| Summary and Discussion

Summary

The present thesis focused on the representations of grasping space based on haptic input. We aimed at identifying their characteristics, and the underlying neurocognitive processes and mechanisms. To this end, we studied the systematic distortions in performance on several orientation perception tasks, and identified some of the circumstances under which they occur. In addition to examining performance of blindfolded sighted participants on several tasks in the first part of this thesis (*Chapters 2, 3* and *4*), we looked at differences between specific groups in the second part. Performances by the early blind, the late blind and the sighted were compared in *Chapters 5* and *6*. In *Chapter 7* differences between male and female performances were examined. In the current, final chapter the main findings of the foregoing chapters are summarized and discussed.

In *Chapter 2*, we studied the effects of delay on performance on the haptic parallel-setting task. We hypothesized delay to result in a shift from egocentric towards allocentric reference frame involvement, which would result in an improvement of performance with delay. Indeed, we found that performance improves when the parallel-setting action is delayed by 10 seconds after the perception of a reference bar. This counterintuitive finding suggests that deviations in parallel-setting result from egocentric reference frame use. We speculated that the improvement may result from cognitive effort (cf. Gentaz & Hatwell, 1999) and/or visuospatial imagery involved in the retention of the reference bar (cf. Millar, 1988, 1994; Thinus-Blanc & Gaunet, 1997).

The goal of *Chapter 3* was twofold. First, having established that egocentric reference frames bias parallel-setting performance in *Chapter 2*, we now examined whether hand- or body-centered reference frames (or both) are responsible for biasing haptic orientation perception. To this end, we introduced a task (the "verbal judgment task") in which bars which were fixed at locations in space with respect to the body, were perceived by either the right or the left hand. Second, we wanted to know to what extent the deviations in haptic perception of orientation depend on specific task characteristics. Therefore, we chose the task characteristics in such a way that we expected them to stimulate mental allocentric reference frame employment and consequently to result in small deviations. By asking blindfolded participants to verbally assign a number of minutes to the haptically perceived orientation we expected to force participants to form a (visuo)spatial image of a haptically perceived bar on a clock face. In addition, orientation was explicitly defined with respect to the edge of the stimulus table, which as such would function as a mental allocentric reference frame. Additional interests were the effect of a 10-

seconds delay in this task, correlation between task performance and performance on a (visuo)spatial imagery task (Paivio's mental clock test (1978)), and the possible relationship between the systematic deviations in orientation perception and another, well documented systematic error in the variability in the perception of orientations ("oblique effect", e.g., see Gentaz and Hatwell (1998, 1999)).

We found that haptic orientation perception, as assessed with the verbal judgment task, is biased by hand-centered reference frames. More specifically, the size of the deviations were systematically related to hand-orientation: the larger the misalignment of hand with the midsagittal plane, the larger the deviations in orientation perception. Importantly, the deviations were very small as compared to performance on the parallel-setting task (*Chapter 2*), suggesting that the accuracy of haptic orientation perception largely depends on task characteristics and is not grossly biased per se. A trend for a moderate positive correlation between performance on the verbal judgment task and the mental clock test suggested that a relationship between haptic orientation perception and (visuo)spatial imagery ability. In addition, delaying the verbal response resulted in a small but significant improvement of only right hand perceptions, suggesting different hemispheric involvement in processes involved in retaining and/or integration of haptic spatial processes (cf. Knecht, Kunesch & Schnitzler, 1996). The haptic oblique effect, as found with the current verbal response, was not affected by hand-orientation nor delay suggesting the oblique effect and the systematic deviation in haptic orientation perception to be independent.

Chapter 4 addressed whether visual allocentric context information (so-called "noninformative vision") improves or otherwise affects haptic parallel-setting performance (cf. Newport, Rabb, & Jackson, 2002). In addition, we examined whether the possible effect of context depends on the orienting direction of head and eyes. We found that both the orienting direction of head and eyes, and the availability of noninformative vision affect parallel-setting performance, but that they do so independently: orienting towards the reference bar facilitated parallel-setting of a test bar in both no-vision and noninformative vision conditions, and noninformative vision improved performance irrespective of orienting direction. These results suggest the effects of orienting and noninformative vision to depend on distinct neurocognitive mechanisms.

In order to investigate the roles of both visual and haptic experience on haptic orientation perception, we compared performance of the early blind, the late blind and the blindfolded sighted on the (delayed) haptic parallel-setting and verbal judgment tasks in *Chapter 5*. Visual experience fulfilled a beneficial role in both tasks. In the parallel-setting task, visual experience resulted in less variable performance indicating that visual experience provides structure to parallel-setting performance. Importantly, with respect to deviation size, only delayed performance revealed a difference between the groups. Whereas the visually experienced groups improved with delay, the early blind did not, suggesting that improvement with delay depends on the ability to engage in *visuo*spatial imagery (cf. Rossetti, Gaunet & Thinus-Blanc, 1996; Gaunet & Rossetti, in press). Interestingly, the sighted improved more than the late blind indicating that becoming blind may lead to a reduced tendency to activate visual memories or to translate haptic input into mental visual images. Importantly, in the verbal judgment task, all groups produced very small deviations as compared to parallel-setting. However, both early and late blind participants displayed larger deviations than the sighted controls. The groups did not differ with respect to the haptic oblique effect, which - like the results of *Chapter 3* - suggests independence of the systematic deviation in haptic orientation perception.

Considering that the differences between the groups occur in the delayed parallel-setting task and verbal judgment task, and not in non-delayed parallel-setting, the results of *Chapter 5* suggest that haptic spatial representation particularly benefits from visual experience in tasks that stimulate allocentric reference frame employment. Despite of the substantial differences between the groups resulting from mental visual processing on these tasks, the small deviations in the verbal judgment task for even the early blind suggest, however, that fairly acceptable allocentric representations can be achieved without mental visual processing. Apparently, other cognitive processes than mental visual ones (e.g., relating bar orientation to the imagined edge of the table, haptic imagery of a clock face, conversion of perceived orientation to a number of minutes) can – to some extent - result in adequate orientation perception.

The foregoing indicates that the extent to which (haptic) spatial information is represented allocentrically may critically depend on the level of processing as triggered by task characteristics. One dimension of particular importance may be that of implicit – explicit. Asking participants to act may address more implicit, egocentric motor representations of space, while asking people to engage in cognitive processing may result in more explicit, reportable, allocentric representations of space (cf. Milner & Goodale, 1995). *Chapter 6* further examined the effects of the explicitness of a task on the performance of the (early and late) blind and the blindfolded sighted. We had early blind, late blind and sighted participants implicitly learn the locations of multiple shapes by matching them to cutouts of a board as fast as possible, in three consecutive trials. After this, we examined their spatial knowledge by having them perform three localization/spatial memory tasks varying in explicitness: implicit speeded matching after rotation of the board, an intermediate non-speeded spatial memory task with a motor response, and an explicit spatial memory task with a verbal response. We found that both blind groups were much faster than the sighted group during both the three learning trials, and the rotation trial. In contrast, no differences between the groups were found in the non-speeded motor placement condition (accuracy, spatial grain). Moreover, with the explicit verbal response, spatial memory was strongest in the late blind group. Together, these findings suggest that beneficial effects of haptic experience may predominantly be expected on implicit haptic tasks, while visual experience becomes increasingly important as tasks require more explicit spatial knowledge.

In *Chapter 7*, sex differences in haptic orientation tasks were explored by addressing possible differences between the sexes in egocentric and allocentric reference employment, both in tasks that do (delayed parallel-setting, verbal judgment and orientation production) and tasks that do not stimulate allocentric reference frame employment (non-delayed parallel-setting). The verbal judgment and orientation production task allowed us to examine whether possible sex differences in haptic performance were due to sex differences in perception or action, or both. In addition, the latter unimanual tasks made it possible to investigate sex differences in lateralization of haptic spatial processing mechanisms.

The findings revealed general as well as specific sex differences in haptic orientation perception. In line with several visual studies that suggest that males have a larger tendency to employ allocentric reference frames (e.g. Geary, 1996; Matthews, 1986; Galea & Kimura, 1993), we found that males were more accurate in non-delayed parallel-setting (cf. Kappers, 2003), delayed parallel-setting and verbal judgment. The extent of mental allocentric reference frame stimulation (delay vs. non-delay) did not affect the sex differences found. In addition, we found that specifically male right hand performance in both the verbal judgment and the orientation production task depended on hand-centered reference frames, which suggests sex differences in lateralization of haptic orientation processing. Finally, comparing performance on the orientation production task - in which bars were rotated to match a verbally presented number of minutes – with that on the verbal judgment task led to an important general finding: orientation production resulted in deviations of the same size as verbal judgment but of opposite sign. The deviations being small indicates that the motor response of rotating a bar, in contrast to what the parallel-setting task may suggest, does not result in large deviations per se (cf. Hermens, Kappers & Gielen, in press). The complementary pattern for verbal judgment and production suggests that biases in production result from biases in perception.

Conclusions and discussion

The findings in the current thesis have shown that systematic biases in egocentric referencing are responsible for the systematic deviations in haptic tasks requiring the representation of orientation. Importantly, it seems that the deviations found in the work presented here ultimately can be traced back to the employment of one and the same egocentric reference frame: the hand. The extent of misalignment of hand orientation with the body's midsagittal plane was found to be related to the size of the deviation (*Chapter 3*). In addition, the deviations all seem to result from biases in *perception*; the complementary pattern of verbal judgment and orientation production suggested that also in tasks that require a motor response the deviations do not result from egocentric reference frames involved in the rotation of the bar (*Chapter 7*). However, the impact of hand orientation on haptic orientation perception appeared to depend highly on the precise task characteristics (*Chapters 2, 3, 4, 5 and 7*). Temporal manipulations *(Chapters 2 and 3)*, orienting direction (*Chapter 3*) and the extent to which a task stimulates specific processes like (mental) allocentric frame employment and (visuo)spatial imagery *(Chapters 3, 4, 5, 7)*, appeared to have direct consequences for the size of the deviation. Basically, the findings suggest that the more allocentric reference frame employment and mental imagery is stimulated, the smaller the deviations in haptic orientation perception. With respect to orienting, we found that, in parallel-setting orienting towards the reference bar enhanced performance.

In addition to task characteristics, we found that the visual status and sex of the observer, as well as hand use affected haptic spatial performance. The effects of visual status seem to depend on task characteristics. *Chapter 5* suggested that visual experience becomes increasingly important in haptic orientation perception tasks that stimulate allocentric reference frame employment. Furthermore, *Chapter 6* suggested that visual experience becomes increasingly important if tasks address more explicit spatial knowledge. In addition, *Chapter 6* indicated that beneficial effects of haptic experience may mainly be expected on implicit (speeded) haptic tasks, that discourage the generation or employment of an allocentric representation. An advantage of haptic experience found in the speeded rotated localization task (*Chapter 6*), and not in the non-delay parallel-setting task (*Chapter 5*), suggests that in addition to the task addressing processing at the implicit haptic motor level, haptic experience may specifically facilitate performance on tasks that require haptic dexterity.

With respect to sex differences, we can conclude that, in general, males outperform females on allocentric haptic orientation tasks, irrespective of mental reference frame stimulation (*Chapter 7*). Interestingly, we found specific sex differences with respect to hand use which seem to be related to a finding in *Chapter 3*. In this chapter, delay in the verbal judgment task resulted in an improvement for right hand performance only, bringing it up to the level of left hand performance. This might suggest that the left hemisphere may code space longer in egocentric coordinates than the right (*Chapter 3).* In *Chapter 7* we found that, without delay but with slightly longer exploration and response times, particularly right hand performances of males reflected hand-centered coding, whereas male left hand performance and female performance in general suggested more midsagittal plane centered coding. Interestingly, male's left hand performance was better than males right hand performance, and than female performance in general. This finding contributes to findings in the visual domain that suggests that males are better in representing space allocentrically. Importantly, it seems that in haptics this only holds for left hand perceptions, as haptic spatial integration mechanisms in males may be more lateralized than in women (i.e., located mainly in the right hemisphere (cf. Knecht et al., 1996)).

The foregoing suggests that in haptic orientation coding, allocentric processing may mean relating the hand to the midsagittal plane, at least in the horizontal plane. In line with this, we consistently found reference bar orientations aligned with the midsagittal plane and (to somewhat lesser extent) those perpendicular to be perceived more accurately (*Chapters 2, 3, 4, 5 and 7*). In addition, we found these orientations to be performed with smaller variability than the oblique orientations, which is know as the haptic oblique effect (*Chapters 3* and *5*). In contrast, however, studies on the oblique effect have shown that a subjective gravitational frame may be causing the haptic oblique effect (Luyat, Gentaz, Corte & Guerraz, 2001).

Taken together, the present findings suggest that hand-centered reference frames bias haptic orientation perception, and that – when no physical reference frames are available - relating hand-centered information to the midsagittal plane centered reference frames may reduce this bias. Importantly, several recent studies have also implicated the use of reference frames comprising the body midline to be vital for adequate performance on haptic orientation perception tasks (Heller, Brackett, Scroggs & Allen, 2001) and other haptic spatial tasks (Millar & Al-Attar, 2002, 2004;

Ballesteros, Millar & Reales, 1998). The effectiveness of relating hand-centered haptic information to the body (or to external reference frames), seems to depend on the specific task characteristics. The present findings have shown that the retention of orientation information, stimulating spatial imagery, providing mental or physical allocentric reference frames, orienting towards an input source, cognitively transforming haptic input, all facilitate haptic orientation task performance. In explaining these effects, we would like to speculate that they rely on only a few key neurocognitive mechanisms, which should explain the effects of specific task manipulations. We will now make an attempt in identifying these mechanisms.

An important finding was that allocentric processing of haptic spatial information does not seem to occur automatically. It seems that, in haptics, transforming egocentric spatial codes into more allocentric ones depends on explicit, cognitive spatial processing; addressing lower level processing at the haptic motor level alone results in predominantly egocentric processing (*Chapters 2, 4, 5* and *6*) and consequently in large deviations (*Chapters 2, 4* and *5*). In contrast, spatial imagery of a clock face and relating the orientation of a bar to a mental image of an external reference frame (via relating it to the body's midsagittal plane (*Chapters 3* and *5*)) *without* visual experience, seem sufficient to produce fairly adequate allocentric representations of haptically perceived orientation. Thus, although allocentric processing may be facilitated by concurrent (*Chapter 4*) and by mental visual processing (*Chapters 2, 3, 5* and *6)*, adequate haptic spatial performance in peripersonal space seems to depend largely on non-visual spatial imagery of allocentric reference frames.

In addition to the extent of engagement in active spatial imagery - either or not helped by (mental) visual processing -, it seems that orienting direction affects haptic orientation perception (*Chapter* 4). Importantly, we found that although the parallel-setting task comprises the perception of two bars - orienting towards the reference bar enhanced performance, whereas orienting towards the test bar did not. This implies that the mere alignment of sensory systems through orienting is not sufficient to result in an improvement in (spatial) perception (cf. Kennett et al. 2001). Rather, it seems that orienting enhances perception by facilitating additional processing, which - in the parallel-setting task - is performed exclusively on reference hand input. Two underlying mechanisms may be considered here. First, it may be that performing the parallel-setting task comprises imagery of the reference bar which is stimulated and/or facilitated by orienting towards it. Second, orienting may facilitate the allocation of attentional resources (Honoré, Bourdeaud'hui & Sparrow, 1989; Driver & Grossenbacher, 1996). Then, the improvement in performance with reference hand orienting may reflect the attentional focus being primarily on the reference hand during task performance. Possibly, these two mechanisms are interlinked: imagery of the reference hand may depend on attentional resources, and in turn, attending a (visuo-tactile) image of the limb itself may be critical, since visually attending a neutral object at the location of tactile stimulation has been found not to boost perception (Kennett, Taylor-Clarke & Haggard, 2001; Taylor-Clarke, Kennett & Haggard, 2002).

We found indications that the right hemisphere (most likely right parietal areas (Knecht et al., 1996)) may be more involved than the left in the integration of haptic spatial information (*Chapters 3* and *7*). With respect to the mechanisms (spatial imagery and orienting direction) mentioned above, we can only speculate about implementations at the neural level. In general, recent studies have suggested that a parietal frontal multimodal network mediates the coding of peripersonal space and our limbs in it by integrating visual, proprioceptive, tactile and possibly auditory inputs (Làvadas, Di Pellegrino, Farnè & Zeloni, 1998; Obayashi, Tanaka & Iriki, 2000; Newport, Hindle & Jackson, 2001; Graziano, 2002; Lloyd, Shore, Spence & Calvert, 2003). Thus, it is likely that haptic spatial representation and imagery of the limbs in space may involve activity of cells in this network.

Our findings indeed seem to suggest that there is more to haptic spatial processing than processing in the primary and secondary sensory cortices and parietal areas 5 and 7. For example, the right intraparietal sulcus has been implicated in the comparison of mentally imaged orientations (Trojano et al., 2000; Sack et al., 2002). In addition, the effects of visual experience and concurrent non-informative vision, suggest visual processing regions to be involved. It may be that the effects of concurrent non-informative visual input changes haptic spatial representations through the effects of particularly conscious visual processing in ventral stream areas on activation of cells in the parietal-frontal network. The effects of mental visual processing may be due to the activation of visuospatial memories, which most likely involve prefrontal cortex, the hippocampus, the ventral visual pathway, and the intraparietal cortex (Lacquaniti et al., 1997; Prather, Votaw & Sathian, 2004). It is also unknown how the facilitating effect of orienting on haptic perception is mediated at a neural level. However, Taylor-Clarke and colleagues (Taylor-Clarke, Kennett & Haggard, 2002) have argued that the effects of *vision* on tactile perception are reflected by a modulation of cell activity in the primary and secondary somatosensory cortex (SI and SII), brought about by back projections from multimodal cortical areas. Importantly, they showed that S1 processing (N80 component) is only enhanced by vision when tactile stimulation is task-relevant, suggesting top-down attentional selection. It might be that the contribution of (visual) imagery and orienting operate in a similar manner, i.e., via back projections from those multimodal areas concerned with visuo-tactile imagery of our moving limbs in space like the intraparietal sulcus (Obayashi et al., 2000; Lloyd et al., 2003) to S1 and S2, with those to S1 depending on task-dependent attentional selection processes.

To conclude, the present thesis has shed new light on the 'hidden' world of haptics as a spatial sense. Its findings suggest that constructing an adequate absolute representation of peripersonal space based on haptic input, is a complex multifaceted process, involving cognitive engagement, multiple stages of egocentric to more allocentric referencing, and the processing in many brain areas, including (some of) those involved in visual and multimodal spatial processing. The quality of haptic allocentric processing may depend on the extent of engagement in spatial imagery of allocentric reference frames, the activation of visual memories, and the orienting towards a haptic input source. As such, the present findings have important implications for the blind. When constructing an absolute representation of space both blind groups should be encouraged to actively use (mental images of) external reference frames as often as possible. In addition, the late blind should be reminded to use their visual imagery ability and to orient towards perceiving hands, as it seems that in the kingdom of the blind, indeed, the man with one eye is king.

References

Ballesteros, S., Millar, S., & Reales, J.M. (1998). Symmetry in haptic and in visual shape perception. *Perception & Psychophysics, 60,* 289-404.

Driver, J., & Grossenbacher, P.J. (1996). Multimodal constraints on tactile selective attention. In T. Inui & J.L. McClelland (eds), *Attention and Performance XVI* (pp 209-235). Cambridge MA: MIT Press.

Galea, L.A.M., & Kimura, D. (1993). Sex differences in route-learning. *Personality and individual differences, 14,* 53-65.

Geary, D.C. (1996). Response: a biosocial framework for studying cognitive sex differences. *Learning and Individual differences, 8,* 55-60.

Gaunet, F., & Rossetti, Y. (in press). Effects of visual deprivation on space representation: Immediate and delayed pointing towards memorized proprioceptive targets, *Perception.*

Gentaz, E., & Hatwell, Y. (1998). The haptic oblique effect in the perception of rod orientation by blind adults. *Perception & Psychophysics, 60,* 157-167.

Gentaz, E., & Hatwell, Y. (1999). Role of memorization conditions in the haptic processing of orientations and the 'oblique effect'. *British Journal of Psychology, 90,* 373-388.

Graziano, M.S. (2002). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Acadamy of Sciences of the United States of America, 96,* 10418-10421.

Heller, M.A., Brackett, D.D., Scroggs, E., & Allen, A.C., (2001). Haptic perception of the horizontal by blind and low-vision individuals. *Perception, 30,* 601-610.

Hermens, F., Kappers, A.M.L., & Gielen, S. (in press). The structure of fronto-parallel haptic space is task dependent. *Perception & Psycholphysics.*

Honoré, J., Bourdeaud'hui, M., & Sparrow, L. (1989). Reduction of cutaneous reaction time by directing eyes towards the source of stimulation. *Neuropsychologia, 27,* 367-371.

Kappers, A.M.L. (2003). Large systematic deviations in a bimanual parallelity task: further analysis of contributing factors. *Acta Psychologica, 114,* 131-145.

Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves the spatial resolution of touch in humans. *Current Biology, 11,* 188-1191.

Knecht, S., Kunesch, E., & Schnitzler, A. (1996). Parallel and serial processing of haptic information in man: Effects of parietal lesions on sensorimotor hand function. *Neuropsychologia, 34,* 669-687.

Lacquaniti, F., Perani, D., Guigon, E., Bettinardi, V., Carrozzo, M., Grassi, F., Rossetti, Y., & Fazio, F. (1997) Visuomotor transformations for reaching to memorized targets: a PET-study. *Neuroimage, 5,* 129-146.

Làdavas, E., Di Pellegrino, G., Farnè, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience,* 10, 581-589.

Lloyd, D.M., Shore, D.I., Spence, C., & Calvert, G.A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience, 6,* 17-18.

Luyat, M., Gentaz, E., Corte, T.R., & Guerraz, M. (2001). Reference frames and haptic perception: Body and head tilt effects on the oblique effect. *Perception and Psychophysics, 63,* 541-554.

Matthews, M.H. (1986). The influence of gender on the environmental cognition of young boys and girls. *Journal of Genetic Psychology, 147,* 295-302.

Millar, S. (1988). Models of sensory deprivation: The nature/nurture dichotomy and spatial representation in the blind. *International Journal of Behavioral Development, 11,* 69-87.

Millar, S. (1994). *Understanding and representing space: Theory and evidence from studies with blind and sighted children.* Oxford, England: Clarendon Press/Oxford University Press.

Millar, S., & Al-Attar, Z. (2002). The Müller-Lyer illusion in touch and vision: Implications for multisensory processes. *Perception & Psychophysics, 64,* 353-365.

Millar S., & Al-Attar, Z. (2004). External and body-centered frames of reference in spatial memory: evidence from touch. *Perception & Psychophysics, 66,* 51-59.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* Oxford, England UK: Oxford University Press.

Newport, R., Hindle, J.V., & Jackson, S.R. (2001). Links between vision and somatosensation: vision can improve the felt position of the unseen hand. *Current Biology, 11,* 975-980.

Newport, R., Rabb, B., & Jackson, S.R. (2002). Noninformative vision improves haptic spatial perception. *Current Biology, 12,* 1661-1664.

Obayashi, S., Tanaka, M., & Iriki, A. (2000). Subjective image of invisible hand coded by monkey intraparietal neurons. *Neuroreport, 11,* 3499-3505.

Prather, S.C., Votaw, J.R., & Sathian, K. (2004). Task-specific recruitment of dorsal and ventral visual areas during tactile perception. *Neuropsychologia, 42,* 1079-1087.

Rossetti, Y., Gaunet, F., & Thinus-Blanc, C. (1996). Early visual experience affects memorization and spatial representation of proprioceptive targets. *Neuroreport, 7,* 1219-1223.

Sack, A.T., Sperling, J.M., Prvulovic, D., Formisano, E., Goebel, R., Di Salle, F., Dierks, T., & Linden, D.E. (2002). Tracking the mind's image in the brain II: transcranial magnetic stimulation reveals parietal asymmetry in visuospatial imagery. *Neuron, 35,* 195-204.

Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory cortical processing. *Current Biology, 12,* 233-236.

Thinus-Blanc, C., & Gaunet, F. (1997). Representation of space in blind persons: Vision as a spatial sense? *Psychological Bulletin, 121,* 20-44.

Trojano, L., Grossi, D., Linden, D.E.J., Formisano, E., Hacker, H., Zanella, F.E., Goebel, R., Di Salle, F. (2000). Matching two imagined clocks: the functional anatomy of spatial analysis in the absence of visual stimulation. *Cerebral Cortex, 10,* 473-481.

Nederlandse samenvatting

Waarnemingen van de ruimte opgrond van tastinformatie: algemeen

Om een indruk te krijgen van de ruimte om ons heen gebruiken we meestal onze ogen. Maar wat nu als het pikkedonker is? Wat nu als je blind bent? In deze situaties ben je grotendeels aangewezen op de tast. Dit proefschrift onderzoekt zowel de karakteristieken van de voorstellingen van de ruimte die we maken op grond van tast- ofwel haptische informatie, als factoren die van invloed zijn op de kwaliteit van deze voorstellingen. We hebben met name gekeken naar de haptische waarneming van oriëntatie, aangezien dit een van de basisaspecten van een ruimtelijke voorstelling is. Eerder onderzoek heeft onder meer laten zien dat geblinddoekte mensen grote systematische fouten maken wanneer ze gevraagd wordt om op de tast staafjes zo te draaien dat ze parallel aan elkaar staan. Figuur 1 geeft de systematische fouten weer van een gemiddelde proefpersoon.

Figuur 1. Grote systematische afwijkingen in de haptische waarneming van parallelliteit: de staafjes voelen voor de waarnemer alsof ze allemaal parallel staan.

In dit proefschrift hebben we onder meer geprobeerd uit te zoeken hoe dit soort fouten ontstaat en welke factoren een modulerende rol spelen in de waarneming van ruimtelijke aspecten. Hiertoe hebben we de performances van verschillende soorten proefpersonen (geblinddoekte zienden, blinden, mannen, vrouwen) onder verschillende omstandigheden geanalyseerd.

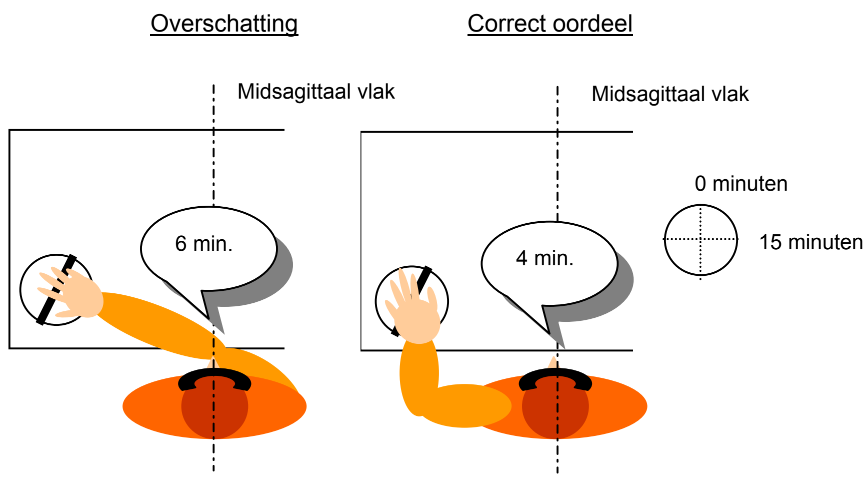
Referentiekaders in haptische ruimtelijke taken

Om het ontstaan van de systematische afwijking in de haptische waarneming van oriëntatie te verklaren, zijn we uitgegaan van het principe dat we om ruimtelijke informatie te interpreteren altijd een of meer referentiekaders nodig hebben. Een referentiekader kan je beschouwen als een soort anker waar nieuwe ruimtelijke informatie aan gerelateerd kan worden. Het kernidee is dat een object altijd ergens is en op een bepaalde manier georiënteerd is ten opzichte van iets anders: je koffiemok is ergens in relatie tot je tafelblad, de telefoon, je hand, je mond. Om een object of lichaamsdeel te kunnen gebruiken als referentiekader moet de locatie en/of oriëntatie van dat object tot op zekere hoogte bekend zijn. Anders zou het gebruik ervan als referentiekader natuurlijk nutteloos zijn. De literatuur onderscheidt grofweg twee soorten referentiekaders, egocentrische (ego = Grieks voor "zelf") en allocentrische referentiekaders (allo = Grieks voor "ander"). Er bestaan aanwijzingen voor dat deze kaders verschillende functies ondersteunen die door verschillende hersendelen worden uitgevoerd. Egocentrische referentiekaders worden geacht gebruikt te worden in doelgerichte acties: om naar een object te wijzen of om het te pakken is het vooral relevant om te weten waar het is ten opzichte van je eigen lijf, of beter nog, ten opzichte van je hand. In pariëtale en frontale cortices bevinden zich gebieden die zich bezighouden met het direct omzetten van zintuiglijke informatie in precieze egocentrische ruimtelijke coördinaten ten behoeve van deze motorische doelgerichte acties. Deze ruimtelijke voorstellingen worden voortdurend ge-update. Ze stellen ons in staat om allerlei handelingen uit te voeren zonder hierover te hoeven nadenken. Meer absolute, cognitieve voorstellingen van de ruimte worden gegenereerd in temporale cortex gebieden en de hippocampus. Dit soort voorstellingen is gebaseerd op allocentrische referentiekaders: objecten hebben een ruimtelijke relatie met elkaar, onafhankelijk van de positie van een waarnemer, zoals in landkaarten. Bij het plannen van een route of het geven van een bewust oordeel over ruimtelijke relaties tussen objecten maken we gebruik van deze allocentrische referentiekaders.

De rol van egocentrische referentiekaders

Om een voorstelling te maken van de ruimte op grond van tastinformatie zijn we aangewezen op onze handen en ons lichaam, zelfs wanneer de uit te voeren taak een voorstelling vereist die onafhankelijk is van de positie van het lichaam of de ledematen. Zo ligt het voor de hand dat ruimtelijke voorstellingen op grond van tastinformatie gebaseerd zijn op egocentrische referentiekaders. Een eerste hypothese van het huidige onderzoek was dan ook dat patronen zoals die in Figuur 1 een gevolg zijn van het gebruik van egocentrische kaders in een poging tot een allocentrische voorstelling te komen: de staafjes dienen parallel aan elkaar te staan onafhankelijk van de positie van het lichaam of de ledematen, maar blijkbaar lukt dit niet helemaal. Om deze hypothese te onderzoeken hebben we gebruik gemaakt van veronderstellingen over referentiekadergebruik die o.a. in het visuele domein heersen. Zoals hierboven opgemerkt wordt bij wijsbewegingen en andere doelgerichte bewegingen over het algemeen gebruik gemaakt van egocentrische referentiekaders. Vanuit de literatuur is echter bekend dat het enige seconden uitstellen van de wijsbeweging naar één van meerdere visuele doelen resulteert in het gebruik van een *allocentrisch* referentiekader: terwijl de landingspunten van directe wijsbewegingen in het verlengde liggen van de wijsbeweging, worden de landingspunten van uitgestelde wijsbewegingen beïnvloed door de locatie van eerdere wijsdoelen, hetgeen het gebruik van allocentrische referentiekaders impliceert. Bij haptisch parallelldraaien zou een dergelijke shift van ego- naar allocentrisch referentiekadergebruik resulteren in een *verbetering* van de performance, aangezien een allocentrische voorstelling nodig is om de taak goed uit te voeren. In *Hoofdstuk 2* hebben we dat onderzocht. We vonden dat wanneer geblinddoekte mensen gedwongen worden om 10 seconden te wachten tussen het voelen van een staafje en het paralleldraaien van een tweede staafje *kleinere* systematische fouten maakt dan wanneer hij direct paralleldraait. Deze tegenintuïtieve bevinding – want waarom zou de 10 seconden oude herinnering aan een waarneming beter zijn dan die waarneming op zich? – duidt erop dat de systematische fouten inderdaad voortkomen uit gebruik van egocentrische referentiekaders.

De bevindingen van *Hoofdstuk 2* roepen echter nieuwe vragen op, bijvoorbeeld: welke egocentrische kaders zorgen voor de afwijkingen in de performance? En, welke processen zijn betrokken bij het onthouden van de oriëntatie zijn verantwoordelijk voor de verbetering? In *Hoofdstuk 3* hebben we onderzocht welk(e) egocentrisch(e) referentiekader(s) verantwoordelijk is/zijn voor de systematische afwijkingen in de waarneming van een staafje. Van de karakteristieken van paralleldraai-performance (Figuur 1) zijn twee mogelijke egocentrische referentiekaders af te leiden: het lichaam (de romp) en de handen. De staafjes vormen een soort waaierpatroon om het lichaam heen, hetgeen er op zou kunnen duiden dat de positie van een staafje ten opzichte van het lichaam bepalend is voor hoe de oriëntatie van zo'n staafje wordt waargenomen. Een andere mogelijkheid is dat de waarneming van de oriëntatie van een staafje beïnvloed wordt door de oriëntatie van de hand waarmee het staafje wordt waargenomen. Om dit te onderzoeken hebben we gekozen voor een taak waarbij telkens niet twee, maar één staafje waargenomen moest worden. Proefpersonen moesten een staafje voelen en aan de gevoelde oriëntatie een kloktijd in minuten koppelen en noemen. In deze zogenaamde "verbale beoordelingstaak" (*verbal judgment task*) lieten we staafjes op verschillende plekken in de ruimte door zowel de linker- als de rechterhand voelen; de oriëntatie waaronder een staafje waargenomen werd was dan voor de linker- en de rechterhand verschillend, terwijl de positie ten opzichte van het lichaam niet veranderde. We vonden dat niet de positie ten opzichte van het lichaam, maar de oriëntatie van de hand waarmee een staafje gevoeld wordt verantwoordelijk is voor het ontstaan van de systematische afwijking in de haptische waarneming van orientatie (zie Figuur 2): hoe meer de oriëntatie van een hand afwijkt van een denkbeeldig vlak door het midden van het lichaam (het "midsagittale" vlak), des te groter de fout. Een afwijking van een waarnemende hand naar rechts resulteerde in een onderschatting van het aantal minuten (ofwel, een afwijking tegen de klok in); een afwijking van de hand naar links resulteerde in een overschatting van het aantal minuten (afwijking met de klok mee). Dit komt overeen met de richtingen van de afwijkingen van de parallelldraai-taak (Figuur 1): een onderschatting van een gevoelde oriëntatie met de rechterhand, ofwel een waarnemingsfout tegen de klok in, leidt tot een overcompensatie in de richting met de klok mee.

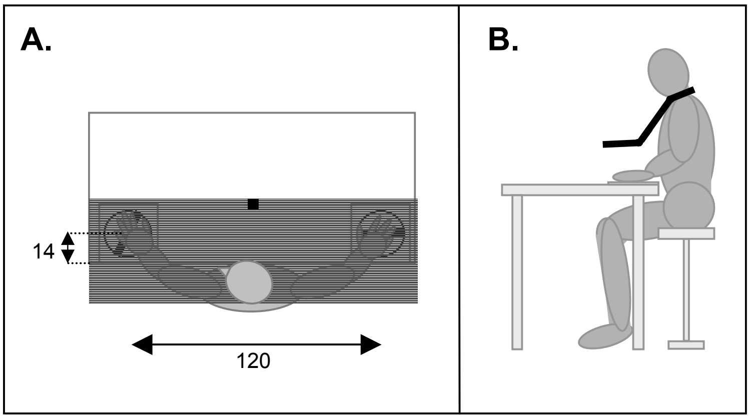


Figuur 2. De Orientatie van de hand ten opzichte van het midsagittale vlak is bepalend voor het verbale oordeel over een gevoelde oriëntatie. Een handoriëntatie parallel aan dit vlak leidt tot een correct oordeel. Het oordeel wordt gegeven alsof het staafje de minutenwijzer van een klok is.

De rol van (mentale) externe referentiekaders

Een opvallende bijkomende bevinding bij de verbale beoordelingstaak was dat de fouten erg klein waren vergeleken met de parallelldraai-taak: terwijl paralleldraaien kan leiden tot afwijkingen tot wel 60º gemiddeld (bijv. *Hoofdstuk 4*), resulteerde het verbaal beoordelen van een gevoelde oriëntatie van slechts 1,2 minuten (≈ 7,2º) bij extreme handoriëntaties. Dit grote verschil moet wel een gevolg zijn van (enkele van) de verschillen tussen de taken. Een belangrijk verschil tussen de paralleldraai-taak en de verbale beoordelingstaak is dat in de eerste een motorische response wordt gebruikt en in de tweede een verbale. Het zou kunnen dat een deel van de afwijking in de paralleldraai-taak wordt veroorzaakt door het draaien van het staafje. In *Hoofdstuk 7* onderzochten we onder andere in hoeverre dit zo is. In een soort omgekeerde verbale beoordelingstaak moesten proefpersonen een staafje zo draaien dat de oriëntatie ervan overeenkwam met een door de proefleider genoemd aantal minuten. We vonden dat deze zogenoemde "oriëntatieproductie-taak" resulteerde in fouten die even klein waren als die van de verbale beoordelings-taak, maar tegengesteld van richting. Dit patroon impliceert dat de basis van fouten in taken met een draairesponse (dus ook de paralleldraai-taak) ligt bij fouten in de waarneming, en niet (ook) bij het uitvoeren van de draaibeweging.

Een ander belangrijk verschil tussen de paralleldraai-taak en de verbale beoordelingstaak is dat in de verbale beoordelingstaak de oriëntatie van een staafje expliciet allocentrisch gedefinieerd was, nl. in relatie tot de rand van de stimulustafel: de proefpersonen werd verteld dat de "klokken" zo op tafel lagen dat de staafjes 15 (of 45) minuten aangaven, wanneer ze parallel lagen aan de rand van de stimulustafel. Het verschaffen van zo'n mentaal extern referentiekader, en het dwingen van de proefpersoon om deze te gebruiken kan tot de verbetering hebben geleid. In *Hoofdstuk 4* vonden we inderdaad dat een extern - in dit geval visueel - referentiekader een faciliterende invloed heeft op de haptische waarneming van oriëntatie. We verschaften proefpersonen visuele contextinformatie terwijl ze de paralleldraai-taak uitvoerden: een doek ontnam hen het zicht op de staafjes, hun armen en schouders, zoals weergegeven in Figuur 3. Performance onder deze conditie werd vergeleken met die wanneer ze geblinddoekt waren. We vonden dat de performance met externe, visuele context beter was dan met blinddoek. Performance was ook afhankelijk van de kijkrichting: performance was het beste met de blik gericht op het (ongeziene!) referentiestaafje (het staafje waaraan het andere staafje parallel gedraaid moest worden). Met het verwijderen van de blik van dit staafje verslechterde de performance. Dit effect trad op in zowel de visuele contextconditie als de geblinddoekte conditie, hetgeen erop wijst dat de mechanismen die verantwoordelijk voor de effecten van blikrichting en contextinformatie onafhankelijk zijn. We stelden dat het blikrichtingseffect een aandachtseffect zou kunnen zijn: bij het uitvoeren van de parallelldraai-taak zou de aandacht dan bij de waarneming van het referentiestaafje zijn, en het richten van de blik op dit staafje zou het richten van de aandacht erop vergemakkelijken. Het visuele contexteffect zou kunnen verlopen via een toename van het aantal geactiveerde neuronen dat de ruimte representeert. De daaraan gerelateerde vergroting van de door de hersenen voorgestelde externe ruimte zou kunnen leiden tot een betere interpretatie van de haptische oriëntatie-informatie in die voorgestelde ruimte.



Figuren 3A and B. Schematisch boven- en zijaanzicht van de experimentele setup in gebruikt in Hoofdstuk 4 in de condities met visuele contextinformatie. Hoewel in Figuur 3A doorzichtig, was het doek in het echt ondoorzichtig.

De rol van mentale visuele processen in haptische ruimtelijke verwerking

Geblinddoekte zienden en mentale visuele beeldvorming

Een ander belangrijk verschil tussen de verbale beoordelingstaak en de paralleldraai-taak is dat voor de uitvoering van de verbale beoordelingstaak de gevoelde oriëntatie vertaald moet worden in een kloktijd. Om dit te kunnen doen genereert een ziende proefpersoon waarschijnlijk een mentale visueel-ruimtelijke voorstelling van een klok. Dit zou wel eens cruciaal geweest kunnen zijn voor de kwaliteit van de ruimtelijke voorstelling van de gevoelde oriëntatie. Visie - in tegenstelling tot de haptiek - wordt namelijk gezien als het meest geschikte zintuig voor het vormen van een absolute voorstelling van de ruimte. Terwijl haptische ruimtelijke exploratie min of meer sequentieel verloopt, stelt visuele exploratie je namelijk in staat om grote hoeveelheden ruimtelijke informatie - van zowel dichtbij als veraf – vrijwel direct te integreren, waardoor het veel makkelijker is om een absolute voorstelling van de ruimte te maken. Zo kan het zijn dat de (visueel) ruimtelijke voorstelling van een klok ook leidt tot een (visuele) voorstelling van het gevoelde staafje in de ruimte, hetgeen waarschijnlijk zal leiden tot een betere ruimtelijke voorstelling van de oriëntatie van dat staafje. Om te kijken of performance op de verbale beoordelingstaak afhangt van het visueel-ruimtelijk voorstellingsvermogen hebben we de performance op een visueel-ruimtelijke voorstellingsvermogen-taak gecorreleerd met performance op de verbale beoordelingstaak (*Hoofdstuk 3*). We vonden een mogelijk verband tussen goede scores op beide taken, hetgeen inderdaad suggereert dat je bij een dergelijke haptische ruimtelijke waarnemingstaak baat hebt bij een goed visueel-ruimtelijk voorstellingsvermogen. In de volgende paragraaf zullen we bespreken wat de rol van visualiseren is in zowel de verbale beoordelingstaak als de paralleldraai-taak aan de hand van ons onderzoek met blinden.

Blinden: de rol van mentale visuele beeldvorming

Blinden zijn natuurlijk een belangrijke groep waar het gaat om haptische ruimtelijke taken. Maar hoewel onze intuïtie ons vertelt dat blinden goed zouden moeten zijn in haptische ruimtelijke taken ten gevolge van hun ervaring, suggereert bovenstaande het tegenovergestelde. De literatuur over ruimtelijke voorstellingen bij blinden ondersteunt dit. Het is bekend dat blinden, en dan met name de blinden die voor hun derde levensjaar blind zijn geworden ("vroegblinden"), moeite hebben met het vormen van absolute voorstellingen van de ruimte, en dat ze geneigd zijn egocentrische voorstellingen van de ruimte te maken. In *Hoofdstuk 5*, onderwierpen we zowel vroegblinden als laatblinden aan de paralleldraai-taak en de verbale beoordelingstaak. Een aanvullende vraag bij de paralleldraai-taak was of (vroeg)blinden een verbetering laten zien met de 10 seconden wachttijd tussen het voelen van het referentiestaafje en het draaien van het teststaafje, hetgeen (zoals hierboven uitgelegd) zou duiden op een shift van een egocentrische naar een meer allocentrische voorstelling. We vonden dat blinden (vroegblinden en laatblinden) net zo slecht zijn in het paralleldraaien van staafjes als zienden: ze maken even grote systematische fouten, en de vroegblinden presteren minder constant dan de zienden en de laatblinden. Tastervaring leidt in deze taken dus niet tot een betere ruimtelijke voorstelling; visuele ervaring maakt de waarnemingen wel constanter, maar maakt de systematische afwijkingen - in directe condities - niet kleiner. Een voordeel van visuele ervaring vinden we echter wél met de 10 seconden wachttijd.

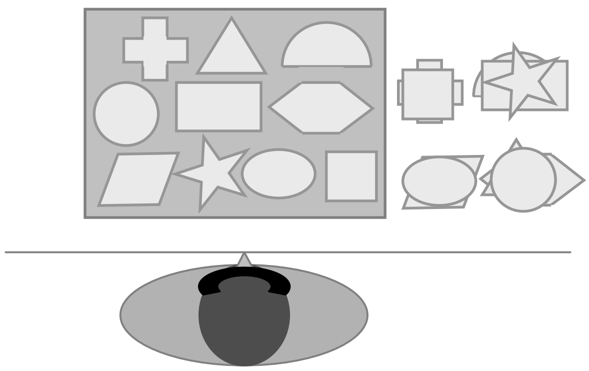
Blindgeborenen verbeteren niet met het onthouden van haptisch waargenomen oriëntatie; laatblinden wel maar opvallend genoeg minder dat zienden. Blijkbaar schakelen zienden en laatblinden hun visuele beeldvormende vermogens bij de paralleldraai-taak pas in bij het onthouden van de oriëntatie, en heeft dit een verbetering in de ruimtelijke voorstelling tot gevolg heeft. Aangezien laatblinden minder verbeteren dan zienden kunnen we concluderen dat blind worden leidt tot een afname van het gebruik van deze mentale visuele processen in ruimtelijke beeldvorming, of het vermogen deze processen in de ruimtelijke voorstellingen te betrekken.

Aangezien visueel-ruimtelijk voorstellingsvermogen een mogelijke rol speelt bij de verbale beoordelingstaak (zie hierboven), verwachtten we ook op deze taak geen voordeel voor de blinden. We vonden inderdaad dat zienden beter presteren dan blinden op deze taak: de afwijkingen in hun verbale oordelen zijn iets kleiner dan die van de blinden. De laatblinden presteerden niet beter dan de blindgeborenen: blijkbaar wordt er ook bij deze taak door laatblinden (i.t.t. de zienden) niet spontaan gebruik gemaakt van mentale visuele processen. Wel moet opgemerkt worden dat ook de blinden relatief kleine fouten maken. Aangezien adequaat presteren op deze taak dus niet geheel lijkt af te hangen van mentale visuele processen, ligt het voor de hand dat andere taakeigenschappen verantwoordelijk zijn voor de goede prestaties. Onze gok is, zoals boven uitgelegd, dat de opgelegde koppeling van de haptische input aan een goed gekozen mentaal extern referentiekader (in dit geval de rand van de tafel) een belangrijke factor is. Op grond van de hier besproken experimenten kunnen we in ieder geval stellen dat visuele ervaring de haptische oriëntatiewaarneming verbetert, maar dat de mate en de aard van het voordeel van visuele ervaring afhangt van de specifieke taakomstandigheden. In de volgende paragraaf bespreken we de rol van bewuste aspecten en onbewuste aspecten van een taak op de invloed van haptische en visuele ervaring.

Blinden en de voordelen van haptische ervaring in ruimtelijke taken

We hebben dus geen voordelen gevonden voor blinden in de haptische ruimtelijke taken die we tot nu toe hebben besproken. Hoewel het de meeste mensen wellicht toeschijnt dat de haptische inschatting van oriëntatie wel degelijk nuttig is in het dagelijks leven van blinden, zou men kunnen beargumenteren dat de tot nu toe gepresenteerde taken niet overeenkomen met de taken die blinden in hun dagelijks leven uitvoeren, en dat ruimtelijke taken die hier meer mee overeenkomen door blinden beter gedaan zullen worden ongeacht of hiervoor een allocentrische of egocentrische voorstelling nodig is. Bijvoorbeeld, men zou kunnen verwachten dat het herkennen van objecten en het leren van hun locaties met de tastzin zou moeten resulteren in voordelen voor de blinden. Weer lijkt de literatuur echter tot tegengestelde conclusies te komen. Zienden en laatblinden zijn over het algemeen meer accuraat waar het gaat om het benoemen van bekende objecten of plaatjes hiervan. Blinden zijn echter sneller - maar niet meer accuraat - dan zienden in het ‘matchen’ van simpele abstracte vormen (= het aangeven of stimuli dezelfde vorm hebben of niet). Het lijkt erop dat visuele ervaring de bewuste benoeming/identificatie van bekende objecten vergemakkelijkt. Diegenen met haptische ervaring hebben (de blinden) lijken vooral sneller te zijn in het herkennen van vormen, zonder dat dit gepaard gaat met een betere bewuste benoeming.

Eerder onderzoek heeft ook uitgewezen dat zienden beter zijn dan blinden in het terugplaatsen van meerdere objecten op hun plek in een goed geleerde ruimtelijke configuratie, met name als de gehele configuratie in zijn geheel gedraaid wordt. Dit is niet verwonderlijk omdat na de draaiing een egocentrische voorstelling van de locaties van de objecten niet volstaat, maar een absolute voorstelling vereist is. Echter, deze resultaten zijn afkomstig van studies waarin de proefpersonen ongelimiteerd de tijd hadden om de objecten en hun locaties bewust uit het hoofd te leren. Als de blinden inderdaad sneller zijn met het meer onbewust herkennen van abstracte simpele vormen, zou men verwachten dat blinden sneller zullen zijn in taken waarbij de locaties van zulke vormen minder bewust geleerd worden, bijvoorbeeld door ze zo snel mogelijk te passen in de uitsparingen van een bord. De verwachte snellere herkenning van vormen en lokalisatie door blinden, zou ook kunnen leiden tot verschillen in de ruimtelijke voorstelling tussen blinden en zienden.



Figuur 4. Schematische voorstelling van het bord met de uitsparingen en de hierin te passen simpele abstracte figuren, zoals gebruikt in *Hoofdstuk 6*.

In *Hoofdstuk 6* lieten we vroegblinden, laatblinden en geblinddoekte zienden zo'n zogenaamde *spatial speeded matching* taak uitvoeren. Figuur 4 is een schematische voorstelling van de experimentele set-up en de stimuli. We vonden dat beide groepen blinden inderdaad veel sneller waren dan de zienden gedurende drie leertrials, waarbij de vormen zo snel mogelijk in de uitsparingen gepast moesten worden. Na deze drie leertrials werd op drie verschillende manieren het ruimtelijk geheugen gemeten. De manieren verschilden in het bewustzijnsniveau waarop we verwachtten dat ze zouden aangrijpen. In één van de condities werd het bord 90º gedraaid, terwijl de taak verder dezelfde bleef. We stelden dat deze speeded matching response waarschijnlijk niet of nauwelijks een bewuste allocentrische ruimtelijke voorstelling aanspreekt. In plaats daarvan draait deze taak waarschijnlijk grotendeels op motorische handigheid en haptische snelheid, waarvoor haptische ervaring waarschijnlijk wél een voordeel is. Inderdaad zorgde de draaiing van het bord hier niet voor een voordeel voor de zienden, i.t.t. de eerder genoemde onderzoeken: de blinden waren ook na draaiing van het bord veel sneller dan de zienden. In een tweede conditie dienden de proefpersonen de figuren zonder tijdsdruk op de juiste plek te leggen op een bord zónder uitsparingen. Deze taak bevat zowel een motorische, onbewuste als cognitieve, bewuste ruimtelijke componenten. We vonden dat blinden en zienden even goed en nauwkeurig waren in het op de juiste plek neerleggen van de figuren. In de derde conditie werd de proefpersonen gevraagd om de locatie van de figuren te beschrijven. Deze conditie beschouwden we als een puur bewuste, cognitieve. De laatblinden wisten met deze verbale response de locatie van meer objecten juist te beschrijven dan de zienden en de blindgeborenen. Uit de resultaten blijkt dat haptische ervaring een voordeel is in ruimtelijke taken die snelle, meer onbewuste herkenning van abstracte simpele vormen en hun locatie vereisen. Visuele ervaring wordt belangrijker naar mate de taak een bewuste, cognitieve ruimtelijke voorstelling vereist.

Sekseverschillen in de voorstellingen van de ruimte op grond van tastinformatie

Naast onderzoek naar verschillen tussen blinden en zienden, vormt het onderzoek naar sekseverschillen in ruimtelijke vaardigheden een belangrijk thema binnen de ruimtelijke cognitie. Opvallend genoeg is bijna al het onderzoek gericht op de visuele modaliteit, en is er nauwelijks onderzoek gedaan naar sekseverschillen in het haptische domein. Uit het visuele onderzoek blijkt dat mannen over het algemeen een beter begrip hebben van de ruimte, en dat ze meer geneigd zijn allocentrische referentiekaders te gebruiken dan vrouwen. Hoewel dit heel goed ook voor haptische ruimtelijke waarneming zou kunnen gelden, kunnen enkele cruciale verschillen tussen visie en haptiek echter resulteren in verschillende uitingen van deze sekseverschillen. Zo leidt haptische input meer tot egocentrische ruimtelijke voorstellingen dan visuele input. Dit zou een effect kunnen hebben op de mannelijke neiging om allocentrische kaders te gebruiken. Hierbij komt dat ruimtelijke functies als ruimtelijke aandacht en ruimtelijke voorstellingsmechanismen bij mannen en vrouwen verschillend verdeeld zijn over de beide hersenhelften. Aangezien informatie vergaard met een hand eerst volledig in de tegengestelde hersenhelft terecht komt, kan het zijn dat haptische ruimtelijke waarnemingen afhangen van handgebruik, en dat deze handverschillen anders zijn voor mannen en vrouwen. Op grond van specifieke verschillen tussen mannen en vrouwen in de verdeling van ruimtelijke functies, verwachtten we dat vooral mannen beter zijn met hun linkerhand. Een ander verschil tussen visie en haptiek is dat de handen - in tegenstelling tot de ogen – onafhankelijk van elkaar bewogen kunnen worden naar de linker of rechterkant van een ruimte. Dit zou kunnen leiden tot onderlinge effecten van handgebruik en aandacht, die specifiek zijn voor de haptische ruimtelijke waarneming, en ook weer voor de seksen anders kunnen zijn. In *Hoofdstuk* 7 hebben we gekeken naar sekseverschillen in performance op de paralleldraai-taak, de verbale beoordelingstaak en de eerder genoemde oriëntatie productie-taak waarbij telkens een staafje zo gedraaid moest worden dat de oriëntatie ervan overeenkwam met een verbaal gegeven aantal minuten. We vonden dat mannen beter zijn in het paralleldraaien van staafjes, hetgeen overeenkomt met het idee dat mannen meer dan vrouwen geneigd zijn om allocentrische referentiekaders te gebruiken. Deze neiging bleek onafhankelijk van de mate waarin een taak allocentrisch kadergebruik stimuleert. Zo resulteerde het stimuleren van allocentrisch referentiekadergebruik door middel van 10 seconden wachttijd niet in een verandering van het gevonden sekseverschil. Ook in de verbale beoordelingstaak en de oriëntatieproductie-taak vonden we een mannelijk voordeel, met name bij waarnemingen met de linkerhand. Dit duidt erop dat de mannelijke rechterhersenhelft mogelijk meer betrokken is bij allocentrische ruimtelijke voorstellingen dan de linker.

Conclusie

Samenvattend kunnen we concluderen dat het empirische werk in het huidige proefschrift heeft laten zien dat:

- systematische afwijkingen in de performance op haptische ruimtelijke taken als de parallelldraai-taak, de verbale beoordelingstaak en de oriëntatieproductie-taak het resultaat zijn van systematische afwijkingen in de haptische waarneming (en niet de productie) van oriëntatie.
- de basis van deze afwijkingen bij de hand ligt: de oriëntatie van de hand heeft een effect op de hoe we oriëntatie haptisch waarnemen. Hoe groter de afwijking van de hand met het (mid)sagittale vlak, des te groter de afwijking in de waarneming. Als een hand naar rechts is gericht is de fout in de waarneming tegen de klok in. Is de hand naar links gericht, dan is de fout in de waarneming met de klok mee.
- de grootte van de afwijkingen in de waarneming afhankelijk is van de mate waarin allocentrisch referentiekaders gebruikt worden door de waarnemer. De mate van allocentrisch kader gebruik is afhankelijk van specifieke taakkarakteristieken, de visuele status (vroegblind/laatblind/ziend) en de sekse van een waarnemer.
- de volgende specifieke taakkarakteristieken van invloed zijn op de mate van allocentrische kadergebruik: de mate waarin visualisatie van de haptische input wordt gestimuleerd; de mate waarin het gebruik van externe referentiekaders wordt gestimuleerd; de mate waarin externe referentiekaders worden aangeboden; de richting van de blik (en mogelijk de aandacht) tijdens de taak.
- visuele ervaring doorgaans een positief effect heeft op de haptische ruimtelijke waarneming. Dit effect is echter afhankelijk van het niveau waarop de taak aangrijpt: hoe meer een taak beroep doet op geheugen, bewuste, cognitieve en/of verbale processen, des te groter de invloed visuele ervaring.
- mensen die op latere leeftijd blind geworden zijn over het algemeen minder goed en/of minder spontaan gebruikmaken van hun visuele ervaring in haptische ruimtelijke taken dan zienden.
- mannen beter zijn dan vrouwen in de haptische waarneming van oriëntatie, met name met hun linkerhand, hetgeen kan duiden op een belangrijke rol van de mannelijke rechterhersenhelft bij het vormen van een allocentrische voorstelling van de ruimte.

Publications

Journal articles and book chapters

Zuidhoek, S., Kappers, A.M.L., Van der Lubbe, R.H.J., & Postma, A. (2003). Delay improves performance on a haptic spatial matching task. *Experimental Brain Research, 149,* 320-330.

Zuidhoek, S., Kappers, A.M.L., Noordzij, M.L., Van der Lubbe, R.H.J., & Postma, A. (2004). Frames of reference in a haptic parallelity task: temporal dynamics and the possible role of vision. In S. Ballesteros, & M.A. Heller (Eds.) *Touch, blindness and neuroscience* (pp 155-164). Madrid, Spain: UNED Press.

Zuidhoek, S., Visser, A., Bredero, M.E., & Postma, A. (2004). Multisensory integration mechanisms in haptic space perception. *Experimental Brain Research, 157,* 265-268.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2005). Effects of hand orientation and delay on the verbal judgment of haptically perceived orientation. *Perception, 34,* 741-755.

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (submitted). Haptic orientation perception benefits from visual experience: evidence from early blind, late blind and sighted people.

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (submitted). Differences between early blind, late blind and blindfolded sighted people in implicit haptic spatial configuration learning and resulting memory traces.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (submitted). Haptic orientation perception: sex differences and lateralization of functions.

Noordzij, M.L., Zuidhoek, S., Van Meggelen, C., Petersen, R., Prinsen, G., & Postma, A. (2004). The influence of perspective on the properties of spatial mental models. In S. Ballesteros & M.A. Heller (Eds.) *Touch, blindness and neuroscience* (pp 281-292). Madrid, Spain: UNED Press.

Noordzij, M.L., Zuidhoek, S., & Postma, A. (in press). The influence of visual experience on the ability to form spatial mental models based on route and survey descriptions. *Cognition.*

Noordzij, M.L., Zuidhoek, S., & Postma, A. (submitted). The influence of visual experience on visual and spatial imagery.

Postma, A., Van der Lubbe, R.H.J., & Zuidhoek, S. (2003). The ventral stream offers more affordance and the dorsal stream more memory than believed. *Behavioral & Brain Sciences, 25,* 115-116.

Conference proceedings

Zuidhoek, S., Kappers, A.M.L. Van der Lubbe, R.H.J., & Postma, A. (2001). Effects of temporal constraints on representations of haptic space. *Poster presentation. Proceedings of the International Symposium on Neural Control of Spatial Coding and Action Production*, *Lyon,* 120-121.

Zuidhoek, S., Kappers, A.M.L. Van der Lubbe, R.H.J., & Postma, A. (2001) Delay improves performance on a haptic matching task. *Oral presentation. Proceedings of the 8th Wintercongres Nederlandse Vereniging voor Psychonomie, Egmond, the Netherlands.*

Zuidhoek, S., Noordzij, M.L., Kappers, A. M. L., & Postma, A. (2003). Visual Imagery and the representation of haptic space. *Oral presentation. Proceedings of the 9th European Workshop on Imagery and Cognition (EWIC), Pavia,* 55.

Zuidhoek, S., Kappers, A.M.L., & Postma, A. (2003). Differences in haptic spatial performance between men and women. *Oral presentation. Proceedings of the 2nd Dutch Endo-Neuro-Psycho Meeting, Doorwerth,* 126.

Zuidhoek, S., Kappers, A.M.L., Noordzij, M.L., & Postma, A. (2003). Visual imagery and the coding of haptic space: Performance by early blind, late blind and blindfolded sighted subjects. *Oral presentation. Proceedings of the XIIIth conference of the European Society for Cognitive Psychology (ESCOP)*, *Granada*, 314.

Zuidhoek, S., Noordzij, M.L., Kappers, A.M.L., & Postma, A. (2003). Blindness and haptic parallelity perception. *Poster presentation. Proceedings of the 9th Wintercongres Nederlandse Vereniging voor Psychonomie, Egmond, the Netherlands.*

Johnson, A., & Zuidhoek, S. (2000). Effects of attentional cueing on the identifications of laterally masked targets. *Oral presentation at the 23rd European Conference on Visual Perception (ECVP), Groningen. Perception, 29, supplement,* 102.

Neggers, S.F.W. Noordzij, M.L., Zuidhoek S., & Schutter D. (2002). A different role for the frontal eye fields in a gap and non-gap saccadic task: a Transcranial Magnetic Stimulation study. *NVP (Nederlandse Vereniging voor Psychonomie) annual meeting, Egmond aan Zee.*

Noordzij, M.L., Zuidhoek, S., & Postma, A. (2003). The influence of perspective on the properties of spatial mental models of blind and sighted people. *Poster presentation. Proceedings of the 9th European Workshop on Imagery and Cognition (EWIC), Pavia,* 96.

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Curriculum vitae

Sander Zuidhoek was born in 't Harde, The Netherlands on May 23, 1972. He completed his secondary education at the Gymnasium Celeanum in Zwolle in 1990. After having broadened his musical skills on the bass guitar, he started studying Psychology at the Utrecht University in 1994. Majoring in Neuropsychology, he studied visual perception and attention with Prof. dr. Addie Johnson and consciousness with Prof. dr. René van Hezewijk, and did a nine month clinical internship at the Department of Medical Psychology of the Eemland Hospital in Amersfoort. His pleasure in studying resulted in obtaining his Master's degree, cum laude, in 2000. In the same year, he commenced the PhD project that resulted in the present thesis. His work with blind people during this project has led to his recent appointment as a psychologist/behavioral scientist at Visio, a Dutch institution for the blind and the visually impaired.