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Touching upon Tactile Processing: Output dependent somatosensory functions in the brain

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**Touching upon Tactile Processing:
Output dependent Somatosensory Functions in the Brain**

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Informatieverwerking in het Brein

(met een samenvatting in het Nederlands)

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Voor mijn grootouders.

*Voor wie mijn kennis en vrijheid
onvoorstelbaar zou zijn geweest.*

*En voor mijn ouders
die het mogelijk hebben gemaakt.*

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CHAPTER I

General Introduction

Ask someone his or her opinion about the importance of touch, and the answer will most definitely be something like: "important, since no human being can survive without feeling the sensation of being hugged by a parent, a partner or a good friend". However, few of us realize how important the sense of touch is for normal interactions with objects in the external world. Although vision might be regarded as the superior sense, perhaps after reading the story about "the disembodied woman" by Oliver Sacks, one will quickly reconsider his or hers opinion. This young woman suffered from brain damage due to medication, leading to dysfunctional somatosensory processes, such that she was unable to perceive information from her muscles and her joints. Most strikingly, she was unable to perceive herself. She could not even identify herself with photographs of the woman she once was. Only when driving a convertible, feeling the wind gently touching her skin, she experienced her self.

Neuroanatomy of the somatosensory system

The Skin

Touching the skin with the sharp end of a pencil, will first of all activate the mechanoreceptors in the skin. These mechanoreceptors are cells sensitive to mechanical strains to the skin and are located in the superficial skin-layers, mainly at the junction of dermis and epidermis (See Figure 1). The two most superficial mechanoreceptors of the four different sub-types are Meissner's-RA I corpuscle, and the Merkel-SA I disc receptor. Meissner's-RA I corpuscle is a rapidly adapting receptor innervating the skin rather densely with about 150 receptors per cm². It is involved in the transference of fine mechanical displacement and responds to stimuli over their entire receptive fields, which are 3-5mm in diameter (Kandel, Schwartz and Jessell,

2000, Johnson, 2001). As such they are responsible for the detection of slip between the skin and an object held in the hand and are most effective at signaling abrupt forces that act on these objects. A Merkel-SA I disc receptor however, innervates the skin less densely as compared to Meissner's corpuscle (100 per cm²) but, it has a high spatial resolution of 0.5mm, although the receptive fields have a diameter of merely 2-3mm. Furthermore, it is a slowly adapting receptor responsible for transmitting compressing strain from the skin and sensitive to points, edges and curvature thereby providing form and texture cues (Kandel, Schwartz and Jessell, 2000, Johnson, 2001).

Deeper into the skin we can find two other mechanoreceptors that are much larger and less numerous as compared to their more superficial siblings. The Pacinian-FA II corpuscle, the larger one of the two, activates in response to rapid indentation of the skin but not to continuous pressure. They are distributed throughout the palm (about 600 corpuscles) and fingers (about 350 per finger) and are extremely sensitive. However, because of their excessive sensitivity and their deep locations these receptors have almost no spatial resolution. They are mainly involved in the perception of high frequency stimuli and the perceptive field can exist of an entire hand (Kandel, Schwartz and Jessell, 2000, Johnson, 2001). The Ruffini-FAII endings are, as is the case for the Merkel disc receptor, slowly adapting receptors and respond to stretch of the skin or bending of the finger nails. They innervate the skin less densely than either SA1 or RA afferents and their receptive fields are about 6 times larger than SA1 afferents. Most importantly, these receptors are of crucial importance for shape perception of grasped objects (Kandel, Schwartz and Jessell, 2000, Johnson, 2001). Note: pain is not a matter of overstimulation of mechanoreceptors but is qualitatively different as it is generated by the activation of nocireceptors. Also, skin temperature is coded by thermal receptors (Kandel, Schwartz and Jessell, 2000).

Proprioception, the sense of position and movement of one's own limbs and body when no visual input is provided, is mediated by mechanoreceptors in skeletal muscle and joint capsules. They have an important role in spinal reflex pathways. Two submodalities can be distinguished: (i) the sense of stationary limb position and (ii) the sense of limb movement.

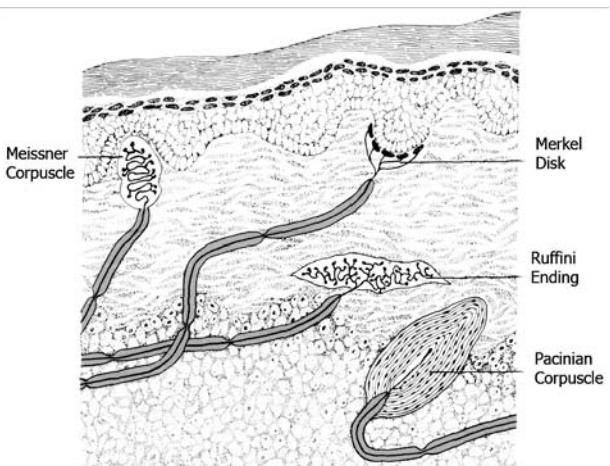


Figure 1: A cross section of the skin with its four mechanoreceptors. (Adapted from Kandel, E.R. & Schwartz, J.H. (1985), Principles of Neural Science, Second Edition. Elsevier Science Publishing Co., Inc., New York).

The spinal cord

After being coded by the mechanoreceptors, the information travels through afferent myelinated nerves towards the dorsal horn of the spinal cord, passing the dorsal root ganglion cells. The dorsal horn consists of two separate systems. The medial lemniscal system is the principal pathway for perception of touch and proprioception, which belong to the epicritic class of somatosensory sensation. Axons of this system ascend in the spinal cord in the ipsilateral dorsal column in the direction of the brainstem. At the level of the brainstem these fibres cross to the contralateral side and ascend further in the direction of the thalamus. The anterolateral system mediates the sensations of the protopathic class such as pain and temperature and of sensations such as tickle and itch. An important aspect of this system is that the afferents entering the dorsal horn first cross the midline before ascending in the anterolateral column in the direction of the brainstem. Via the thalamus, the information ascends further to the somatosensory areas in the postcentral gyrus of the cerebral cortex¹. In both systems the somatotopic organization of the axons relaying the input is maintained throughout the entire somatosensory pathway.

The brain

Thus, somatosensory perception is processed along an ascending pathway and via the brainstem the axons ascend further to the contralateral thalamus, terminating directly in the ventral posterior lateral nucleus (VPL). Projections from the VPL to the cerebral cortex allow the information to enter the primary sensory cortex (SI). However, information can also be transported directly to the secondary somatosensory cortex (SII), posterior parietal cortex and insula via small projections from VPL and other thalamic nuclei (Whitsel, & Petruccielli, 1969). Below I will further describe the functional importance of this shortcut in the section “Impairments after stroke”.

The classical view of the first somatosensory cortex (SI) is that it consists of four different Brodmann areas, 3a and 3b, 1 and 2. However, recently it has been suggested that only area 3b can be regarded as the SI (Kaas 1983; 2004) and therefore the term anterior parietal cortex (APC) will be further used to address the early processing areas. Each Brodmann area contains a somatotopic map of the contralateral half of the body and each body part is represented according to the degree of innervation density (see Homunculus Figure 2). Area 3a and 2 mainly receive input from joint (3a) and muscle receptors (Merzenich, Kaas, Sur, & Lin, 1978) but the parts in 3a also contain skin receptors. However, most skin receptors are located in area 3b and 1. The ultimate task of the brain is to integrate the fragmented tactile information that is obtained from touching an object.

¹ Note: for reasons of brevity the somatosensory system of information regarding the face is not described here.

An important characteristic of the organization of the somatosensory system, allowing for such integration, is that in the early processing stages the characteristics of the tactile information are directly representing the stimulation applied to the peripheral nerves. Further on in the APC, the response properties become more complex. For example the responses represent simple features such as texture or the direction of movement of a stimulus whereas in SII the responses are even more complex since the simple features are combined to more complex representations. Indeed, SII, extending laterally to the insular cortex, contains neurons with larger receptive fields and respond to ipsilateral as well as contralateral stimulation. Besides reciprocal connections with the APC, SII maintains ipsi- and contralateral connections with area 7b of the posterior parietal cortex (PPC; areas 5 and 7). This area receives visual as well as tactile and proprioceptive information which allows the integration of stereognostic and visual information. Major cortical outputs from the PPC project back to the SII and to the motor areas of the frontal lobe, the limbic cortex and the superior temporal sulcus (Kaas, 2004). The PPC, mainly area 5, is found to be involved in the guidance of goal directed movement (e.g. Colby, 1998), such as goal directed movement to one's own body and exploratory hand movements. At the same time different parts of the PPC are involved in perceptual recognition of the body and of the object. Specifically, the superior PPC, the intraparietal sulcus and the neighbouring inferior parietal lobule is suggested to be involved in body related perceptual processes (Bonda, Petrides, Frey, & Evans, 1995, Ehrsson, Holmes, & Passingham, 2005).

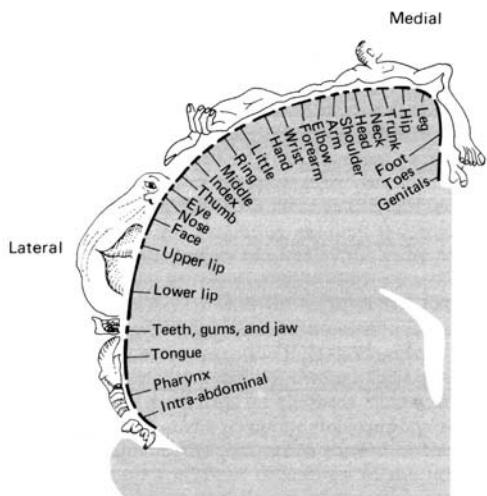


Figure 2: The representation of the body parts in the somatosensory cortex "Somatosensory Homunculus" (Adapted from Kandel, E.R. & Schwartz, J.H. (1985), Principles of Neural Science, Second Edition. Elsevier Science Publishing Co., Inc., New York).

Behavioral characteristics of simple touch

Many studies examined the characteristics of the tactile sensory system using various types of tasks, such as tactile pressure detection, two-point discrimination and point localisation. An important step forward in this area was made by Weber (1834; in Ross & Murray 1996) when he observed that the perception of distance applied to the skin varied with the receptor density and spatial acuity. According to Weber, the sense of localisation "consists of our being able to distinguish between two sensations... excited at different places on our body or in our organs of touch". However, when discriminating two simultaneously applied points, one is

merely judging the relative location of one stimulus to another and not the location related to the rest of the body. In his second investigation of cutaneous space relations Weber tested the perception of location (Weber, 1852; in Hamburger, 1980), by asking blindfolded participants to indicate a touched location on the skin as accurate as possible. After the first "landing" on the skin, participants were allowed to grope around the skin until they thought they found the correct location. It was considered that the average error implies an absolute measure of the local sensitivity of the skin. In an attempt to overcome methodological shortcomings, Pillsbury, (1895) and Parrish (1896) modified Weber's experiment. In this study, investigations were restricted to the volar side of the arm. Although only few participants were measured and only some of them are discussed in the article, it seemed that the amount of error decreased in a proximal to distal direction with the highest errors for the region near the elbow (35.30mm) and the smallest errors for the region near the wrist (25.19mm; note: these scores are obtained from one participant only).

A well documented study by Weinstein (1968), which reported additional statistical tests, discusses effects of body part, sex and laterality on tactile sensitivity, measuring tactile pressure sensitivity, two-point discrimination and point-localization. Here, the point localisation test can be viewed best as a two-point discrimination but with a short-term memory component, and tests the perception of one location relatively to that of another location. The results confirmed the above described observations of Pillsbury that the amount of error decreases from proximal to distal when measured at the upper extremities. Also, this author did not observe substantial differences in localisation performance between males and females. However, with respect to simple pressure sensitivity, females were overall more sensitive. Furthermore, left-right differences were variable over the different measures, indicating that there is not an overall difference in tactile perception performance.

Higher order somatosensory functions

Body representations

A complex and important function of the somatosensory system is that of providing a representation about the body. This allows us to perceive ourselves as distinct from the external world and it guides automatically all actions of the self in this external world. To achieve this, tactile and proprioceptive input has to be integrated with information provided by the other sensory systems. The question of how the body is represented in the brain has received extensive attention throughout the last century and terms as "body image", "body schema", or, longer ago "postural schemata", have been used to capture the variety of complex functions involving our own body. Moreover, many studies have been set up to investigate dissociations between several sub-categories of the body representation (e.g. Sirigu, Grafman, Bressler and Sunderland, 1991, Paillard, 1999, Schwoebel & Coslett, 2005; Gallagher, 2005). And recently, an extensive review has been published by Dijkerman and De Haan (2007) aiming to interpret the subdivision in body image and body schema (Gallagher, 2005; Paillard, 1999) alongside the ac-

tion perception dichotomy (Milner & Goodale, 1995, 2008). However, in line with a suggestion made by De Vignemont (response to Dijkerman & De Haan, 1999) it could be argued to give up making subdivisions all together. Nevertheless, the most commonly used distinction is that between Body Image and Body Schema and will be described below.

According to Paillard (1999), Body Image can be described as a "perceptual identification of body features" and these bodily features such as size and the normal configuration of the body parts are directly related to somatosensory and motor input. The information represented is accessible to conscious experience and can be regarded as rather stable since adaptations to a changed situation are rather slow. On the other hand the Body Schema can be regarded as a representation used for the guidance of action and is derived from short term information in the sensorimotor system. As such, it constantly monitors the position and the changes in the current position of the body parts. In contrast to the Body Image one cannot become aware of this information and as such the functions subserved by this representation can be regarded as implicit. At the same time this representation is dynamic and highly adaptive. The latter is nicely shown for example by studies investigating the incorporation of tools into the Body Schema (see for review Maravita & Iriki, 2004).

Haptic object recognition

An important function of the somatosensory system, closely linked to the function of the body representation, is that of haptic object recognition. Explorative finger movements allow us to collect haptic information and integrate it into a percept of the explored object. Most of the time we have additional visual information about what we are exploring, however, when for example searching for a pen or keys in a hand bag we are almost entirely dependent on our haptic abilities.

Both touch and proprioception are important for haptic object recognition; accurately directing the finger movements determines whether the appropriate tactile information is gathered (Lederman & Klatzky, 1987; see for review Klatzky & Lederman, 1993). This suggests a close relation between perceptual processes and finger and hand movements that support these perceptual processes. Generally, exploring objects by touch alone involves several fingers and somatosensory information from these different fingers needs to be integrated to perceive object properties. Moreover, multiple tactile and proprioceptive signals need to be integrated across space but also over time. Unless an object is small enough to enclose it entirely with one hand, it is impossible to sense it from simultaneous acquired information. Larger objects therefore, are explored bit by bit in an attempt to collect a stream of haptic information. The mechanism underlying this integration process, however, remains to be determined. For example Soechting, Song and Flanders, (2006) explored the idea that haptic perception of complex shapes is constructed from primitives, or geometric elements, such as straight lines, arcs or even ellipses. Although participants were successful in reproducing the features of the constituent elements, such as the size and the shape of individual components, when drawing a previously

explored object, the main conclusion entailed that subjects selectively focused attention to regions of high spatial contrast. Also, exploratory strategy introduced distortions in the haptically perceived shapes.

A different perspective in studying the integration of information during object recognition is taken by Ernst and Bülthoff (2004). The authors take a more general crossmodal approach, defined within a Bayesian framework and include the effects of visual and tactile information. Their starting point is that of “the ambiguous world”; how can we create a robust percept in an ever changing environment, which sometimes provides conflicting information. A common solution of our brain to overcome such conflict is to gather more and more information about the perceptual event until the ambiguity will be resolved. However, in order to prevent an extensive delay in behaviour, the brain decides on one source of information and uses it to calculate the required response. These decisions are facilitated by prior knowledge about the perceptual event and will affect sensory input in a top-down fashion. In the natural world correlations exist between perceptual events from different modalities. Implicit knowledge about these correlations is build up by experience acquired throughout the life span and is an important source of information when sensing the world. So, the most common situation for that particular perceptual event will guide the decision of the brain in picking the signal. For example, the best side to view an object is that corresponding most to the view in which we initially learned the object (usually the front). In the tactile modality, the best orientation to recognize the object is that most common to the fingers to explore (Newell, Ernst, Tjan, and Bülthoff, 2001). Tactile and visual experience builds up from early childhood and the ability to use visually guided grasping movements and more differentiated finger movements (+/- 6 months of age) provides the fundamental tool to the development of exploratory procedures that correspond to a specific object property (Piaget, 1952; Bushnell and Boudrau, 1993). Also, an important consequence of tactile experience is that it continues to shape the perceptual configuration of our hands and fingers, even in adult life.

Uncommon somatosensory situations and tactile perception

The position of body parts can influence the way the haptic world is perceived and a simple way to induce an uncommon situation is to cross body parts. A good example of this is provided by “Aristotle’s illusion”. When two fingers of the same hand are crossed, and a pencil is placed between these crossed fingers, most of the time a sensation of two pencils rather than one is experienced (in Shore, Spry, and Spence, 2002). More recently, Benedetti (1985, 1988) investigated this effect and tested how two tactile stimuli presented to the middle and the index finger are perceived both in fingers crossed and uncrossed position. Participants were required to indicate the position of a stimulus (a sharp point) applied to the middle finger relative to that of a reference stimulus applied to the index finger (a small ball). The results showed that tactile stimuli were always perceived as if fingers were uncrossed. However, finger position sense itself was preserved, even in the conditions where correct localization of the stimuli

was lost. Based on these studies he suggested that spatial localization of tactile stimuli may be independent of knowledge of the body part location. In addition, it was suggested that it might be dependent on the functional range of finger excursion.

As was indicated above, tactile experience continues to shape the perceptual information even in adult life. This characteristic of the somatosensory system is elegantly shown by Benedetti, (1991). In that study, participants were asked to tape their middle and index finger together and were required to perform the above described experiment. After 30 days, merely one participant was able to correctly perceive the location of the tactile stimulus in a fingers crossed position. The other five participants needed even more days to accomplish such performance (up to 4 months). Furthermore, the effects of learning did not transfer to other fingers. It was suggested that perceptual learning was responsible for enlarging the functional range of action and as such, it was concluded that the perceptual organization of the human hand depends on experience rather than on a rigidly determined genetic basis.

Impairments after stroke

Both theories concerning body representations, as well as theories about haptic object recognition are complemented, or sometimes triggered, by studies investigating impairments after a stroke. In the next session I will further describe common impairments in higher order functioning after stroke.

Lesions of the anterior parietal cortex (APC) will lead to impairments in tactile perception. Most often, tactile pressure sensitivity is declined as well as joint position sense and two-point discrimination. Peripheral input will not be transferred to higher order areas and therefore, functions such as tactile object recognition, or accurately grasping of objects will be impaired as well. As was remarked above in the neuroanatomical section, the short-cut from the thalamus to the somatosensory areas higher up in the processing stream (SII, PPC, Insula) can allow for preserved residual behaviour in reaction to tactile information. For example, a patient with a parietal lesion described by Paillard et al., in 1983 was unable to perceive tactile stimuli in a detection task. Nevertheless he was able to localize the stimulus when forced to point towards it. This relatively intact localizing behaviour could be explained by spared direct projections from the thalamus to higher order somatosensory areas. As such, the PPC received enough input to program a goal-directed movement towards it. Similar observations were described by Rosetti et al., (1998) when studying a patient with a thalamic lesion. Again this patient's performance was relatively intact when forced to immediately point towards the stimulated area, despite his severe problems with stimulus detection. In addition the authors tested the pointing performance under different conditions. For example the patient was asked to point on a drawing of a hand where he thought he was touched. Again, performance was highly impaired. Together these results suggest that it is not so much of "how" the pointing response is performed, but more about "where" the response has to be aimed at. Therefore it could be suggested that location information is only available for guided movements directed towards ones

own body and not when this information has to be transferred into another coordinate system, such as required when pointing towards a 2D visually defined drawing of a hand.

After lesions of the PPC impairments in tactile object recognition as well as in body related processes may occur. For example the inability to perceive the common configuration of ones own body parts can be disturbed; i.e. autopagnosia. Pick reported this impairment already in 1922 and defined it as an incapacity to localize body parts on verbal command. Often it is observed in association with aphasia, apraxia, reaching disorders and spatial neglect. More recently Buxbaum and Coslett (2001) described a patient with autotopagnosia. Interestingly, he was able to localize and grasp coherently to body parts despite his inability to point towards these parts on verbal or visual command, both on himself or others.

Besides impairments affecting the perception of more general configuration of the entire body, more specific impairments are observed as well. For example finger agnosia is an impairment affecting, most often amongst other cognitive deficits, specifically the fingers. These patients have difficulties individuating between their own fingers, or fingers in general. Specifically, they are unable to identify them by verbally naming, or by indicating them on for example a map of a hand (see for extensive reports Benton, 1959; Ettlinger, 1968). It has been suggested by Kinsbourne and Warrington (1962) that the neural boundaries of the fingers are damaged and as a consequence, the fingers are merged into a solid lump.

An overview given by Berlucchi and Aglioti (1997) and Haggard and Wolpert (2004) teaches that many different types of phenomena can occur. For instance pathologies of segmentation such as autotopagnosia and finger agnosia are reported, but also impairments in updating the somatosensory system, such as when patients perceive an extra limb, pathologies of bodily coherence, such as anosognosia (unaware of own illness) and pathologies of somatoparaphrenia, a condition in which patients attribute their affected limb to someone else.

However, another type of impairment is that of impaired tactile object recognition, or, tactile agnosia. It has been suggested that tactile agnosia arises from impaired low-level somatosensory acuity or from more general dysfunction in spatial perception. However Reed et al., (1996) observed that tactile shape perception can be impaired independently from: (i) general spatial and tactile ability, (ii) manual exploration of the object or (iii) the perception of more low level features such as metric length of a tactile stimulus. Binkofski, Kunesch, Classen, Seitz and Freund l., (2001) further confirmed the independence between tactile object perception and exploratory movements of the hand and introduced tactile apraxia as a dysfunction of hand movements for use of, and interaction with an object. Valenza et al., (2001) investigated the contribution of active exploration to tactile object recognition and tested a patient on his ability to scan 2D sandpaper objects. As performance was rather impaired, the authors investigated the tactile recognition performance of passively perceived objects. To that purpose the experimenter drew shapes onto the palm of the hand, using a wooden stick and now the patient was significantly better in perceiving the shape of the object. It is important to emphasize that all patients described in the studies of Binkofski et al., and Valenza and co-workers do not experience gross

motor impairments, therefore, the exploration difficulties are entirely restricted to the goal directed movement aiming to identify an object. Together these results imply that tactile object recognition can be impaired independently from the perceptual driven exploratory procedures and that these procedures can be impaired even if motor function in general is intact.

Task dependent effects of somatosensory processing

A large body of visual processing literature reports on task dependent processing mechanisms. The "Two visual streams" model by Milner & Goodale (2005, 2008) is developed aiming to capture the functional and structural organization of the visual system. In this model it is the task at hand that determines where (in the brain) and how the information is being processed as opposed to input defined theories. Milner and Goodale specifically argue that the visual processing for perception and action is functionally and anatomically separate. An important starting point for the model to develop was that of the investigation of a patient DF who was suffering from visual agnosia. At that time, the main function of the parietal cortex was suggested to be that of processing spatial information. However, other studies were investigating the parietal cortex in terms of its contribution to motor responses such as reaching and grasping. Testing DF on grasping and reaching experiments in reaction to visual objects, which she could not recognize or discriminate, revealed that she was still able to process visual object information. For example, she was unable to recognize a post card, but performed relatively well when inserting a post card in a slot. In reaction to these observations it was suggested that the latter behaviour would be a function of the posterior parietal cortex thereby constituting the by now accepted "dorsal stream", as opposed to the visual object recognition defined "ventral stream". In contrast, impairments of the dorsal stream might lead to a situation in which patients are able to recognize visual objects, but fail to process the visual information in order to compute a goal directed movement. These optic ataxia patients further confirm the suggested parallel processing of visual information used for the guidance of action and used for conscious recognition (see for overview of the literature Milner & Goodale 2005, 2008).

Within the somatosensory system this model can be of similar importance as task dependent processing might be a more general organization of the brain. Visual perceptual illusions have been used to investigate differential effects on implicit motor responses and conscious perceptual judgements in healthy participants (see for review Carey, 2001; Franz, 2001). Few studies have used haptic illusions to study task dependent differences in healthy participants. For example Westwood and Goodale (2003) investigated how grasping and matching responses were affected by a size-contrast illusion. Participants were instructed to manually explore with the left hand two objects, a target and a flanker object. After touching the objects, they either had to grasp the target object or estimate its size (right hand). The size of the flanker object was identical, smaller or larger compared to the target object. Consistent with several previous visual illusion studies (e.g. Aglioti, DeSouza, and Goodale, 1995; Haffenden & Goodale, 1998), size estimation was affected by the illusion (albeit, for the larger flanker object only) whereas

grasping was not. A limitation of the Westwood and Goodale study is that the size contrast illusion is likely to induce visual imagery processes, which means that the observed differences between matching and grasping might be related to differences in visual rather than somatosensory processes.

Recently Dijkerman and De Haan (2007) reviewed a substantial amount of literature that can be explained in terms of a division between touch for action and touch for perception. Moreover the authors distinguished between somatosensory processing for the guidance of action and somatosensory perception for conscious recognition, each being subserved by separate neural processing streams. An important aspect of the model is that the conscious recognition is likely to be affected by higher-order processes such as illusions, whereas the processing of information in order to compute an action response will be less affected. However, more evidence is needed in order to further confirm whether output defined processing mechanisms capture the organization within the somatosensory system.

Thesis Outline

The study of touch and in particular, the study of the relationship between low-level and high-order processes in the somatosensory system might provide insight in how the brain is functionally organized. The paradigms used to investigate these interactions are diverse and the responses that are used mainly vary along the action-perception dimension. Moreover, effects of perceptual illusions and mental operations will be studied as well as the effects of low-level and higher order perception impairments in patients who suffered a stroke. Finally, these effects are compared for action and perception tasks separately in order to investigate the suggested independence of tactile processing for programming an action as opposed to its conscious recognition.

My first aim is to focus on how somatosensory information such as simple tactile stimuli and more complex stimuli, such as an entire body part, are localized and how these processes are affected by brain lesions causing lower- and higher- order tactile perceptual impairments. A frequently used paradigm to investigate localization performance in the somatosensory system is that of pointing movements. In **Chapter 2**, we examined how healthy participants perform when executing pointing movements to localize unseen tactile targets on the volar side of the forearm, the hand and the fingers. Most studies have found increasing localization performances with increasing tactile acuity. However, on basis of studies revealing that fingers are somewhat special, we expected that performance might be different for finger directed movements, especially before tactile location feedback was provided. Also, we studied the effects of proprioceptive input by manipulating the posture of the stimulated limb and hypothesized that additional input about the position of the entire limb would enhance localization performance in general. However, the suggested uniqueness of our fingers is difficult to capture using a point localization task. Therefore in a second study, described in **Chapter 3**, we reported on the localization performance of stimuli presented to the fingers taking a more perceptual

approach as opposed to the action task used in the previous chapter. Also, to investigate the effect of proprioception on the processing of tactile information, we tested finger localization in three different postures: (1) fingers together (2) fingers spread and (3) fingers interwoven. In **Chapter 4** we investigated tactile localization processes by directly comparing performance on a perceptual and on an action task in two stroke patients. In the action task the patients were asked to directly localize a tactile stimulus presented on their own hand using a pointing response towards the touched location on their hand. The perceptual task however, required to localize a tactile stimulus presented to their hand using a pointing response towards the touched location on a drawing of a hand. **Chapter 5** deals with a similar comparison of tactile and perceptual responses to tactile stimuli but here we investigated the localization of an entire body-part, such as the finger, in patients suffering from finger agnosia due to stroke. Finger agnosia is a condition characterized by a specific loss in finger identity which most commonly leads to confusion of the middle three fingers. Also, stored long term knowledge about common finger configuration is affected. All patients had suffered a stroke affecting brain areas within the somatosensory system. Therefore insight in the relation between brain areas and somatosensory behaviour might be provided additionally.

My second aim is to investigate the relation between higher order representations and bottom-up tactile processes. For example stored long term knowledge affects tactile processing in a way that information is always processed under default circumstances, which allows the system to be as economical as possible. With respect to the position of our body-parts, this default can be regarded as “body-parts are always located in a functional position. A striking tactile illusion is therefore perceived when someone touches an object with crossed fingers. In this view the question arises whether patients with finger agnosia are still affected by long term knowledge about common finger configuration. Therefore in **Chapter 6** we examined the effects of such an illusion in a patient with finger agnosia using a relative location discrimination task of tactile stimuli presented to two neighbouring fingers testing two posture conditions: (1) fingers crossed (2) fingers uncrossed. Furthermore, it has been suggested that the neural boundaries of the fingers are affected by the stroke and the fingers are therefore fused into one solid lump. So, are patients with finger agnosia still able to accurately perceive and integrate tactile information perceived by the fingers? This question was investigated in a second experiment testing the same patient with finger agnosia but with a haptic search paradigm. Another way in which stored knowledge can influence behaviour is by mentally generated sensations through imagery. Mental operations tend to influence behaviour and most insights in these effects are derived from visual research. However, it is likely to expect tactile imagery to affect tactile processing similarly to the effects observed in the visual system. Therefore in **Chapter 7** we investigated the influence of tactile imagery on auditory and tactile perception and the effects of auditory imagery on auditory and tactile perception.

Chapter 8 again reports on the effects of a tactile illusion, that is, Weber’s illusion, and we compared its effect on both an action and perception response. From visual literature we learned

that action responses towards visual stimuli are, under most circumstances, insensitive for the effects a perceptual illusion generally causes. Therefore in this chapter we examined whether a similar robustness for the effects of a tactile illusion on an action response.

Finally, in **Chapter 9** I will reconsider all the observed results and contrast these with the most recent findings presented in the literature.

CHAPTER II

Where have I been touched? Localizing tactile stimuli on the fingers, hand and forearm

H. A. Anema, E. Habets, and H. C. Dijkerman

Abstract

The processing of tactile location information is highly relevant in many daily situations, for example when wanting to scratch an itch on your back, or trying to squash a fly on your arm. Previous studies investigating tactile localisation revealed an increase in performance for body-parts with increasing tactile acuity. These studies used a variety of methods, such as relative position judgements and marking the perceived location with a pen, which can be regarded as more perceptual responses as opposed to active motor responses. Here we investigated how above-threshold tactile stimuli on the dorsal side of the forearm hand and middle three fingers, are localised using direct pointing movements. In addition, the effect of recurrent proprioceptive input on the localisation performance and the effect of tactile feedback were investigated. The data confirm earlier observations of better tactile localisation performance for areas with higher tactile acuity. However, we failed to observe considerably better localisations of tactile stimuli on the fingers as compared to the hand and this effect was most pronounced when tactile feedback had not yet occurred. After feedback a finger stimulus was better localised as compared to the localisation of a hand stimulus. After feedback the corrections were substantial enough to reveal a better performance for stimuli on the finger as compared to the hand, suggesting that higher tactile acuity is particularly important for online adjustments at the end of the movement. Finally, localisation performances did not improve with recurrent proprioceptive input in the arm.

Introduction

How somatosensory information is derived from the external world is a question investigated already in the early 19th century (see for overview of the literature until 1940: Boring, 1942). Most of those early studies have been set up to disentangle how tactile stimuli are detected and localized. Using different types of responses, such as tactile pressure detection, two-point discrimination and point localisation, these studies observed many characteristics of the tactile sensory system. An important step forward in this area was made by Weber (Weber, 1834; in Ross & Murray 1996) when he observed that the perception of distance applied to the skin varied with the receptor density and spatial acuity. According to Weber, the sense of localisation "consists of our being able to distinguish between two sensations... excited at different places on our body or in our organs of touch". However, when discriminating two simultaneously applied points, one is merely judging the relative location of one stimulus to another and not location related to the body. In his second investigation of cutaneous space relations Weber tested the perception of location (Weber, 1852; in Hamburger, 1980), by asking blindfolded participants to indicate a touched location on the skin as accurate as possible. After the first "landing" on the skin, participants were allowed to grope around the skin until they thought they found the correct location. It was considered that the average error implies an absolute measure of the local sensitivity of the skin. In an attempt to overcome

methodological shortcomings, Pillsbury, (1895) modified Weber's experiment. In this study, investigations were restricted to the volar side of the arm. The experimenter touched a point on the skin with a charcoal point (1mm diameter) after which participants (eyes closed) were asked to indicate the point with another, similar charcoal point (1mm diameter). The error was measured by means of a compass and a scale. Although only few participants were measured and only some of them are discussed in the article, it seems that the amount of error decreased in a proximal to distal direction with the highest scores for the region near the elbow (35.30mm) and the smallest scores for the region near the wrist (25.19mm; note: these scores are obtained from one participant only). Also, observations revealed that errors were most pronounced in the direction of the wrist, possibly caused by movement parameters. In a follow-up study by Parrish (Parrish, 1896), using a slightly adjusted paradigm as was used by Pillsbury, the data again revealed an overshoot in the direction of the wrist. Also, overshoots were observed to a rightward direction for pointing movements to the right (left pointing arm to right stimulus arm) and vice versa. Again these observations were explained in terms of movement parameters and not by actual processing mechanisms of the tactile stimulus and its location. The most important difference with Pillsbury's paradigm is the lack of tactile feedback and as a consequence, the following corrections, which ultimately led to a larger amount of endpoint error. Although based on observations and introspection, these results are still of importance in terms of guiding us to unravelling the mechanisms behind tactile localisation.

A first well documented study by Weinstein (1968), which reported additional statistical tests, discusses effects of body part, sex and laterality on tactile sensitivity, using a variety of objective tactal measures. Most important here is the point localisation test. In this test the experimenter pressed a Y shaped grid on the skin of the volar side of the forearm, hand or finger, with its tail pointing distally. At the centre of the Y a point stimulus was presented (through a small hole) which served as the reference. Next, the experimenter stimulated the skin through one of the other holes (separated by 1 or 2.5mm) in one of the Y-arms and participants were asked to judge whether the second stimulus was located at the reference point or not. This test can be viewed as a two-point discrimination but with a short-term memory component, and tests the perception of one location relatively to that of another location. The results confirmed the above described observations of Pillsbury that the amount of error decreases from proximal to distal when measured at the upper extremities. Also, the author did not observe differences in localisation performance between males and females.

An elegant series of experiments was conducted by Hamburger, (1980) in an attempt to find a clinically useful and applicable method to measure the ability to localize tactile stimuli on the skin. The author defined this process as Locognosia, or, the gnosis of a location, emphasizing that this process is one of the cognitive apparatus and not merely of mechanoreceptors. Participants were asked to locate an unseen tactile stimulus on the skin, by marking the felt position with a pen. Stimulus locations were marked with red ink and localisations

were performed under visual feedback conditions. Participants wore a pair of red goggles to prevent them from seeing the red ink marked target spots but enabled them to view their own arm and hand. The stimuli were marked within eight different areas, that is, the dorsal and volar surfaces of the right and left hand and of the right and left forearm. As part of the hand area, the dorsal and volar sides of the distal phalanges fingers were marked as well. The results showed, in line with the literature, that the errors were larger near the elbow than on the fingertips and most often made in the proximal-distal direction of the arm. Also, points stimulated on the elbow and wrist joints were localised better as compared to stimulated points on the forearm itself. Finally, the results did not reveal any differences in performance between fingers, which was however expected on basis of cortical size differences between the various fingers and overall performance did not differ between dorsal and volar stimulation. However, two out of 23 participants produced errors at points stimulated at the middle and ring finger. As indicated by Hamburger (1980), the middle fingers differ in the amount of cortical tissue, rendering them less represented.

An in depth study of how tactile stimuli presented to the fingers are localized is provided by Schweizer, Maier, Braun and Birbaumer (2000). These authors observed that participants erroneously localised a near threshold tactile stimulus presented to a finger as if it was perceived by a neighbouring finger. Also, this type of error was more frequently observed as compared to errors to other fingers. It was suggested that finger overlapping receptive fields might have accounted for the observed pattern of results. Also, fingers are special since we have many of them on the same limb and the middle fingers are visually very much alike. Some authors suggested that there might be a separate finger schema, apart from the hand and the rest of the body (Benton, 1959; Haggard, Kitadono, Press, & Taylor-Clarke, 2005). For instance, Benton argued on basis of the results provided by an extensive investigation of finger agnosia that a separate finger schema could exist. This is a condition which is characterized by specific finger identification impairments in the absence of more general body part identification difficulties. In the study by Haggard et al. (2005), it was observed that tactile information applied to the hands and fingers were processed separately, as the configuration of the hands, hands on top of each other and fingers interwoven, did not affect the indication of which finger was stimulated, but did affect the performance when participants were required to indicate which hand was stimulated.

Put together, even though these suggestions are based upon results derived from rather perceptual tasks, as opposed to more action related goal directed responses, it could be argued that fingers are somewhat special as compared to other body parts such as the hands or arms.

An important aspect of the somatosensory system is its sensitivity to ongoing stimulation and lack of recurrent, new input. Most researchers argue that proprioception drifts when it is not continuously recalibrated with visual information about the current position of the limb (Craske and Crawshaw, 1975; Velay, 1984; Wann and Ibrahim, 1992). For instance Wann and

Ibrahim (1992) observed that when short glimpses of visual information were allowed, the drift ended. A similar effect was observed for a minor re-positioning of the limb, providing new and more veridical posture information. But, both types of recalibration do not refresh the somatosensory system to its original state. On the contrary, Desmurget et al., (2000; see also: DelRey and Lichter, 1972; Lee and Kelso, 1979) failed to observe that proprioception drift in the absence of visual information. Instead, the authors suggested that there might be a more accurate multimodal visuo-proprioceptive representation. The observed drift after visual occlusion might therefore be caused by a shift between the multi-modal and the less accurate multimodal prioprioceptive representation.

In all, tactile localisation has been studied rather extensively and several common mechanisms have been revealed. For example localisation performance is better for distal as compared to proximal body parts when tested at the upper extremities. Also, performance is likely to be more accurate when localisations are near anchor points such as joints or other markers on the skin. Furthermore, left/right and dorsal/volar differences have not often been observed. However, these findings are derived from experiments using rather perceptual responses, that is, marking a perceived position with a pen can be regarded as qualitatively different as compared to localizing a perceived position by means of a direct pointing movement. For instance, in visual literature it has been suggested that perceptual responses such as conscious recognition of an object is qualitatively different from action responses such as grasping the object. Also, both these responses are subserved by separate neural pathways. The suggestion that a similar division in action and perception responses exists in the somatosensory modality, has previously been reviewed by Dijkerman and De Haan (2007). In their study it was suggested that somatosensory information for the direct guidance of action towards the body is differently processed as compared to somatosensory information processed for conscious recognition. To date, no study has been set up investigating the kinematics of direct pointing to localize movements in healthy participants using tactile stimuli on the forearm, hand and fingers. In addition, the literature about different representations of hands and fingers encourages to hypothesize that localisation performance might be different for the fingers as compared to the hand and or the arm. Therefore the current study investigated how above-threshold tactile stimuli on the dorsal side of the forearm, hand and middle three fingers are localized, by means of direct pointing movements. Two posture conditions were tested, both a stable posture condition (no proprioceptive update in between trials) and an active moving posture condition (proprioceptive update in between trials). Furthermore, end-point positions both before and after tactile feedback were investigated. We expect total error to decline with recurrent proprioceptive input and after tactile feedback occurred. Finally, if fingers are somewhat special, we would expect more total error for finger directed localisations as compared to hand directed localisations, but only before tactile feedback occurred. After tactile feedback, we expect localisation performance to increase with increasing tactile acuity, inline with the results of previous studies.

Method

Participants

Twelve students of Utrecht University (1 male, 11 female, mean age 22.05 ± 2.46 years) with no medical or neurological condition, who were naïve as to the purpose of the experiment, participated in this study and received either a small payment or course credits required as part of their studies. All of them stated to be right-handed.

Experimental set up

Blindfolded participants were seated at a table with their hands placed on top (palms down, 30 cm apart; see Figure 1A). Tactile stimuli consisted of an above threshold pressure Von Frey hair tactile applications (10g target force/applicator 5.07). Pointing movements towards the stimulated area were executed with the non-stimulated (right) hand and were recorded by means of a Minibird 3D magnetic movement tracker (Ascension Technologies) sampling the 3D position of an electro-magnetic marker attached to the tip of the index finger at 86.1Hz.

Stimulated areas were evenly distributed across subjects and located on the left three middle fingers (two dots each), hand (6 dots) and arm (6 dots). These locations were predefined by marked dots on the skin (see Figure 1B) and were defined on basis of body-part boundaries. To make certain that the tactile target locations would have exactly the same location in external space (crucial for calculating endpoint error) throughout the entire experiment, the hand and fingers were pressed into a piece of clay. That way the edges in the clay would prevent the fingers from moving sideways. Also, it would keep the entire forearm in the same position. Even so, if the participant wanted some rest, the hand could easily be returned to the starting position.

Procedure & Design

After the experimental procedure was explained and the informed consent was signed the experiment started. Blindfolded participants were seated at a table with their hands placed on top

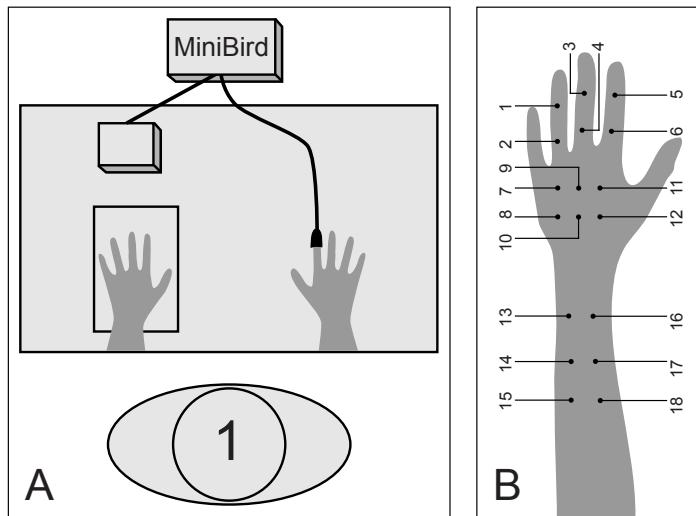


Figure 1 (A): Experimental set up (B): Stimulus locations on the lower limb

(palms down; see Figure 1A) and the experimenter was positioned opposite the subject. Next, the stimulation locations were marked on the skin of the left limb. A trial started with a warning signal which indicated that the tactile stimulus would be applied. Immediately afterwards, the experimenter pressed the tactile stimulator for 1 second on one of the predetermined locations. Participants were required to respond directly after the stimulation or at least within 5 seconds, by pointing with the non-stimulated finger towards the touched location. After the experiment finished, participants removed the blindfold and pointed, using visual feedback, to the 18 target locations after which the position was sampled.

Two experimental conditions were tested in blocks: one in which the arm would remain stationary throughout the entire experiment (Static), and a second condition in which the arm was actively lifted up and down in between trials (Move). Block-order was counterbalanced across subjects. Each tactile target location (18 in total) was stimulated 2 times, adding up to a total of 36 stimulations per block. Together the independent factors were measured using a within-subjects repeated measures design with factors Posture (Static, Move) and Body-part (Finger, Hand, Arm). By analysing the endpoint positions in two different moments in time just before participants hit the target and after tactile feedback, a third factor (Time) with two levels was added to the design. More specifically, these endpoints were determined when participants were near the target and moved 50mm/s, or when the participants finally stopped moving (0mm/s; see below) after several corrections.

Data analyses

3D kinematic data were analyzed off-line using MATLAB programming environment (Mathworks Inc.) The data were filtered using a polynomial filter (Press, Teukolsky, Vetterling & Flannery, 1994). Movement onset was defined as the first sample after velocity exceeded 50 mm/s. To obtain the third factor (Feedback) in our design, movement offset was defined as: (1) the first sample after velocity dropped below 50 mm/s, or (2) the first sample after velocity dropped to 0mm/s. XY-coordinates of the offset sample were subsequently used as endpoint position. For each velocity condition (at 50mm/s and at 0mm/s), endpoint errors were calculated by comparing the endpoint position in the xy-plane of each trial to that of the target coordinates. Next, for each velocity condition, endpoint errors were averaged per target and per subject, for each task condition separately. Other kinematic parameters such as peak velocity (PV) and the percentage of time spend to reach peak velocity (relative time to peak velocity; rTPV) were calculated from the position data between the first sample after velocity exceeded 50mm/s and the first sample after velocity dropped below 50mm/s.

A $2 \times 3 \times 2$ analysis of variance (ANOVA; repeated measures) was calculated on the total xy-endpoint errors with factors Posture (Static, Move), Body-part (Finger, Hand, Arm) and Feedback (BFB, FB). Repeated contrasts were calculated to explore significant main effects whereas paired sample t-tests were used to further explore significant interaction effects. Means (mm) and their standard error are notated in the text as e.g. (30(2.3). Finally, the kinematic variables

were analysed using a 2×3 ANOVA with factors Posture and Body-part. Again, post-hoc repeated contrasts and paired samples t-tests are calculated to further explore significant main and interaction effects.

Results

The average endpoint-errors in XY together are depicted in Figure 2A. A main effect was found for Body-part ($F(1,11) = 11.80$, $p < 0.01$). Repeated contrasts revealed that the xy-error in the Finger conditions (14mm (0.68)) did not significantly differ from that of error in the Hand condition (16mm (1.52)), whereas the xy-error in the hand condition differed significantly from that in the Arm condition (22mm (2.01), $F(1,11) = 11.51$, $p < 0.01$). Another main effect was found for Feedback, that is, overall more xy-error in the endpoint position was observed before tactile feedback (20mm (1.26) as compared to the final position after feedback (15mm (1.24), $F(1,11) = 45.54$, $p < 0.01$).

Furthermore we observed an interaction effect between Body-part and Feedback ($F(2,22) = 4.123$, $p < 0.05$). Paired samples t-tests revealed that in the Before feedback condition (BFB) the difference in the amount of xy-error between Finger (18mm (0.89) and Hand (19mm (1.77) did not reach significance ($t(11) = -0.825$), whereas after feedback (AFB) it did (Finger = 10mm(0.80), Hand = 14mm(1.50), $t(11) = -2.463$, $p < 0.05$). The other Body-parts significantly differed from each other in the amount of xy-error both before and after feedback

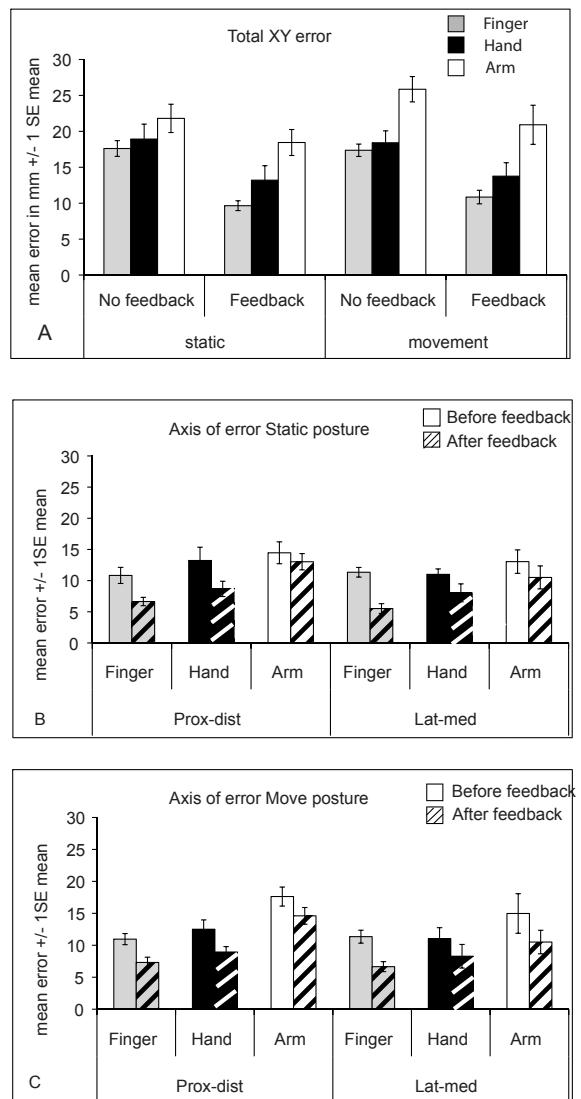


Figure 2 (A): Average xy-error for separate body part, feedback and posture conditions. (B) Average error for separate body part and feedback localisations in lateral-medial and proximal-distal direction in the Static posture condition and (C) in the Move posture condition. Note: error bars are between subject standard error of the mean.

(BFB: Hand = 19mm (1.50), Arm = 24mm (2.09), $t(11)=-2.664$, $p < 0.05$; AFB: Hand = 14mm(1.77), Arm = 20mm(2.10), $t(11)=-3.93.6$, $p < 0.01$).

Also, when testing the effect of feedback on the localization performance for each body part separately, we further confirmed the overall main effect of Feedback (Finger BFB = 18mm (0.89) vs AFB= 10mm(0.80), $t(11) = 7.091$; Hand BFB = (19mm (1.77) vs Hand AFB = 14mm(1.77), $t(11) = 4.240$, $p < 0.01$; Arm BFB = 24mm (2.09) vs Arm AFB = 20mm(2.10), $t(11) = 5.061$, $p < 0.01$.

We observed a marginally significant three-way interaction between Posture, Body-part and Feedback $F(2,22) = 1.857$, $p = 0.09$). On basis of our expectations about the effects of proprioceptive input we decided to further explore this effect. Examination of Figure 2A, reveals that the overall effect of feedback is rather similar between the two posture conditions. However, separate ANOVA's on the data of each Posture condition (Static, Move) revealed a significant interaction effect between Body-part and Feedback in the Static condition ($F(2,22) = 7.421$, $p < 0.01$) indicating a difference in correction magnitude after feedback for the various body parts as described above, but not in the Move condition ($F < 1$). Therefore in the Move condition the magnitude of correction after feedback is similar for all body-parts and this is most likely caused by an increase in correction magnitude in the arm condition. As revealed by Figure 2A, arm directed localisations in the Move condition before feedback had occurred (26mm (2.72) are less accurate as compared to the same situation in the static condition (22mm (1.97), $t(11) = -1.821$, $p < 0.05$; see Figure 2A left and right panel, left white bars. On the other hand, After Feedback, the performance was similar to that observed in the Static condition (arm AFB Static = 19mm (1.76); arm AFB Move = 21mm (2.75)).

One aspect of our results requires further investigation. As we hypothesized, error decreased from proximal to distal. However, the decrease in error for finger directed localisations did not differ significantly from that observed for the hand. Moreover, taking into account the impact of haptic feedback, the results indicate that this relative poor performance for finger directed localisations is only observed before feedback occurred. As was described in the introduction, fingers are somewhat special and sometimes participants become confused about finger identity. As such, we would expect that more error is observed for localisation movements towards the fingers in the lateral-medial directions (indicative of uncertainty about finger position) as compared to the proximal-distal directions. To test this hypothesis we calculated averages per target for each task condition for the absolute X errors and Y errors separately. Subsequently these X and Y errors were treated as levels (X = Lateral-medial, Y = Proximal-distal) of a fourth independent factor: Axis. Next, we computed a 3 (Part) x 2 (Time) x 2 (Axis) repeated measures ANOVA for each Posture condition separately. The results are depicted in Figure 2B and C.

In the Static condition we observed main effects for Body-part ($F(1,11) = 9.931$, $p < 0.01$) and Feedback ($F(1,11) = 42.07$, $p < 0.01$), similar to the omnibus ANOVA described above. Also, Body-part, Feedback and Axis interacted significantly ($F(2,22) = 2.930$, $p < 0.05$). Indeed, as is revealed by Figure 2B and C, the effect of Feedback on the amount of error differed between

the performances in the Proximal-distal direction and the Lateral-medial direction. And this seems most pronounced for the Finger and Hand. Separate 2 (Feedback) x 2 (Axis) ANOVA's on the performance in the Finger, Hand and Arm condition revealed, besides the earlier observed main effects for Feedback in all Body-parts, a marginally significant interaction effect of Feedback and Axis, albeit for the Finger condition only ($F(2,22) = 2.825, p = 0.06$). As can be observed from Figure 2B, the decrease in error after feedback is slightly larger in the Lateral-medial direction as compared to the Proximal-distal direction. In the Move condition (Figure 2C) we only observed main effects of Body-part ($F(1,11) = 9.060, p < 0.01$) and of Feedback ($F(1,11) = 35.01, p < 0.01$), similar to the main effects observed in the above described xy-error ANOVA.

Other kinematic variables

With respect to the Peak Velocity, a significant main effect was observed for factor Body-part ($F(1,11) = 88.203, p < 0.01$). Post-hoc contrasts revealed both significant differences between finger (720mm/s (40)) and hand (780mm/s (44)) ($F(1,11) = 53.64, p < 0.01$) and between hand and arm (928mm/s(60); $F(1,11) = 78.87, p < 0.01$), indicating that peak velocity decreased from proximal to distal. Next, for the time that peak velocity was reached, we observed a significant main effect of Body-part ($F(1,11) = 17.89, p < 0.01$). Post-hoc comparisons revealed significant differences between finger (32% (0.9)) and hand (35%(1.0); $F(1,11) = 14.54, p < 0.01$) and between hand and arm (37%(1.4); $F(1,11) = 13.64, p < 0.01$), indicating that the time necessary to reach peak velocity is shortest at the fingers and increases proximally.

Discussion

The current study investigated how tactile stimulations are localized by means of pointing movements. Overall, we observed the smallest amount xy-error for localizations on the body-part with the highest tactile acuity (fingers) and the largest amount of xy-error on the body-part with lower tactile acuity (arm), in line with our hypotheses about the relation between tactile acuity and localisation performance. However, localisations on the fingers were not more accurate as compared to the localisations on the hand, as might be expected on basis of their acuity difference. Nevertheless, after tactile feedback, when corrections were made, new information about the current location of the pointing finger allowed for better localisations on the finger as compared to those directed to the hand. In contrast, for localisations on the arm and the hand we did not find such a large effect of tactile feedback, which might be indicative of relatively less uncertainty about the touched location for these body parts, before tactile feedback occurred. Although we failed to observe any overall differences in the amount of error in the proximal-distal direction and the lateral-medial direction between the body parts, after feedback had occurred we found more corrections in the lateral-medial dimension as compared to the proximal-distal axis. However, this was observed for stimuli presented to the fingers in the static posture condition only. It could be suggested that participants were con-

fused which specific finger was stimulated and this confusion prolonged until tactile feedback had occurred. Reasons for such confusions could lie in finger overlapping receptive fields. As was mentioned in the introduction, Schweizer et al., (2000) suggested that finger overlapping receptive fields caused subjects to erroneously attribute a near threshold tactile stimulus to a neighbouring finger, more often than to any other finger. Even though we applied above threshold stimuli, stimulating an area on one finger might lead to co-activation of a neighbouring finger. Perhaps this introduced extra noise in the signal, leading to the relatively large amount of error for finger stimuli before tactile feedback was available. An additional factor that could have accounted for this increase in lateral-medial error might be provided by an increase in uncertainty, induced by the small landing surface in this direction.

Finally, we failed to identify any general differences between localisation performances when new proprioceptive input was available, and localisation performances when such information was not available. As was described in the introduction, several studies reported mixed results with respect to proprioceptive drift after visual occlusion. Nevertheless, we expected that an update in proprioceptive information by moving the arm up and down in between trials would at least improve localisation performance as compared to a situation where no proprioceptive update would be available during the testing. Our results, however, suggest that a proprioceptive update did not improve tactile localisations, indicating that either no drift occurred, or the perceived location of the limb did not influence the perceived location of a tactile stimulus presented to that limb. Some authors have suggested that when a goal directed movement is programmed towards a touched location, tactile information needs to be combined, or integrated with proprioceptive information (both from pointing and target hand). To allow for such coupling, tactile information is coded in an (egocentric) external reference frame (Haggard and Wolpert, 2005; Bonda et al; 1995; see for overview of the spatial processing role of tactile information: Gallace and Spence, 2008). Although these findings are primarily based on cross-modal, visuo-tactile experiments which consisted of tasks aiming to identify external spatial, or temporal, characteristics of the stimulus, our blindfolded participants could have developed visuo-spatial strategies in order to perform in an optimal manner, perhaps through visual imagery of the arm. This might imply that proprioceptive information plays a less dominant role in a tactile localisation task. Therefore, manipulation of such information might not sort any effect. However, posture information about the current location of the arm is in fact influencing tactile localisations, as is found in a study by Rossetti, Stelmach, Desmurget, Prablanc and Jeannerod (1994). The authors observed that viewing the hand prior to movement onset decreased pointing variability. Therefore, it could be suggested that in the current study, the posture manipulation might not have been salient enough to generate a substantial effect. Merely extending and flexing the arm once refreshed the input of the ligaments and tendons near the elbow joint but not that of the wrist and fingers. Instead, moving the entire limb and its digits might be more efficient to improve localisation performance.

Furthermore we observed differences in peak velocity for the different body-parts. More spe-

cific, we observed highest velocities for arm directed movements and the slowest for finger directed movements. Also, the time necessary to reach that peak in velocity was earliest for the finger directed movements and latest for the arm directed movements. In an earlier study by some of the current authors, similar effects were observed for arm and hand directed movements in a similar set up (Anema, Wolswijk, Ruis, & Dijkerman, 2008). In this study rectangular objects were placed either on the dorsal side of the forearm or on the arm. Subsequently blindfolded participants were asked to grasp the object and the starting position of the grasping hand was similar as in our experiment. Peak velocity appeared to be significantly higher when grasping movements were directed to the forearm. Also, it emerged significantly later in time for the arm compared to hand directed responses. We hypothesized that these difference were caused by a distance difference between grasping movements to arm and the hand involving different biomechanical characteristics. Indeed, a second experiment in which the grasping movements were directed to the same location in external space (by moving the hand and forearm between trials), and thus, of similar length, the differences in peak velocity and relative time to peak velocity disappeared. This suggests that the observed differences in peak velocity in the current study are a result of different biomechanics between forearm and finger directed movements, rather than differences in spatial acuity.

Some aspects of our study require some discussion. First of all, even though fingers have a better tactile acuity, we did not observe overall more accurate localisations for stimuli presented to the fingers, as compared to hand stimuli. As was described earlier, under certain circumstances participants might be uncertain about which specific finger received the tactile stimulus. This could have caused the relatively large error on for finger stimuli as compared to stimuli on the hand. However, an alternative explanation could be that the overall localisation performance on the fingers reached a ceiling effect due to noise in the motor system. So, perhaps noise in the motor system induced by motor variables such as muscle contraction, movements of joints etc, does not allow pointing movements to be more accurate than around 18mm away from the target (error observed for finger and hand stimuli). Further improvement would therefore be impossible. However, Prablanc, Echallier, Komilis, & Jeannerod, (1979) showed that open-loop pointing movements to visual targets (open loop: no visual input about the pointing hand) are performed with an accuracy of < 5 mm. So, when visual information about a location is processed, and a motor response (pointing movement) is generated on basis of such information, generated noise caused by motor parameters still allowed for pointing movements with an accuracy of 5 mm from the target. But, visual location information is more accurate and decays less rapidly (Bliss et al., 1966) as compared to tactile location information, which might lead to more precise open-loop pointing movements on basis of visual location information.

Secondly, the localisation of stimuli on the arm was even worse in the moving posture condition as compared to the static condition, specifically before feedback had occurred. As such, motion in the elbow joint seems to interfere with tactile localisations of arm stimuli but not

with hand and finger stimuli. In fact, the exact contribution of moving the arm up and down in between trials remains somewhat unclear and in itself is in need for further investigation. Finally, if it is somehow more difficult to localise tactile stimuli perceived on the fingers, one could hypothesize that more salient stimulation will enhance processing and therefore localisation performance. Although we used far above threshold stimuli, we used stimulus presentations of 1 second and participants were asked to point immediately after the target had been stimulated. This forced participants to maintain the perceived location in short-term memory. It could therefore be suggested that prolongation of the stimulus presentation until participants are near the target location, would allow for more elaborate processing of the tactile stimulus in terms of the correct finger. In turn, more online adjustments of the pointing response can occur. Therefore, future studies should further investigate the observed relative increase in pointing error for finger applied stimuli, especially in the lateral-medial direction, before tactile feedback is available.

In sum, the data reported confirm the earlier observations of improving tactile localisation performance for areas with better tactile acuity. However, we failed to observe considerably better localisations of tactile stimuli on the fingers as compared to the hand. Moreover, this effect was most pronounced before tactile feedback had happened and in the medial-lateral direction. After tactile feedback, the corrections were substantial enough to reveal a better performance for stimuli on the finger as compared to the hand. Finally, localisation performances did not improve with recurrent proprioceptive input in the arm.

CHAPTER III

Finger position influences whether you can localize tactile stimuli

K.E. Overvliet, H.A. Anema, E. Brenner, H.C. Dijkerman, J.B.J. Smeets

Abstract

To investigate whether the positions of the fingers influence tactile localization, participants were asked to localize tactile stimuli applied to their fingertips. We measured the number and locations of errors that participants made in three configurations: fingers together, fingers spread and fingers interwoven. We reasoned that if there are spatially defined tactile receptive fields that normally span more than one finger, localisation will improve when the fingers are spread. We indeed found that fewer errors were made when the fingers were spread. However, the reduction of errors was not specific to the neighbouring fingers. This suggests that more distinct information about the positions of the fingers can improve tactile localization.

Introduction

If you want to identify an object by touching it with several fingers of your hand, you must have information about the positions of the fingers. You then need to integrate the tactile information collected by your fingertips with proprioceptive information about the spatial coordinates of the fingers. Already in 1964, Natsoulas and Dubanoski showed that tactile perception is influenced by limb position: the final perceptual experience of tactile stimulation depends on the orientation of the stimulated skin with respect to an external reference frame. More recently, Yamamoto and Kitazawa (2001) demonstrated that the subjective temporal order of two stimuli delivered to the two hands depends critically on whether the two arms are crossed or uncrossed. When the arms were crossed, participants sometimes misreported the order of the stimuli. They suggest that participants ordinarily base their judgments on a reconstruction of the spatial locations of the stimuli in the external world, a process that takes time and requires information about the locations of the two hands. Thus tactile localisation appears to depend on posture as well as on the local sensibility.

Tactile perception is also influenced by effects of spatial proximity between two neighbouring limbs. In a study by Soto-Faraco, Ronald and Spence (2004) participants were required to make judgments about the presence and location of a vibro-tactile stimulus presented to the thumb or index finger of one hand, while attempting to ignore distractor stimuli on the thumb and index finger of the other hand. They showed that when the position of the target and distracter were on congruent digits (index-index finger) the reaction times were shorter and error rates were lower. The difference between congruent and incongruent presentations was smaller when the positions of the target and distracter in external space were further apart: since the separation between the arms determined how strongly the stimuli influenced each other. Apparently the effect does not (only) depend on the stimulated skin sites, but also on the position of the stimulated body parts.

With respect to the influence of spatial proximity of separate body parts on tactile perception, our fingers constitute an example of several body parts that usually operate in a fixed configuration within a small space. This, together with the high spatial acuity of the tactile receptors make fingers particularly suited for identifying and manipulating objects. Thus the fingers are

somewhat special, and several lines of evidence suggest that there may be separate representations for the fingers and hand within the brain. For example, Haggard, Kitadono, Press and Taylor-Clarke (2006) argued for separate representations for hands and fingers. They looked at the effects of various configurations of the hands and fingers in tactile processing. Participants were asked to either detect a tactile stimulus applied to the fingertips, indicate which finger (but not of which hand) was stimulated, or indicate which hand (but not which finger) was stimulated. This task was performed both with hands next to each other and with fingers interwoven. There was an increase in error rate when the fingers were interwoven when participants had to identify the stimulated hand, but not when they had to identify the stimulated finger. Therefore it was suggested that hands and fingers were processed separately, and that the configuration of the hands did not have an effect on the identification of the stimulated finger.

Other evidence of finger posture influencing tactile processing comes from a study by some of the current authors (Overvliet, Mayer, Smeets, & Brenner, 2008). In their study, participants had to detect the absence of a line segment under one of their fingers when their fingers were in different configurations: all fingers positioned on a single straight line which had a gap just beneath one of the fingers, or the fingers in a relaxed posture with separate line segments under all but one finger pad. In the condition in which the fingers were on a straight line detection of the "gap" was much faster than when the fingers were in an extended position (with separate line segments). Apparently, the configuration of the fingers influenced detection. In that paper it was concluded that the integration of the perceived line segments into an object was the critical component for observing the faster gap detection times. However, it could also be that the fingertips have overlapping receptive fields when they are closer together, making it easier to integrate information across the fingertips.

As we know, our fingers are very sensitive tools for extracting tactile information (Weinstein, 1968). But, how accurate are we in localising tactile stimuli? An extensive investigation of how accurate we are in localizing near threshold tactile stimuli (Von Frey hair applications) on the fingers by Schweizer, Maier, Braun and Birbaumer (2000) showed that potential stimulation points that were close to the actual stimulation point were selected more frequently than ones that were further away. Close stimulation points were even selected more frequently than expected on the basis of chance when they belonged to a neighbouring finger. Schweizer et al. concluded that digit-overlapping receptive fields are responsible for the errors made to neighbouring fingers. The idea of digit-overlapping receptive fields in the somatosensory cortex is far from new (Iwamura, Tanaka, Sakamoto, & Hikosaka, 1983a, 1983b; McKenna, Whitsel, & Dreyer, 1982). However, if these overlapping receptive fields are linked to skin location, proximity of two adjacent fingers would not change the distribution of errors. Since we saw that the (relative) positions of the hands and fingers are relevant when processing tactile information, overlapping somatotopical receptive fields cannot be the whole explanation. Perhaps, the receptive fields are not purely linked to skin location but are linked to space surrounding the

finger, in which case enlarging the distance between the fingers should improve localisation. In particular, spreading the fingers should decrease the tendency to choose the adjacent position on the neighbouring finger, because the distance is increased.

To test this hypothesis we used a variation on the paradigm used by Schweizer, Maier, Braun and Birbaumer (2000). We studied the errors that participants made in localizing a near-threshold stimulus presented to one of thirty locations at the fingertips. We used three different finger configurations: fingers together, fingers spread and fingers interwoven. If somatotopically overlapping receptive fields are involved, participants will make the same errors to the neighbouring finger in ‘fingers spread’, ‘fingers together’ and ‘fingers interwoven’ conditions. However, if spatially overlapping receptive fields are involved, the errors will be distributed differently for each finger configuration.

Experiment

Participants

Ten participants, two male and eight female, with an average age of 27.5 (range 20-38) participated in this experiment. One participant reported to be left-handed, and the others reported to be right-handed.

Stimuli and Setup

We used a point localization test. The stimulus that was used was a Von Frey hair of 0.07 grams (North Coast Medical, Touch-Test, Sensory Evaluator Size 2.83). We chose this size, because earlier findings by other experimenters indicated that this generated an error rate of about 50% (Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer, Maier, Braun & Birbaumer, 2000). Three finger configurations were measured: fingers together, fingers spread and fingers interwoven (Figure 1A-C). We marked 3 evenly distributed and aligned dots in the middle of each finger pad of both hands of the participant, at 0.25, 0.5 and 0.75 of the total finger width. A screen with a curtain prevented the participant from seeing his or her hands. A map of the two hands with the numbered positions (Figure 1D) was attached to the screen in such a way that the participant could easily read it.

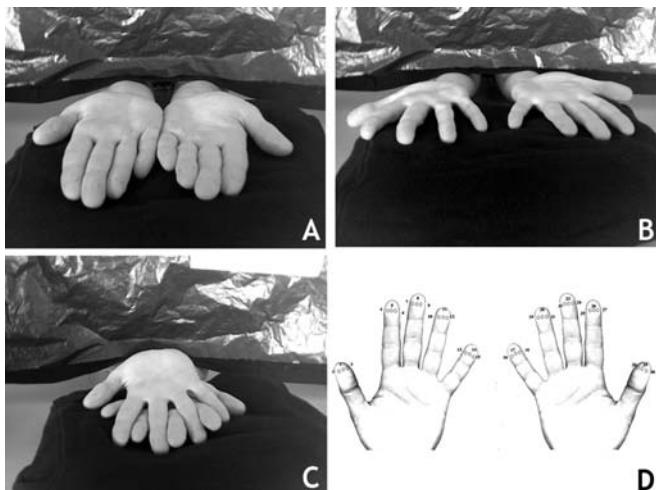


Figure 1. The different finger configurations used in the experiment: (A) fingers together, (B) fingers spread, and (C) fingers interwoven. (D) The map of the two hands that was shown to our participants, with numbered dots indicating the possible stimulation sites.

There were 150 trials for every finger configuration: 5 repetitions for each of the 30 possible stimulation locations. The three finger configurations were measured in different blocks, counterbalanced in order across participants. Within a block the 150 trials were presented in a random order.

Procedure

After the experimental procedure was explained to the participant and the informed consent form was signed, participants were seated behind the screen. They were asked to stretch their arms through a hole in the screen and place their hands with their palms up on a pillow, assuming one of the three finger configurations (Figure 1A-C). A warning signal indicated that the stimulus was going to be applied, after which the stimulus was applied at one of the thirty marked locations. The location was touched with the hair applying just enough force for the hair to start bending which resulted in 1.5s of stimulation. The participant's task was to name the location, as indicated by the numbers on the map, at which they felt the stimulus. They were allowed to take as much time as necessary. However, if they did not feel the stimulus and spent too much time thinking, they were encouraged to guess. The experimenter entered the named location in the computer and the next trial started.

Results

Correct responses

Overall task performance per condition was calculated by determining the percentage of correct responses for each participant. The average and standard error of the mean could then be compared with the performance reported in the study by Schweizer, Maier, Braun and Birnbaumer (2000).

The proportions correct were 0.44 +/- 0.04 (between subject standard error of the mean), 0.56 +/- 0.05 and 0.31 +/- 0.04 for fingers together, finger spread and fingers interwoven respectively. Schweizer, Maier, Braun and Birnbaumer (2000) found a similar proportion of 48 % correct trials, similar to our value for fingers together. In their study, the positions of the fingers with respect to each other were not experimentally controlled.

Mislocalization

We found a main effect of finger configuration on the proportions correct (Repeated Measures ANOVA; $F(2,18)=57.9$, $p<0.001$). Paired samples t-tests (Bonferroni corrected) revealed that all configurations differed significantly from each other. Thus, increasing between-finger distance appears indeed to lead to more accurately locating tactile stimuli. However, this could just have to do with the posture itself or with the extend to which the fingers touched each other. The hypothesis of spatially overlapping receptive fields makes a more specific prediction: the additional errors in the fingers together condition should be on the neighbouring finger of the same hand. We therefore determined the proportion of responses that was correct, that was

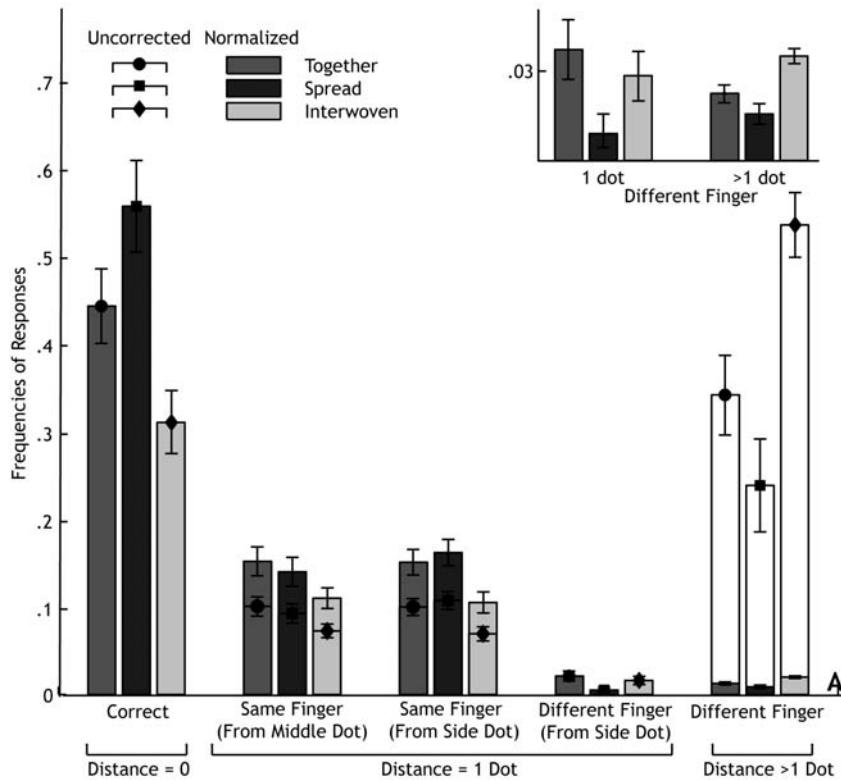
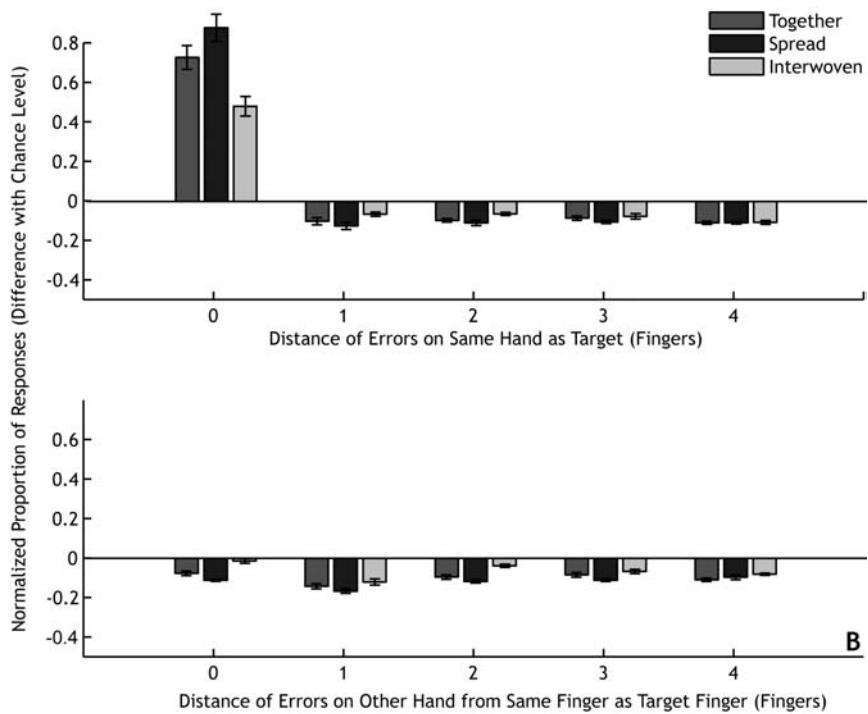


Figure 2. Proportion of responses averaged over all participants (with standard errors). (A) Symbols (transparent bars): the proportions of responses. Bars: proportions normalized by the number of response options (e.g. for responding at the neighbouring point within a finger when the central point was stimulated there are two possibilities). In the inset enlarged bars of the normalized responses to a different finger are shown. Fig 2(B) Normalised frequencies (as above) for all possible numbers of fingers from the target on the stimulated hand (upper panel) or the other hand (lower panel). The positions on the other hand are calculated as if the same finger of that hand were stimulated.

shifted by one position within a finger when the middle dot was stimulated, that was shifted by one position within a finger when one of the side dots was stimulated, that was shifted by one position to the neighbouring finger (which can obviously only happen when one of the side dots was stimulated), and the proportion of shifts of more than one position. We corrected the proportion of responses for the number of trials in each response category (e.g. there were only 50 trials in which the middle dot was stimulated and only 100 in which one the side dots was stimulated). These values are plotted in figure 2A (transparent bars with symbols). The values of these bars add up to 1 for each finger configuration.

We defined a shift to the neighbouring finger in spatial terms, which is to a finger of the other hand in the interwoven condition. It is clear that spreading the fingers does not specifically



reduce the number of responses to the neighbouring finger (at a distance of 1 dot), but also to positions further away. This indicates that spatially overlapping receptive fields alone cannot explain the results.

In order to check whether the neighbouring finger is chosen more often than other fingers, we normalized all the frequencies of responses in relation to the number of response possibilities, so for responses on the same finger from the middle dot, we divided the total number of responses by two, since there are two response possibilities in this condition. For the responses to a different finger we divided the total number of responses by 27. For all the other bars there is only one response possibility (dark bars in figure 2A). Doing so clearly shows the errors relatively frequently involve selecting the wrong position on the stimulated finger ("same finger"). The probability of choosing the neighbouring dot on the next finger was not clearly higher than that of choosing any other dot on another finger in any condition. A repeated measures ANOVA on the normalized frequency of errors with factors finger configuration (together, spread, interwoven) and response position (neighbouring dot on the next finger, any other dot on an incorrect finger, inset in figure 2A) revealed no main effect of response position, but a main effect of finger configuration ($F(2,18)=11.02$, $p<0.01$). We also found an interaction effect between finger configuration and response position ($F(2,18)=5.17$, $p<0.05$). This interaction is mainly due to a small but significant difference between the response positions in the fingers spread configuration ($t_{df=9}=3.41$, significant for a Bonferroni corrected p of 0.0167). This difference is in the opposite direction than expected: there were relatively few responses to the

neighbouring dot on the neighbouring finger, compared to the number of responses at any other location. However, the total number of responses to the neighbouring finger is the same as the number of responses to any other finger (see below).

In order to determine whether the identity of the hand matters in localizing the stimulus, we also plotted the distance of the response from the target finger in terms of the number of fingers rather than positions on the fingers (figure 2B). The distance from the stimulated finger to a selected finger within the target hand is shown in the upper panel and the distance from the corresponding finger of the other hand is shown in the lower panel. To obtain a comparable measure for all distances despite the different number of possibilities we normalized the responses: the bars shown in figure 2B are the difference between the proportion of response made and the proportion of responses that we would expect to have been made if participants were randomly guessing. To test whether the normalised responses were evenly distributed across the fingers, we performed a Repeated Measures ANOVA on all incorrect responses (thus excluding distance 0 on the same hand). We found a main effect for both finger configuration and distance ($F(2,18)=56.75$, $p<0.001$ and $F(8,72)=15.64$, $p<0.001$ respectively) and also an interaction between these two factors ($F(16,144)=3.83$, $p<0.001$). The number of responses in the fingers interwoven configuration on the same finger of the opposite hand seems to be somewhat larger than in the other two configurations. Paired samples t-tests (Bonferroni corrected) reveal that this is significantly different from distances 1, 3 and 4 on the opposite hand, but not significantly different from distance 2.

Discussion

In the current study we tested the effect of finger configuration on a tactile localisation task. Our hypothesis was that there would be fewer errors to the neighbouring finger in the fingers spread configuration than in the other two configurations, because in the latter cases one would have a larger overlap of the (spatial) receptive fields. We indeed found fewer errors in the 'fingers spread' configuration compared to the 'fingers together' and 'fingers interwoven' configurations. However, in all three conditions there were many more errors to the neighbouring dot on the same finger than to the neighbouring dot on the next finger (figure 2A). Moreover, errors to the neighbouring finger occurred as frequently as errors to any other finger. These results show that the only difference between the conditions is the likelihood of correctly identifying the target. This indicates that spreading the fingers helps in localizing the target, but not because spreading separates the otherwise overlapping receptive fields. Instead, spreading the fingers may make each individual finger appear more distinct and therefore reduces the across finger misidentifications.

In the fingers spread and fingers interwoven configurations the configuration of each hand is the same, so the proprioceptive information from the fingers is presumably also the same. However, we found more errors in the fingers interwoven configuration. This indicates that not only proprioceptive information about finger configuration is relevant. Having your fingers

interwoven is a somewhat unusual posture which is likely to generate uncommon combinations of tactile information from the sides of the left and right fingers and proprioception from the arms. In turn this could have generated more noise and as such have caused the higher proportion of errors.

It is quite surprising that we did not find relatively more responses to a neighbouring finger like Schweizer, Maier, Braun and Birbaumer (2000) found. This may have been caused by the differences in the amount and distribution of the response options used in the experiment. Participants in the current study had to choose between thirty possible response options, distributed over the upper segments of the fingers of both hands. The participants in the study of Schweizer et al. had to choose between 42 response options, which were distributed over all segments of the fingers of one hand. It could be suggested that receptive fields only overlap across the digits for the lower segments of the fingers. Unfortunately, Schweizer et al. did not specifically test differences in error distribution for each finger segment separately and so this needs further investigation.

Finally, Haggard, Kitadono, Press and Taylor-Clarke (2006) claimed that the hands are localized separately from the fingers. If that were so one would expect an exceptionally large number of responses to the same finger of the opposite hand. We did not find this for two of the three finger configurations (together and spread), that is, the responses are below chance level (figure 2B). However, in the most difficult task (interwoven configuration) there was an increase in the number of responses to the same finger on the opposite hand. This hand/finger configuration is very unusual and leads to the most errors of all the configurations. The hands are not located at either the left or the right side (but on top of each other) and therefore could cause more confusion in knowing where the fingers are located. So, perception of the position of the hands and fingers are probably influenced by the same spatial information.

In summary, we found fewer errors in the fingers spread configuration. However, the distribution of the errors was similar in all three finger configurations. This suggests that more distinct information about the positions of the fingers can improve tactile localization.

CHAPTER IV

Double dissociation between somatosensory processing for perception and action

H. A. Anema, M. J.E. van Zandvoort, E. H.F. de Haan, L.J. Kappelle, P. L.M. de Kort, B. P. W. Jansen and H. C. Dijkerman

Anema, H.A., Van Zandvoort, M.J.E., de Haan, E.H.F., Kappelle, L.J. de Kort, P.L.M., Jansen, B.P.W. and Dijkerman, H.C. (In press).

*Double dissociation between somatosensory processing
for perception and action. Neuropsychologia.*

Abstract

Human neuropsychology suggests that there are two distinct body representations. Body image and body scheme are, respectively, thought to be involved in conscious perceptual judgments and unconscious sensorimotor guidance. The evidence is based on the double dissociation between disorders of perceptual detection and sensorimotor guidance. Until now, research focused on cases that had impaired tactile pressure sensitivity and comparisons of performance were of cases suffering from different types of lesions (peripheral and central). Here, we report a unique double dissociation in two stroke patients with intact basic somatosensory processing (tactile detection). One patient was poor at identifying the position of where she had been touched on a line drawing of a hand but was able to point accurately towards the actual position on her/his hand itself. The reverse pattern was observed in the other patient. This finding provides further support for separate processing for body image and body scheme.

Introduction

One of the key questions in sensory processing is that of the organisational principles that determine the functional and neural characteristics of the brain. Many of the earlier studies implicitly assumed that the organisational structure (e.g. different neural areas for the processing of colour, shape and space) are governed by characteristics of incoming sensory input. One of the most important advances of the ‘two visual streams: what & how’ hypothesis (Milner & Goodale, 1995, 2008) is that it is the task at hand that dictates where (in the brain) and how the information is being processed. Milner and Goodale specifically argue that the visual processing for perception and action is functionally and anatomically separate. In a recent literature review we suggested that task dependent processing may also be important for the organisation of cortical somatosensory processing (Dijkerman & de Haan, 2007). Paillard, Michel, and Stelmach, (1983) provided the first well documented evidence for such a dissociation in the somatosensory system (for similar findings see: Rosetti, Rode and Boisson, 1995, 2001). Paillard et al. reported a stroke patient with a left parietal stroke who was unable to detect tactile stimulations on the hand. Nevertheless he was capable of localising these stimulations by pointing towards it with the intact arm. Halligan, Hunt, Marshal, and Wade, (1995) presented a stroke patient with a left-sided parietal stroke, who demonstrated the opposite pattern of performance. This patient demonstrated relatively intact tactile detection while he was impaired at localising the stimulus when pointing towards it. The authors suggested that, together with the findings by Paillard et al., (1983) these observations provided evidence for a double dissociation of detection and localisation of light pressure stimuli. In 1999, Paillard presented a peripherally deafferented patient who was able to detect somatosensory stimuli such as pain and thermal sensation applied to the hand, but was impaired when asked to localise these stimuli on her own hand. In contrast, she was able to localise these stimuli on a line drawing of a hand. Overall, Paillard suggested that these findings indicated a double dissociation.

tion between a somatosensory “what” and a “how” system, analogous to the model proposed by Milner and Goodale (1995). However, Milner and Goodale defined their “what” processes as involving higher order, cognitive processes. Nonetheless, the problems encountered by the patients suffering from somatosensory perceptual deficits as described by Paillard et al., were restricted to the mere low level detection of tactile stimuli. Recently, we made a first attempt to investigate this dissociation in higher order somatosensory processing in patients with finger agnosia (Anema et al. in press). We reported patients with finger agnosia who were impaired at indicating the location on their hand where they had been touched on a line drawing of a hand, but remained able to localise where they had been touched by pointing on their own hand with the other hand.

In the current study, we present a double dissociation with respect to tactile localisation capacities for perception and action in two patients who both had suffered from a stroke but who had intact somatosensory detection. These patients were both tested with a similar pointing paradigm as was developed by Rossetti et al. (1995), but using tactile stimuli far above the detection threshold.

Methods

Participants

Patient 1 (KE), a 60 year-old right-handed male (in 2006) suffered from an ischemic stroke in the ventral posterior lateral nucleus (VPL) of the right thalamus (see Figure 1). On admission he showed left-sided somatosensory loss with left-sided weakness and distorted motor function of the left upper and lower extremity. There were no language disorders.

At four days post stroke KE was further tested on somatosensory and motor capacities. Grip strength was tested using a hand dynamometer (Lafayette instrument; model 78010). There was weakness of the left hand (first attempt = 30 kg, second attempt = 26) as compared to the

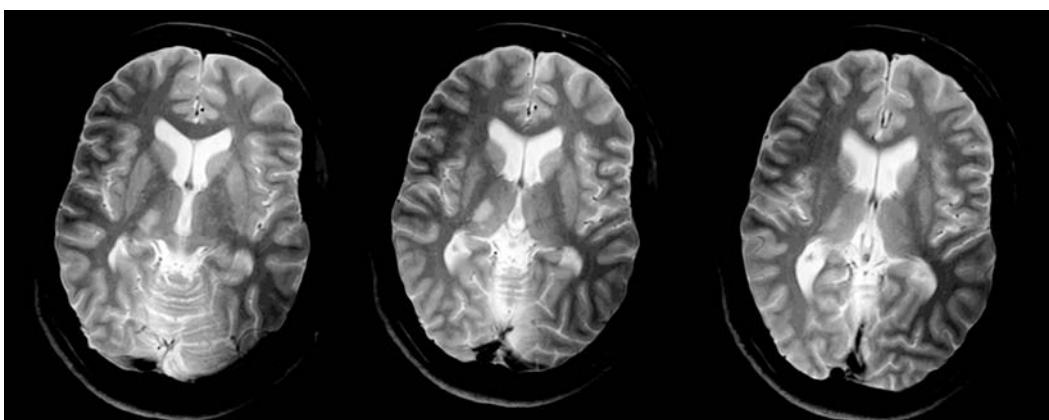


Figure 1: Three successive scans of patient KE [MRI T2/ FLAIR] MRI, magnetic resonance imaging.

right hand (first attempt = 48kg, second attempt = 50kg; average of 50 year old male: 33kg, non-dominant hand). Informal observations again revealed impaired skilled motor behaviour. A three-down/ one-up stair case procedure (Matlab Inc) with Von Frey hair tactile applications (VFA; Touch-Testtm sensory evaluators, North coast medical Inc.) was used to measure tactile pressure sensitivity (TPS, threshold at 79% correct). The threshold of the left hand was impaired (10.0g target force/ VFA 5.07) as compared to age matched healthy controls (mean = 0.04g target force SD = 0.12g/ VFA 2.44), indicating a loss of protective sensation but intact deep pressure sensation (see instructions Touch-Testtm, North coast medical Inc.). The ability to perceive joint position (JPS) was tested by passively moving the distal phalanx of the index finger (12 trials) and the thumb (12 trials). KE was required to detect whether the movement was upwards, or downwards and correctly indentified 20 out of 24 movements (thumb = 4 errors, index finger = 0), while age matched controls detected on average 23.67 out of 24 (SD = 1.3). This renders KE's performance considerably below average, though still far above chance (chance = 50%; % correct = 84%. The right hand thresholds for TPS (0.02g target force/ application 2.36) and JPS (24/24) were intact. Finally, we tested visual, auditory and tactile extinction as well as visual field defects, using a short clinical test. During the extinction test we randomly applied single or double tactile (light tap on the hand), auditory (click of a pen), or visual stimuli after which the patient was asked to state whether the stimulus came left or right (from the body midline). With respect to the visual condition: the experimenter was positioned in front of the patient who was asked to fixate at the tip of the experimenter's nose. The experimenter randomly moved either his left or right fingers or both. The experimenter's hand and fingers were initially positioned on the outer boundaries of the visual field (checked with verbal report). In subsequent trials, the experimenter changed the position of the moving fingers such that it covered all 4 quadrants. Therefore, in this test both visual extinction and visual field defects were tested. This clinical test revealed that KE showed no sign of visual, tactile or auditory extinction and no visual field defects.

Patient 2 (JO) was a 79-year-old right-handed female (in 2007) with a partial infarction in the supply area of the left middle cerebral artery. On admission she showed a right-sided hemiparesia, motor aphasia and dysarthria. No signs of hemispatial neglect or hemianopia were observed using clinical assessment.

On testing 14 days after stroke onset, some problems in speech fluency were observed as well as a mild right-sided hemiparesis. Furthermore, TPS was impaired for the right hand (0.6g target force/ VFA 3.84), indicating a diminished protective sensation, and intact for the left hand (0.04g target force/ VFA 2.44). JPS was intact in both hands (24/24) and grip strength was similar between the two hands (LH = 20kg and 24; RH = 18kg and 16), which is similar to the average strength of fifty years old females (Lafayette norms). Finally, no signs of visual, tactile or auditory extinction or visual field defects were observed.

The control group consisted of 5 stroke patients; 4 males and 1 female (mean age = 63, SD = 11;

mean TPS = 0.07g, SD = 0.01g; mean JPS = 23/24 correct, SD = 1.4; Grip strength = 29kg, SD = 8kg); two had a left and three had a right hemisphere lesion and none of them showed signs of extinction or visual field defects. Data was collected on basis of pointing movements towards the stimulated contralesional hand. All control patients were tested in a similar sub-acute state (mean days post stroke = 4.6, SD = 1.5). The study was approved by the local medical ethics committee (UMCU) and written informed consents were obtained from all participants according to the declaration of Helsinki.

Experimental set up

Participants were seated at a table with their hands placed on top (palms down; see Figure 2A). Tactile stimuli consisted of a far above threshold pressure (100% detection; 300g target force/VFA 6.65). Pointing movements were recorded by means of a Polhemus-Liberty 3D magnetic movement tracker which sampled (240Hz) the 3D position of an electro-magnetic marker attached to the tip of the index finger. The line drawing of the hand consisted of a drawing of the participant's own hand which was obtained by the experimenter by following the contours of the hand with a pencil which is further referred to as "Map". This map was positioned centrally on top of the wooden board.

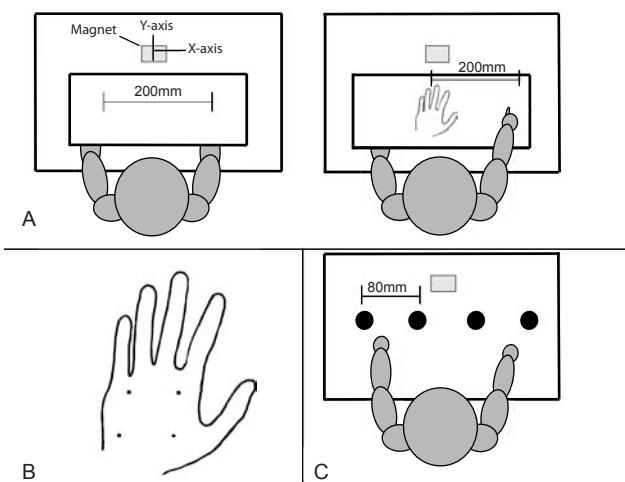


Figure 2. Experimental set up. (A): Pointing to own hand condition (left panel). Height of the wooden board was 100mm. Pointing to map condition (right panel). (B): Approximate target locations on participant's hand. (C): Visual control condition; Diameter of Visual targets was 14mm.

Procedure & Design

Four different localisation conditions were tested using a within-subject factor design; direct pointing with the unstimulated hand to the stimulated hand (Pointing-hand), direct pointing with the unstimulated hand to a map of the stimulated hand (Pointing-map), a pointing localisation task of visual targets to control for gross perception and motor problems (Visual control). Before a trial started, participants were instructed to keep the pointing hand at the starting point. Next, the experimenter stimulated (1sec) one of the four designated areas (see

Figure 2B). Each area had a unique position on the X and Y axis. In the Pointing-hand task, participants were required to point fluently towards the stimulated area immediately after the

tactile stimulation. In the Pointing-map task, participants were required to point towards the perceived location of the tactile stimulus on the map of the hand. Data collection started when the experimenter stimulated the area and finished after the participant reached the target. Each area was stimulated four times.

Finally, a pointing task with four differently coloured visual targets (Diameter = 14mm; similar spatial locations as proprioceptive targets: see Figure 2C) was used to control for gross reaching problems. A trial started when the experimenter named one of the four targets (yellow, black, blue and green) after which the participant was required to point towards the visual target. Each area was stimulated four times. Tasks (Pointing-map/- hand, Proprioceptive and Visual control) were randomized using a Latin square and target areas were randomized within each task.

To further control for proprioceptive input impairments (see Case description for clinical JPS-test) we tested whether participants were able to remember a previously held position of their underarm. We marked four different target positions on the top of the table (see Figure 2C) and positioned the arm of the blindfolded participant so that their index finger was exactly placed at the target. After 1 second the experimenter placed the arm back to the starting position. Thereafter participants were required to wait for 2 more seconds before they actively returned their arm to the previously held position. A trial finished when participants returned to the starting position. Each area was stimulated four times.

Data analyses

3D kinematic data were analyzed off-line using MATLAB programming environment (Mathworks Inc.) The data were filtered using a polynomial filter (Press, Teukolsky, Vetterling & Flannery, 1994). Movement onset was defined as the first sample after velocity exceeded 50 mm/s whereas movement offset was defined as the first sample after velocity dropped below 50 mm/s. XY-coordinates of the offset sample were subsequently used as endpoint position, therefore the endpoints were determined before a correction based on tactile feedback could have been made. Endpoint errors were calculated by comparing the endpoint position in the xy-plane of each trial to that of the target coordinates.

Second, unsigned endpoint errors were averaged per target for each task condition for both KE and JO and the control group. That way, we were able to obtain a measure of the total deviation within an axis (medial-lateral, proximal-distal), irrespective of overshooting or undershooting the target. A 2×4 analysis of variance (ANOVA) was calculated on KE's and JO's endpoint errors with factors Subject (KE and JO) and Task (Pointing-hand, Pointing-map, Proprioceptive-control, Visual-control). In case of a significant main effect of Task, repeated contrasts were calculated to test the differences between its four levels. Paired sample t-tests were used to further explore a significant interaction effect. Paired sample t-tests were also calculated on the endpoint errors of the control group to detect significant differences between the four tasks. Means (mm) and their standard error are notated in the text as e.g. (30(2.3).

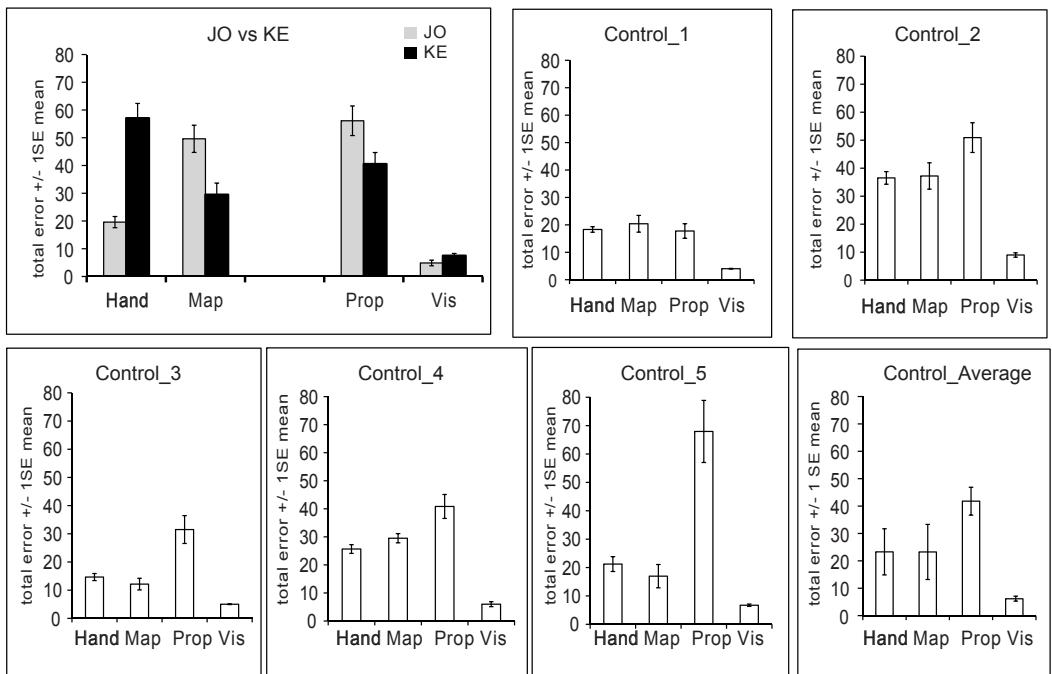
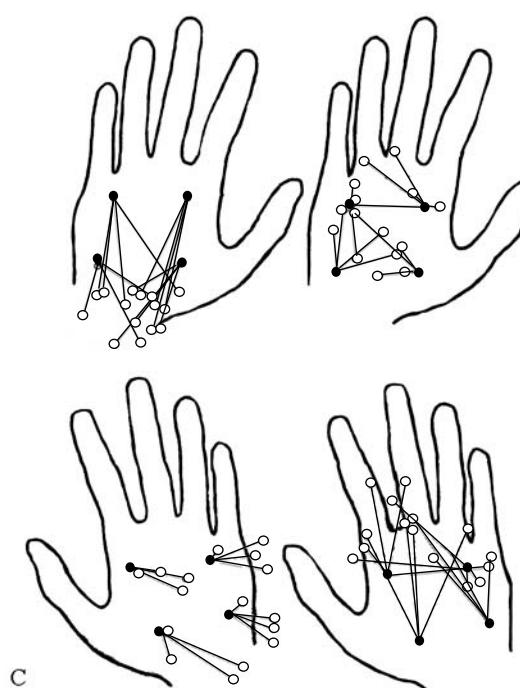


Figure 3. Average end-point positions for patients (A) and brain lesion controls (B) separately. Mean pointing error in mm: Error bars = between trial error of the means (KE & JO and separate controls) or between participants error of the means (Control_Average). Note: HA = Pointing-hand condition, MA = Pointing-map condition, PR = Proprioceptive control, VI = visual control. (C) Average end-point and target positions of KE (top panel) and JO (bottom panel) for the two tasks (Left: Pointing_hand. Right: Pointing_map. Note: these figures are schematic.

Results

Figure 3A shows the results of our patients whereas Figure B shows that of the brain lesion controls. As can be observed from Figure 3B, the controls performed rather similar on the two different tactile localization tasks, which is confirmed by non significant planned comparisons between the two tasks ($t(DF) < 1$). The performance on the visual localisation control task (6(0.84)), however, is better than performance on the Proprioceptive-control task (42(8.5) and the two tactile localisa-



tion tasks (Visual-control compared to Proprioceptive-control, $t(4) = -4.495$, $p < 0.02$; Visual control compared to Pointing-hand ($23(3.8)$), $t(4) = 5.623$, $p < 0.01$; Visual-control compared to Pointing-map ($23(4.5)$), $t(4) = 4.331$, $p < 0.02$).

KE & JO

The results of KE and JO summarised in Figure 3A show a classic double dissociation between the performance of the Pointing-hand and the Pointing-map task. The 2×4 ANOVA revealed a significant main effect for Task (Pointing-hand = 38 (3.1), Proprioceptive-control = 48(3.8), Pointing-map = 40 (3.8), Visual-control = 6 (0.6) $F(3,45) = 31.30$, $p < 0.01$). Planned repeated contrasts failed to reveal significant differences between Pointing-hand and Pointing- own ($F < 1$), but significant differences were observed between Pointing-map and Proprioceptive-control ($F(1,15) = 64.88$, $p < 0.01$) and between Proprioceptive-control and Visual-control ($F(1,15) = 147.40$, $p < 0.01$). More importantly, Subject interacted significantly with Task ($F(1,15) = 18.58$, $p < 0.01$). Paired sample t-tests (planned contrasts) revealed that the interaction is based upon opposite differences in performance between the Pointing-hand and Pointing-map task (JO Pointing-hand = 19(2.0) versus KE Pointing-hand = 57(5.3), $t(15) = -7.166$, $p < 0.01$; JO Pointing-map = 50(4.9) versus KE Pointing-map = 29(4.2); $t(15) = 3.930$, $p < 0.01$). Performance on the other two tasks however, did not significantly differ (JO Proprioceptive-control = 56(6.8) versus KE Proprioceptive-control = 41(4.1); $t(15) = 1.883$, $p = 0.79$ and JO Visual-control = 5(1.0) versus KE Visual-control = 7(0.83), $t(15) = -1.745$, $p = 0.10$).

Figure 3C shows a schematic picture of the target and pointing positions for the Pointing-hand and map conditions. Visual observation of the data might suggest that even though the performance is rather impaired, a spared relation between the target and pointing position still exists. As such, we can test the hypothesis of whether a difference exists in the relation between target and pointing position, either in lateral-medial or proximal-distal direction, in the Pointing-hand task and that in the Pointing-map task, for each patient separately. Therefore we first calculated the regressions of target and pointing position for each task and axis separately and subsequently tested the slope differences using an independent samples t-test.

On basis of the ANOVA results we would expect the task (Pointing-hand or Pointing map) with the least amount of error to have a more pronounced linear relation between target and endpoint as compared to the task (Pointing-hand or Pointing map) with a higher amount of error (irrespective of axis). Then, we compared the slope for the Pointing-hand condition to that of the Pointing-map condition for each axis separately, using dependent samples t-tests (one-tailed). On basis of the observed task differences found in the ANOVA analyses, we would expect the two regressions (calculated for each axis separately) to differ significantly. However, since we only measured four trials per position positions (four positions in total), we need to be cautious when interpreting the data.

Calculating the regression for KE for the proximal-distal axis using the data of the Pointing-hand condition, we observed that the target position explained a proportion of variance (R^2 :

R square) of 17% which was not significant ($F(1,14) < 1$; Pearson's $R = 0.34$, $p = 0.1$). On the other hand, when analysing the proximal-distal values of the Pointing-map condition, the target position explained a significant proportion of variance ($R^2 = 40\%$, $F(1,14) = 9.238$, $p < 0.01$; Pearson's $R = 0.63$, $p < 0.01$). Also, a dependent samples t-test revealed a significant difference between the slopes of the two tasks ($t(df=15) = 1.85$, $p < 0.04$). For the medial-lateral values, the target positions in the Pointing-hand condition explained a marginally significant proportion of the variance ($R^2 = 23\%$, $F(1,14) = 4.164$, $p = 0.06$; Pearson's $R = 0.48$, $p < 0.05$). Similarly, in the Pointing-map condition we observed that only a marginally significant proportion of 20% explained the variance ($R^2=20\%$, $F(1,14) = 3.503$, $p = 0.08$; Pearson's $R = 0.45$, $p < 0.05$). Moreover, the comparison of the two slopes failed to reveal a significant difference between the two ($t(14) = 0.09$, $p = 0.98$).

With respect to the performance of JO in the Pointing-hand task, the proximal-distal target positions explained a significant proportion of variance ($R^2= 87\%$, $F(1,14) = 93.7$, $p < 0.01$; Pearson's $R = 0.93$, $p < 0.01$). In contrast, analyses of these values in the Pointing-map task failed to reveal a significant proportion of variance explained ($R^2 = 0.04$, $F(1,14) < 1$; Pearson's $R = -0.062$, $p = 0.4$). Comparison of the two slopes revealed a significant difference between the two ($t(df=15) = 4.56$, $p < 0.01$). For the lateral-medial values, we observed a significant proportion of variance explained for the target positions in the Pointing-hand task ($R^2 = 73\%$, $F(1,14) = 37.14$, $p < 0.01$; Pearson's $R = 0.82$, $p < 0.01$), whereas we failed to observe a significant proportion of variance explained in the Pointing-map task ($R^2 = 14\%$, $F(1,14) = 2.200$, $p = 0.160$; Pearson's $R = 0.37$, $p = 0.08$). Again, a dependent samples t-test revealed a significant difference between the two slopes ($t(df=15) = 2.56$, $p < 0.05$).

Discussion

We examined two stroke patients on two tactile localisation tasks, one aimed to identify the location of tactile stimuli on the hand and another to identify locations of tactile stimuli on the hand on a line drawing of that hand. The results clearly show a functional double dissociation between the two tasks; KE was impaired when locating tactile stimuli on his own hand but could reasonably well localise the stimuli on a map of a hand. In contrast, JO produced smaller errors when localising stimuli on her own hand as compared to localising these stimuli on a map of a hand. Also, this pattern of results cannot be explained by more general impairments in pointing to localize movements, or by a disruption of low-level tactile or kinaesthetic input. Moreover, this is the first time such a double dissociation is reported in patients using a within-subjects design with above detection threshold tactile stimuli.

Although one must be cautious when interpreting the following results, a thorough observation of the relation between the target location and the location of the pointing response in the two tasks, suggests that in the own hand condition, patient KE is mainly impaired in the proximal-distal direction. Interestingly, there seems to be a spared relation within the lateral-medial direction, and this spared relation is also observed when pointing to a drawing of the hand.

As such the difference in performance between the two tasks is mainly explained by the error produced in the proximal-distal direction. This might imply that KE cannot use that particular aspect of the location in order to direct the pointing hand to the target hand when performing an own body directed pointing response and points to his wrist instead. On the other hand, the location of the touched position in the lateral-medial direction was relatively more preserved (as compared to the proximal-distal direction). With respect to the performance of patient JO, the results are more clear-cut. In both directions, proximal-distal and lateral-medial, the relation between target and pointing location is stronger when pointing to the own hand as compared to the drawing of the hand, further confirming the above mentioned dissociation between the two tasks.

Together, it could be suggested that the dissociations reported here are derived from selective higher-order deficits, as opposed to the dissociations between basic sensory detection and localisation as reported by Paillard et al. (1983) and Halligan et al. (1995; but see Harris (2004, 2006) for attempting to find this dissociation in healthy individuals).

In 1999, Paillard interpreted the tactile localisation differences as originating from tactile processes mediated by a body schema representation or a body image representation (see for similar idea's Gallagher, 2005). Dijkerman and De Haan (2007) elaborated further on this distinction and integrated it with the idea of separate task dependent sensory processing for perception and action (Milner and Goodale, 1995, 2008). The authors defined the body schema as a representation responsible for the programming and guidance of direct actions towards the body, whereas the body image was defined as a representation necessary for the recognition of the body as an object (e.g. size, configuration of parts). When localising a tactile stimulus on a map of the body, the location information is processed in somatotopic coordinates and subsequently translated to 2D external coordinates as provided by the map. Doing so, the somatotopic location needs to be combined with stored knowledge about the normal configuration of the hand and fingers, their relative spatial relations, as well as similar information of ones own hand. This type of static, "long lasting", knowledge is suggested to be stored in the body image representation. Recently studies using bodily illusions in healthy individuals have provided further evidence for this distinction. Although, tactile localisation has not been studied directly, evidence for different task-dependent representations has been observed for proprioceptive limb position (vibrotactile illusion, Kammers et al., 2006) and tactile size of objects (Anema et al., 2008). Considering that certain studies fail to replicate dissociations in healthy individuals that have previously been observed in neurological patients (Harris et al., 2004, 2006), these results are important as they provide further converging evidence for the idea of task dependent processing of bodily signals.

Dijkerman and de Haan (2007) not only described a functional dissociation between body representations, but also suggested differences with respect to the underlying neural processes. The body image is considered to involve a network of cortical areas including SII (integration of input from different body halves), the posterior parietal cortex (PPC) and especially the

anterior part of the intraparietal sulcus (AIP) (for metric aspects of body representation) and the insula (sense of ownership and emotional aspects). The body schema involves a somewhat different network including direct projections from the thalamus to the posterior parietal cortex, and cortical projections between SI, and the superior part of PPC either directly or via SII. Considering the clear functional dissociation observed between patients JO and KE it may be useful to consider their lesion locations in light of the above described cortical processing characteristics. Patient JO showed an impairment when pointing to a drawing of the hand which would presumably be mainly related to a body image related deficit. Unfortunately, little is known about the precise lesion location of JO. A clinical description based on an acute clinical CT scan suggests an infarction in the area of the left medial cerebral artery, which indeed could affect posterior parietal areas involved in metric aspects of body image. This would be consistent with our recent report on three patients with finger agnosia who were impaired on a similar map pointing task after (left) angular gyrus lesions (Anema et al., in press).

For KE, who showed body schema related impairments, we do have a detailed MRI scan showing a distinct right-sided thalamic lesion, affecting mainly the VPL nucleus. VPL is considered to be the main relay station of somatosensory input to the cortex and as such can be expected to affect perceptual as well as sensorimotor processing. Interestingly, the numb-sense patient JA described by Rossetti et al. (1995, 2001) also suffered a thalamic lesion affecting among others the VPL nucleus. These findings seem contradictory in that KE shows impaired pointing to his own hand with intact pointing to a line drawing, while JA was at chance when pointing to the line drawing, but above chance when pointing directly to the stimulus on his own hand. However, JA's lesion was more extensive with not just VPL, but also the posterolateral part of the thalamus being affected and extending into the thalamoparietal projections. As a result, JA suffered a complete deficit in detecting tactile stimuli, with reduced, but nevertheless residual processing for direct pointing. This residual pointing was possibly subserved by projections from the posterior thalamic complex to the posterior parietal cortex. Patient KE also showed reduced direct pointing abilities that were not at chance. Indeed the errors made by KE in the direct pointing condition (average of almost 6 cm) were better than those reported by Rossetti et al. (1995) for JA (almost 9 cm). In KE, these were accompanied by essential normal pointing performance to the line drawing, while in JA this was almost entirely lost. This is likely to be the result of differences in the extent of the thalamus lesion. As such, the main difference between JA and KE was with respect to the perceptual detection and map-localisation, resulting in an opposite pattern of performance. This raises questions about the absoluteness of the body schema-body image dichotomy, a point also discussed in a more theoretical context by others. For example de Vignemont (2007) raises the question of "how many body representations do we really have", emphasising the risk of being overly redundant when modelling body related processes. Taking a more generally accepted Bayesian approach, it is suggested that how somatosensory information is processed depends on how informative, or reliable, the current information is for the task at hand. For example in the review of Ernst and Bülthoff,

(2004) the authors argue that to perform optimally the brain must have on-line access to an estimate of sensory information and its reliability. Depending on the amount of noise in the signal, the brain uses the information from a certain channel (modality) with the highest reliability to generate an accurate response. Similarly the functional dissociations of KE and JO may be explained by different weighting of information sources. The map pointing task required the integration of current somatosensory location information with stored knowledge about own hand characteristics such as size as well as visual input from the drawn map of the hand. In contrast, the pointing hand condition relied mainly on online processing and integration of proprioceptive and tactile input of ones own hand. It could be suggested that in case of impaired processing, the integration of different types of information (tactile, visual, online and stored) seems to be disturbed while the direct own body localisation on basis of online information is still reliable enough to compute an accurate response. On the other hand, in case of impaired computation of a localisation response on basis of online somatosensory information, performance might be enhanced when other types of information are available for integration with the online somatosensory information. Therefore we consider this explanation to be compatible with the distinction between two different underlying representations for either a goal-directed action or conscious recognition as these may be based on different sources of information (see Gallagher, 2005). Nevertheless the current double dissociation supports the idea that the nature of the task at hand is also an important characteristic of processing mechanisms within the somatosensory system. Future studies will be necessary to specify such impaired functions after stroke in terms of a model specifically aimed at a combination and integration of multiple sources of sensory information in a task dependent manner.

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CHAPTER V

Differences in finger localisation performance of patients with finger agnosia

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*Anema, H.A., Kessels, R.P.C., De Haan, E.H. F., Kappelle, L.J. Leijten, F. S.,
Van Zandvoort, M.J.E., and Dijkerman H.C. (2008). Differences in finger
localisation performance in patients with finger agnosia. Neuroreport*

Abstract

Several studies have suggested parallel processing of somatosensory input when pointing to a touched location on one's own hand (body schema) and when pointing to a touched location on a map of a hand (body image). Usually these reports describe patients with impaired detection, but intact sensorimotor localisation. Here, we examined three finger agnosia patients with intact somatosensory processing. These patients performed normally when pointing towards the touched finger on their own hand but failed to indicate this finger on a drawing of a hand. The findings provide converging evidence for the dissociation between body image and body schema and, more importantly, reveal for the first time that this distinction is also present in higher-order cognitive processes selectively for the fingers.

Introduction

A long-standing division in body representations is the distinction between body image and body schema [1-3]. Although different definitions have been used, the body schema is generally considered to be a representation essential for the guidance of body movements that is not accessible to consciousness. As such, it continuously receives input about the position and the changes in the current position of the body parts. In contrast, the body image is a consciously accessible representation that is used for a perceptual experience of the body. It contains knowledge about bodily features such as size, and the normal configuration of the body parts [3,4]. In a recent model of cortical somatosensory processing [5], it has been proposed that the inferior posterior parietal cortex is mainly involved in the body-image representation, while sensorimotor guidance (body schema) relies on subcortical and superior parietal processing. These ideas are supported by a double dissociation between certain neurological patients with impaired perceptual detection, but intact sensorimotor guidance towards a tactually stimulated location (i.e. "numbsense") and vice versa [3].

Several studies have suggested that the representation of fingers may be separate from representations of the rest of the body [6-8]. This idea is supported by the occurrence of specific impairments in identifying the fingers (e.g. finger agnosia) in patients with lesions to the angular gyrus. The distinction between body image and body schema therefore provides us with a framework in which impairments in finger representations and identification, that is, finger agnosia, can be examined in more detail. We can test whether a dissociation is present between body image and body schema impairments even when impaired function is restricted to the fingers. In contrast to other studies that have investigated dissociations in body representations in patients with "numbsense" [3,9,10], basic tactile perception (e.g., pressure sensitivity and spatial acuity) in finger agnosia patients is generally intact. However, awareness of this tactile stimulus in terms of relating it to the finger that has been touched is suggested to be lost [7], which is most commonly observed for the fingers of both hands [6]. Together, this provides us with a unique opportunity to investigate dissociations in body representations on a higher-order cognitive level in patients with intact somatosensory processing.

We investigated finger gnosis in three patients with lesions affecting the angular gyrus by ask-

ing them to localise a touched finger using three different response modes. They were required to either point towards the touched finger on their own hand, on a drawn map of a hand, or by means of naming the targeted finger. We compared the results with the findings in five healthy controls. Based on previous findings [3,9,10] we expected to observe intact localisation of a stimulated finger when immediately pointing (with the other hand) towards the touched finger, which presumably involves the body schema. In contrast, localisation of the tactually stimulated finger on a line drawing of the hand is expected to be impaired, since tactile information about the targeted finger has to be transferred to an abstract hand representation based on the body image [3,4]. Also, performance is expected to be impaired for the fingers of both hands. Secondly, information about lesion site may provide further converging evidence that the body image representation is dependent on inferior parietal areas and more specific, the angular gyrus [11,12].

Methods

Participants

Patient 1: GO is a 52 years old right-handed woman who had suffered bilateral watershed infarctions in the parieto-occipital region at the boundary between the supply area of the middle cerebral artery (MCA) and the posterior cerebral artery (PCA) including the angular gyrus. No signs of additional subcortical damage were observed (see Figure 1a). As a result she presented with a transient left-sided hemiparesis and a permanent right-sided hemiparesis, but there were no signs of profound somatosensory loss. Neuropsychological assessment revealed impairments in writing, mental arithmetic and spatial orientation (left/right dissociation, mental rotation, and visual construction). No impairments in memory, executive function or language were found. As she exhibited several symptoms of Gerstmann's syndrome (acalculia, agraphia and left/right disorientation), GO was subsequently tested on finger gnosis which indeed was impaired. GO scored 8 out of 10 correct when naming fingers of a drawn hand, 6 out of 10 when her own fingers had to be named and 5 out of 10 when the fingers were to be named in response to an unseen touch. The visual fields were intact. Two years later, when the experimental data were collected, she still experienced minor residual problems in writing and calculation, although these could no longer be confirmed in formal testing. Both proprioception and tactile pressure sensitivity were intact.

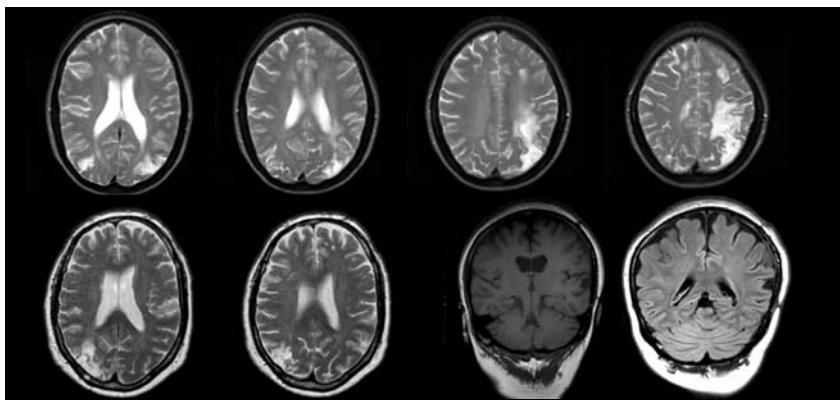


Figure 1: Scans of patient 1 [(A) MRI T2/FLAIR] patient 2 [(B) MRI T2/FLAIR] and the postoperative scan of patient 3 [(C) MRI T1]. MRI, magnetic resonance imaging.

when tested at the distal phalanx of the right index finger.

Patient 2: BU is a 59 years old man who suffered from a right occipital ischemic stroke in the supply territory of the right PCA including the angular gyrus (Figure 1b). There were some minor white-matter lesions visible on magnetic resonance imaging (MRI), but no signs of profound subcortical damage. He exhibited diminished visual capacities in the left visual field (left lower quadratopia), dysarthria and left-sided distal hemiparesis with intact coordination capacities. Both proprioception and tactile pressure sensitivity were intact when tested at the distal phalanx of the left index finger. Neuropsychological assessment revealed (mild) deficits in working memory, constructional praxis and finger gnosis. No executive or language impairments were found. BU scored 7 out of 10 correct when naming touched fingers (without vision), and 12 out of 20 when naming two simultaneously touched fingers. Experimental data were collected both 4 and 10 days post stroke.

Patient 3: MA is a 31 years old woman who underwent a chronic subdural electrode investigation and surgery for intractable left temporal-lobe epilepsy by removal of a circumscribed epileptogenic focus caused by focal cortical dysplasia. The resection consisted of a superficial cortical ablation of about 5 cm² in the left posterior superior temporal gyrus and temporal part of the angular gyrus (Figure 1C). A postoperative MRI scan did not show subcortical damage. Neurological examination was normal. Both proprioception and tactile pressure sensitivity were intact when tested at the distal phalanx of the right index finger. A short examination after the surgery did not show signs of finger agnosia (naming own fingers; 10/10 and fingers on a drawn map; 10/10 hand). Neuropsychological assessment revealed impairments in picture naming, a mild language-comprehension deficit and intact memory and executive functions. Experimental data were collected both 3 and 12 days post-surgery.

Control participants: Five healthy right-handed female participants (mean age 58.8 years; range 56-62 years) of comparable age and educational background participated in this study as controls. Written informed consents were obtained from all participants according to the declaration of Helsinki and the study was approved by the medical ethics committee.

Procedure

Participants were seated at a table on which the forearms and hands (palm down) rested during testing. Tactile stimuli were applied by the experimenter for 1.5 seconds using Semmes-Weinstein monofilaments (North Coast Medical Inc.; no. 5.18/ 10g target force). The participants' hands were placed underneath a wooden board to prevent them from relying on visual feedback.

First, body schema representation was assessed by asking the participants to point towards the touched finger itself (further referred to as "Pointing-own"). After tactile stimulation of the finger, participants were required to immediately point with the non-stimulated hand towards the stimulated finger and to subsequently return to the starting position. All ten fingers were examined four times each in a random order, resulting in a total of 8 trials per finger.

Second, the body-image representation was investigated using identical tactile stimuli. However,

pointing movements were now aimed at a drawing of a hand mounted on top of the wooden board. Both hands were represented on this drawing (further referred to as "Pointing-map") and consisted of a simple scaled line drawing from a dorsal perspective including details such as nails and skin creases, but without objects, such as a watch or a ring. The number of trials was identical to that of the body schema task.

To obtain a classic measure of finger agnosia, finger localisation was also tested by asking the participants to name the touched finger (further referred to as "Verbal"). The procedure of this task was similar to the one described above. Finally, to prevent the occurrence of order effects, the presentation of the three tasks was randomised across participants using a Latin Square. In a follow-up test session the three finger tasks were retested to confirm the observed results from the first test episode (GO: after two months, BU: after six days, MA: after eight days). The number of days between the first and second test was determined by logistics and was not part of the manipulation. To control for gross localisation problems of body parts in general, we examined the localization performance of other body parts separately in the first test episode. In this task patients were required to locate their own body parts (left and right knee, shoulder and ear) on verbal command under full vision. All side by body part conditions were tested twice, resulting in a total of 12 trials.

Data Analyses

For each task percentages correct were calculated both for the patients and the control participants. The chance of randomly guessing a certain finger is 1 out of 5 (20%), when hand identification (left or right) is not impaired. Therefore, percentages were corrected by subtracting chance level from the percentages correct (resulting in a maximum percentage of 80). Next, performance of the patients was compared to that of the control subjects using Crawford and Garthwaite's test for the abnormality of test scores since ceiling effects were expected to be present in healthy controls [13]. In case of a perfect performance of the controls ($SD=0$) abnormality cut-off scores would be defined as "less than 99% accuracy (79% when corrected for chance levels)". Also, to test for performance differences between left- and right-hand fingers, we performed a standard nonparametric test for frequencies of two related samples (McNemar test) for each task with the percentage correct as dependent variable.

Results

Figure 2a shows the corrected percentages correct for each task and participant. The healthy controls showed near-perfect performance on the finger gnosis tasks (Pointing-own: mean = 80.0 ($SD = 0.0$); Pointing-map: mean = 79.0 ($SD = 2.2$); Verbal: mean = 80.0 ($SD = 0.0$)).

Visual inspection of the finger-gnosis data revealed that all patients showed a similar pattern of results (see Figure 2A), that is, near-normal performance on the Pointing-own task in combination with impaired performance on the Pointing-map and Verbal task. The Crawford and Garthwaite test indeed confirmed the impaired performance on the Pointing-map task for all three patients (significantly different from control group; all $p < 0.001$). However, overall

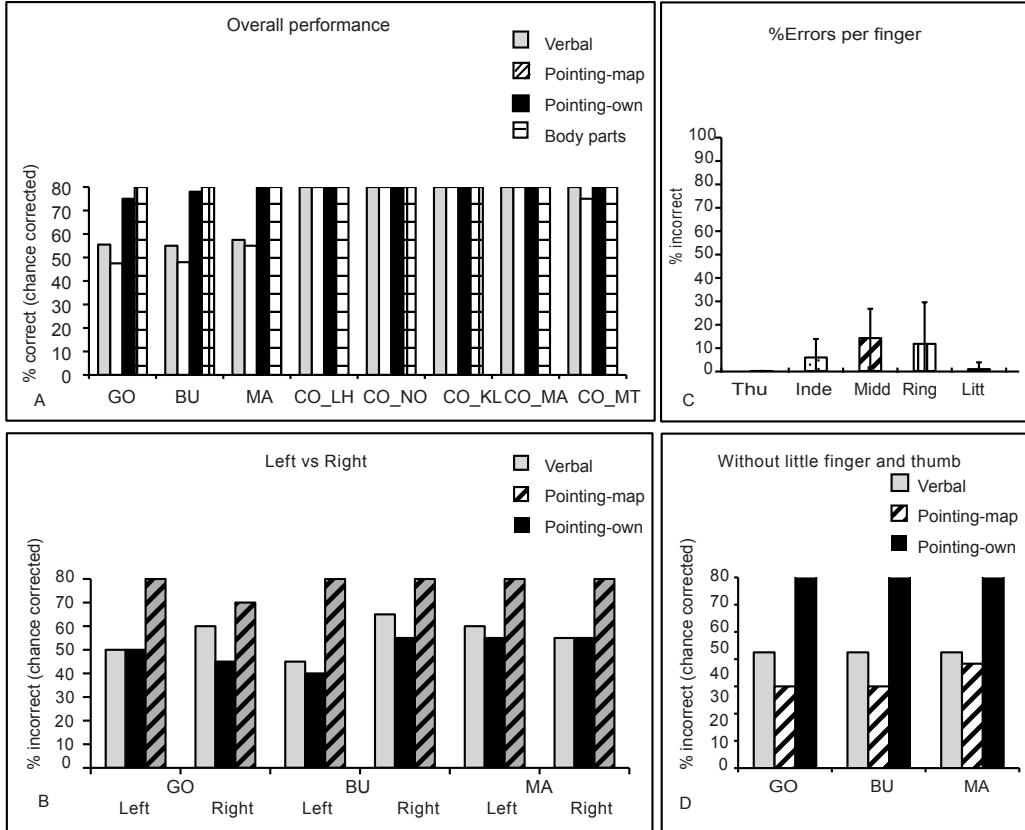


Figure 2: (A) Accuracy results (% correct - 20% chance level) of the patients and the age-matched control participants on the Pointing-own (TACTOWN), Pointing-map (TACTMAP) and Verbal (TACTVERB) tasks.

(B) Performance for left and right hand fingers for each task and patient separately (% correct - 20% chance level) (C) Distribution of errors over the different fingers, across hands, tasks and patients. The error bars represent +/- 1 standard error of the mean. (D) Performance for each patient per task calculated on basis of ring, middle and index finger only (% correct - 20% chance level).

performance of the three finger agnosia patients was well above chance level, as is indicated by the 0% correct level. This clearly shows that at least some information about finger identity is preserved. The pattern of performance is similar for right- and left-hand fingers. Indeed, no significant differences were observed between left and right hand performance as was revealed by the McNemar tests (all $p > 0.2$; see Figure 2B).

The distribution of incorrect responses (Fig. 2c) showed that across tasks and patients, most errors were related to the middle three fingers, whereas the thumb and little finger were identified almost perfectly. Figure 2D shows the performance of each patient when ignoring the thumb and little finger. Performance in the Pointing-map and Verbal tasks is reduced compared to when all fingers were included, but still above chance level, which is indicated by the 0% level.

Finally, all patients showed a perfect performance on the Body Parts localisation task indicating

that the localization of other body parts is intact (GO: 12/12, BU: 12/12, MA 12/12). Normative scores of this task have been determined previously in a separate age-matched healthy control group ($n = 20$) and revealed a perfect score of 12 out of 12 in all participants.

Observation of the data of the second test episode revealed a consistent pattern, with normal performance on the Pointing-own task and impaired performance on the two body image tasks (GO: Verbal = 38%, Pointing-map = 48%, Pointing-own = 70%; BU: Verbal = 65%, Pointing-map = 63%, Pointing-own = 80%; MA: Verbal = 65%, Pointing-map = 60%, Pointing-own = 80%). In addition, an overall higher accuracy was observed for all patients in the second test episode (GO +2%; BU +9%; MA +4%). Paired samples t-tests comparing the first and second episode revealed that only the difference observed in BU reached statistical significance ($t(40) = 2.56$, $p < 0.05$).

Discussion

We examined different types of finger representations in three patients with lesions in the angular gyrus who were suspected of having finger agnosia. The results clearly showed a similar pattern in all three patients, despite differences in aetiology and lesion side. All patients exhibited impaired performance on the task that was hypothesized to activate the body image, that is, a perceptual or semantic representation of the fingers. This deficit was found in naming a touched finger or pointing towards this finger on a schematic drawing, and was not due to language problems or motor deficits. In contrast, the patients performed normally when asked to point directly to the touched finger without the aid of visual feedback. This latter task condition is considered to involve the body schema, a sensorimotor representation of the fingers that is not consciously accessible and is used for guiding motor action.

Together, the current findings demonstrate a dissociation between perceptual and sensorimotor responses which is in line with previously reported studies on body representations [3,9]. These previous studies however, have investigated "numbsense" patients who have intact localisation abilities in the absence of conscious touch perception, but who performed at chance level when pointing towards the touched location on a map of the body. Extending these findings, we tested patients who were entirely aware of the tactile stimulations on the fingers, but most remarkably remained unable to localize the tactile stimulation on a drawing of a hand. Thus, this is the first time that such a dissociation is reported in patients with specific higher-order impairments leading to impaired identification of the fingers. Furthermore, the intact performance when localizing tactile stimuli on other body parts suggests that the impairment is indeed restricted to the fingers, confirming the notion of a separate finger representation [6,8].

We suggest that the specific location of the target finger in terms of its relative position within the other fingers, is lost in our patients. This caused the impairments in localizing touched fingers on a drawing of the hand. In order to associate tactile information about the target finger with the appropriate finger name, one must be aware of the specific location of the finger amongst the other fingers, hence the impaired performance on the Verbal task. In contrast, the intact localization abilities when pointing to tactile stimuli on one's own hand indicates that spatial information about the relative position of the finger that had been touched is not crucial

for programming a motor response targeted at the touched skin. This action is computed on the basis of the skin location, which can be classified as direct sensorimotor coupling and occurs without elaborate cognitive processing.

Finger agnosia is often reported after lesions of the angular as well as the supramarginal gyrus e.g. [11,12]. Neuroimaging data of our patients confirmed involvement of these regions. In line with the observed lesion data, Dijkerman and de Haan [5] have suggested that with respect to immediate guidance of action (pointing to self), somatosensory information is processed both by subcortical and cortical routes from the somatosensory cortex to the superior parietal lobule. In contrast, conscious perception and memory, which are required when pointing towards a touched location on a map of the hand, are mainly subserved by cortical routes to the posterior insula and posterior parietal cortex. The authors assigned the inferior parietal lobule, which includes the angular gyrus, to be involved in conscious perception and memory with respect to metric aspects of the body and its parts.

Finally, some aspects about this study require discussion. First, finger agnosia impairments are heterogeneous and finger identification involves many complex higher-order functions which each can be impaired, such as executive functioning, spatial awareness language or memory. The current findings are unlikely to be caused by impairments in these cognitive domains, since none of our patients presented with profound impairments in executive functioning, spatial awareness or memory. A second issue is the location of the lesion. The aetiologies (stroke) in two of the three patients were such that the lesion was unlikely to be restricted to only one cortical area. In the third patient however, the lesion was made surgically and was mainly restricted to the cortex of the angular gyrus. Nevertheless, we were able to identify unique overlay of the lesions in this brain region. Finally, it must be noted that even in the absence of severe finger-gnosis deficits in a short clinical examination (MA), impaired finger identification performance can be demonstrated when tested more extensively.

Overall, the current study further confirms the hypothesized dissociation between body image and body schema representations and most importantly suggest that such a dissociation applies even at the higher-order level of the fingers.

CHAPTER VI

Integration of tactile input across fingers in a patient with finger agnosia

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Abstract

Finger agnosia has been described as an inability to explicitly individuate between the fingers. Haptically exploring objects usually involves several fingers and to provide the parts for the construction of a stable object percept, the input from these different fingers needs to be integrated. This implies that some distinction between the fingers has to be maintained. It has been suggested that finger agnosia is caused by fused neural representations of the fingers, possibly indicating that the fingers cannot be kept separate. Nevertheless, finger agnosic patients have not been reported to suffer from impaired haptic object recognition. Therefore, the suggested fusion must occur at a different processing level. The apparent contradiction between intact haptic object recognition in patients with finger agnosia and the inability to differentiate between and identify different fingers has yet received little attention. We report data from a patient with finger gnosia (GO), who was tested on two tasks that measured the ability to integrate somatosensory information perceived by the individual fingers level. Our results show that GO's ability to use information about the relative positions of the fingers to interpret tactile information at the fingertips was comparable to that of age-matched controls, despite her difficulties in explicitly identifying the fingers. We discuss these results in the context of forming a better understanding of finger agnosia and possible effects of stored knowledge about common body part configuration on haptic object recognition processes.

Introduction

Our hands and fingers are powerful tools when interacting with the external world. Explorative finger movements allow us to collect haptic information and integrate it into a percept of the explored object. Most of the time we have additional visual information about what we are exploring, however, when for example searching for a pen or keys in a hand bag we are almost entirely dependent on our haptic abilities. Both touch and proprioception, provided by the finger movements, are important for haptic object recognition; accurately executing the required finger movements determines whether the appropriate tactile information is gathered (Lederman & Klatzky, 1987; see for review Klatzky & Lederman, 1993). Generally, exploring objects by touch alone involves several fingers. Before object recognition can occur, somatosensory information from these different fingers needs to be integrated to perceive object properties such as edges or corners. This implies that some distinction between the fingers has to be maintained, especially at the early stages of haptic object recognition. When these elements are put together, conscious recognition of the object can occur. However, the process of combining information from the finger, of which it is suggested that fingers must be kept separated, can be regarded as implicit as it occurs without awareness.

Finger agnosia, a condition in which patients are unable to explicitly distinguish between their fingers (e.g. Benton 1961; Ettlinger, 1963) is suggested to be caused by the inability to maintain distinct neural representations of their fingers (Kinsbourne & Warrington, 1962; (Haggard &

Wolpert, 2004). Moreover, these patients who generally have lesions in the angular gyrus (e.g. Roux, Boetto, Sacko, Chollet, & Tremoulet, 2003; Mayer et al., 1999), present with difficulties in the identification of their own fingers or fingers in general. As was noted by Kinsbourne and Warrington, these patients have difficulties to couple a tactile stimulus to the finger which receives the tactile stimulus. Interestingly, these patients do not automatically suffer from impaired haptic object recognition as, to our knowledge, no study has reported (or even investigated) impairments in haptic object recognition (see for example: Ettlinger, 1963; Roux et al., 2003; Carota, Di Pietro, Ptak, Poglia and Schnider, 2004; Mayer, et al., 1999; Poeck and Orgass, 1969; Kinsbourne & Warrington 1962). This intuitively suggests that the fingers are not "fused" at the level of implicitly integrating tactile information over the fingers. On the other hand, it could be suggested that an impairment in this specific function will not entirely disrupt tactile object recognition as many other factors contribute to the perceptual reconstruction of a haptically explored object (e.g. weight perception, holding the object, material characteristics perceived by the skin of the hand palm). However, it remains to be clearly demonstrated whether finger agnosia patients perform normally when tested on their ability to integrate somatosensory information over several fingers.

As mentioned above, both touch and proprioception are important for haptic object recognition. A study by some of the current authors (Overvliet, Mayer, Smeets, & Brenner, 2008), targeting the search strategies of simple tactile features such as line segments, provides an example of how proprioceptive input can affect the speed of tactile processing. In this task, the proprioceptive input, informative of the position of the finger, was manipulated using two different finger configurations, either fingers stretched and placed on several tangible line segments (line segments condition) or fingers bent rather awkwardly in order to be aligned on one tangible continues line (continuous line condition). The effect on tactile processing was measured using a speeded haptic search task. The participants were required to lift the finger that did not feel a part of a line. The results showed that healthy participants have faster response times in the continuous line condition, as compared to the line segments condition. It was concluded that the alignment of the fingers in the continuous line condition allowed the participants to integrate the input perceived over the fingers into one object, which led to faster detection of the target. This effect can only be achieved if information about the relative positions of the fingers, provided by the proprioceptive signal, is combined with the tactile information about the stimulus and is integrated into one percept.

Another task in which integration of tactile and proprioceptive input across fingers is required was first described by Benedetti (1985, 1988). In the these studies the author asked participants to judge the spatial position of a tactile stimulus (a small ball) perceived by the tip of the index finger relative to the spatial position of another tactile stimulus (a sharp pin) perceived by the ring finger. The finger positions and the tactile stimuli applied to the fingers were varied with respect to each other (crossed or uncrossed). This task therefore requires spatial judgements that depend upon a coupling of a particular tactile stimulus (ball or pin) to a specific finger,

and subsequently on the integration of proprioceptive input about the finger position with the tactile input. Benedetti observed that participants were able to judge the relative spatial positions of their fingers. Participants were also able to judge the relative positions of the tactile stimuli, except in a fingers crossed position, where the stimuli were always perceived as if the fingers were uncrossed. It was concluded that integration of tactile and proprioceptive input is accurate when the fingers are uncrossed, but beyond the functional range of the fingers, position sense is not sufficient for localizing tactile stimuli correctly in space. An important difference with the above-described study by Overvliet et al., (2008) is that the task reported on by Benedetti, includes two, instead of six stimuli. As the task requires a relative spatial judgment of two tactile stimuli that are simultaneously presented to two neighbouring fingers one needs to scale the position of one to the position of the other. Therefore it is important to accurately combine the perceived tactile stimulus with the finger which receives the stimulus in order to perform the task.

Together, both studies provide insight in how tactile information processed by the fingers can be mediated by the proprioceptive information about the relative positions of the fingers. Most studies set up to investigate finger agnosia target the explicit processing of stimuli in relation to the finger which perceives the stimulus, whereas the processes in support of haptic object recognition such as the integration of information over fingers, are implicit and do not necessarily involve awareness. In order to explore whether finger agnosia patients perform as healthy controls when implicitly integrating somatosensory information over fingers, we tested a finger agnosia patient (GO) who failed to explicitly indicate and name touched fingers. GO was tested on both the above-mentioned implicit tasks reported by Overvliet et al (2008) and Benedetti (1985, 1988). The haptic search experiment consisted of simple line segments which are a good example of features that normally provide the building blocks for more complex objects. As such this task allowed us to investigate the early stages of haptic processing, necessary for object recognition. If we observe that GO, like healthy controls, benefits from the position where fingers are bent and aligned and placed on a continuous line, than GO is most likely able to integrate the perceived information over the fingers. The Benedetti experiment provides for an additional investigation of the ability to keep separate the tactile information perceived by the fingers but here we used a response of which it is assumed that it requires more elaborate processing of the spatial position of the perceived information. Again, if GO's performance falls within normal ranges, than we can suggest that any fusing of neural representations of the fingers happens at a processing stage at least further as compared to the early stages of the integration of input over fingers.

Case Description

GO is a 52 year old right-handed woman who had suffered a left hemisphere watershed infarction in the parieto-occipital region including the angular gyrus (see Figure 1A). Shortly after the stroke she exhibited a mild right-sided hemiparesis and complained about her concentra-

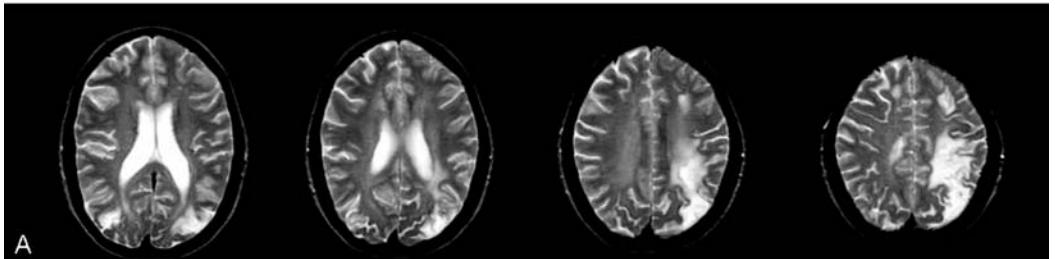
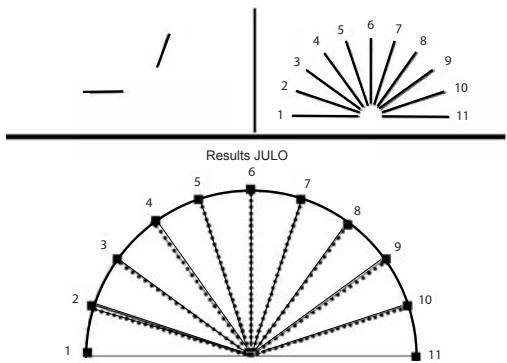


Figure 1 (A): A T2/ FLAIR scan of the finger agnosia patient GO; It shows a lesion in the left parieto-occipital cortex, including the angular gyrus.

(B) Visual Judgement of Line Orientation test (JUL0); corresponding line segments. The lines segments in the left upper panel have to be matched to one of 11 possibilities in the right upper panel (3 trials per position)
Note: GO completed a short version of the task.



tion and memory capacity. Furthermore, right hemispheric damage was observed on the boundaries between the supply area of the cerebral medial artery (CMA) and the cerebral posterior artery (CPA) resulting in a minor left distal hemiparesis, which was dissolved on admission. A neuropsychological examination four weeks after admission revealed impairments in writing, mental arithmetic and spatial orientation (left/right dissociation, mental rotation, and visual perception/construction). As she exhibited several symptoms of Gerstmann's syndrome (acalculia, agraphia and left/right disorientation; Gerstmann, 1930), GO was subsequently tested on finger gnosis which indeed was impaired. GO scored 8 out of 10 when naming fingers of a drawn hand, 6 out of 10 when her own fingers had to be named and 5 out of 10 when the fingers were to be named in response to an unseen touch. In contrast, localizing and naming other body parts such as shoulder, knee, hip, etc. was unimpaired (10/10). No memory or language impairments were found. About twenty months later when the experimental data were collected, she still reported minor residual complaints regarding these cognitive functions such as agraphia and acalculia, although these could no longer be confirmed on formal testing. However, she still exhibited finger localization difficulties both when localizing her own fingers (6/10) as well as indicating fingers on the map of a hand (4/10). Overall, the errors GO made were mainly in response to the middle fingers. In only two out of a total of 60 trials (all tasks and test episodes) GO erroneously indicated her thumb.

To re-assess her visual perception performance we tested GO on the Judgement of Line Orientation (JULO). In this task GO was required to visually judge the orientation of a line, and respond by selecting a line with an identical orientation as the target line, out of 10 possible outcomes (see Figure 1B).

Although GO in total made more errors than was expected on the basis of her age, gender and education (10/15), rendering her performance significantly differed as compared to matched healthy controls, she never selected a line further than 1 response option away from the target (see Figure 1B). As such, GO was still able to process visuospatial information as she was able to judge the spatial relation. At that time sensibility measures could be obtained and pressure sensitivity measures (with Von Frey hair applications) appeared to be different between the left (0.02g target force) and right hand (0.04g) although within the normal range (mean = 0.04g SD = 0.12g). Furthermore, proprioception as measured by a clinical joint position sense test for the upper phalanx of the thumb appeared to be intact (24/24).

Methods

Participants

GO's performance was compared to that of 5 age matched right handed controls (mean age = 59; SD = 1.8) without history of psychiatric or neurological illness. Participants received a small payment for their participation and written informed consent was obtained before the start of the study. This study was approved by the Utrecht ethical medical board and has been conducted in according with the declaration of Helsinki.

Experiment I

The first experiment consisted of the experiment reported earlier by Overvliet et al. (2008) which was described in the introduction. By testing GO with this haptic search experiment we investigated her ability to process simple features perceived by the fingers, and to subsequently integrate them.

Experimental set up

The experimental set up was similar to that of Overvliet et al (2008; see introduction). The participants were seated at a table and a screen with a curtain was placed between the apparatus and the participants in order to prevent visual input of the stimuli. The three middle fingers of both hands were positioned on the apparatus which consisted of six force sensors, designed to have pieces of ZY®-TEX2 Swell paper (Zychem Ltd., Cheshire, England) attached to them. The stimulus items were horizontal lines with a line width of 1.4 mm, which protruded about 1 mm from the surface of the swell paper. Each separate sensor could be accurately positioned to fit the hand size and stimulus positions. The sensor measured whether the finger was in contact with the stimulus. The fingers were always separated in order to prevent them from touching the neighbouring fingers, which could give additional information, as well as to prevent them

from touching a neighbouring sensor. The apparatus and both experimental conditions (see below) are shown in Figure 2A and B.

Procedure

Two different search conditions were measured. In the first condition, the stimulus consisted of separate 2 cm line segments that were positioned under the participants' finger pads (index, middle and ring finger of both hands). In this condition, the hands were in a comfortable (natural), though stretched position (Figure 2A). The target stimulus was a piece of swell paper without a line segment. In the second condition a continuous 14.5 cm line was used instead of line segments. A 2 cm gap in this line served as the target. Participants then had to adjust their finger positions to the line (Fig. 2B).

Each condition was tested in a separate block consisting of 40 trials. In 25% of the trials the stimulus did not contain a target. Both blocks were repeated twice and presented in an ABBA design. Before each trial, the participant was asked specifically to position the fingertips on the sensor to prevent her from misplacing the fingers and consequently missing the target. When the fingers were in the correct position, participants lifted the fingers and maintained that position, while the experimenter placed the next stimulus on the sensors. The experimenter started each trial by presenting a 4500 Hz tone. As soon as participants heard the tone they had to lower the fingers onto the stimulus. Moving the fingertips over the line stimuli was allowed as long as the fingers remained on the sensors. Participants were instructed to lift the finger under which the target (no line) was positioned as soon as it was detected. Anema, Kessels and Dijkerman (2006) previously showed that a fingeragnosia patient had preserved direct sensorimotor coupling even at the level of the fingers. In an attempt to find the underlying mechanism of fingeragnosia, Ettlinger (1963) already revealed that most finger agnosia patients were able to lift their finger in response to tactile

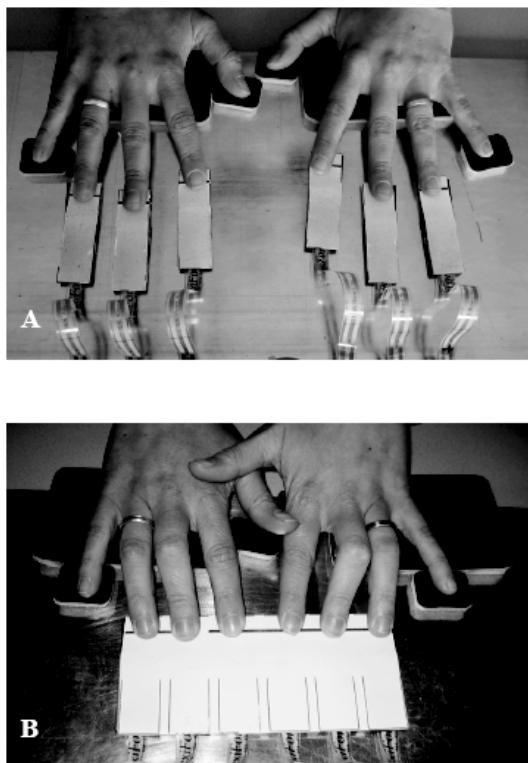


Figure 2: The setup of experiment I. In the upper panel (A) a subject is performing the haptic search task with line segments (the target (no line) is below the middle finger of the left hand) and in the lower panel(B) a subject is performing the haptic search task in the continuous line condition (the target is below the middle finger of the right hand).

stimulation. For trials in which the target was absent (all fingers were presented with a line), participants were instructed to lift all the fingers as soon as they detected the absence of the target. This procedure (and the analysis presented below) was successfully applied in an earlier study by some of the current authors (Overvliet et al., 2008)

Design and Data Analyses

On both target present and absent trials, the reaction time was defined as the time from when the first finger contacted the sensor until a finger was lifted. Trials were excluded on the basis of three different parameters. First, trials with reaction times shorter than 100 ms were discarded as such a fast response was considered physiologically implausible. Second, trials with reaction times longer than 2 SD above the mean of the participant in question (either control or GO) were excluded as they were considered outliers. Third, trials in which participants lifted the wrong finger were also excluded from analyses. Next, for each condition (separate line segments, continuous line) the median search time was computed for the remaining trials. To increase the power of our experiment, we added the control data ($N=10$) from the Overvliet et al., (2008) study to the data of the age matched controls ($N=5$), following the procedure of Bukach, Bub, Gauthier, & Tarr, (2006; experiment 4). Thus data analysis for the healthy control subjects involved a 2 (target condition: target absent, present) \times 2 (line condition: continuous line, separate line segments) \times 2 (group: student controls, age matched controls) design with both target condition and line condition as within subject factors and group as between subjects factor. Only significant effects are reported.

To test whether GO exhibited a similar benefit of the continuous line condition as compared to the line segments in detecting a target, or detecting the absence of a target, we tested the results in these conditions against that of age matched healthy controls using Crawford and Garthwaite's test for abnormality scores in single case studies (Crawford & Garthwaite, 2002). In the target present condition only the left hand trials were analysed, to rule out the influence of basic tactile sensitivity differences between GO's left and right hand (see Case Description).

Results

Data of the controls and GO are plotted in Figure 3. The ANOVA on the healthy control subject reaction times showed a significant main effect of Target condition ($F(1,13) = 12.83$, $p < 0.01$) as reaction times were faster in the Target present condition (2011 ms) as compared to the Target absent condition (2694 ms). Also, a main effect of Line condition was observed ($F(1,13) = 9.533$, $p < 0.01$) indicating that search time decreased when fingers were positioned on one continuous line (2168 ms) as compared to the positioning on line segments (2537 ms). Furthermore this effect did not differ between groups ($F(1,13) < 1$). However, the age matched control group was overall slower as compared to the younger control subjects (age matched = 3469 ms/ young controls = 1235 ms; ($F(1,13) = 78.29$, $p < 0.01$)). To rule out possible effects of age, GO's performance was therefore directly compared to that of the age matched controls only.

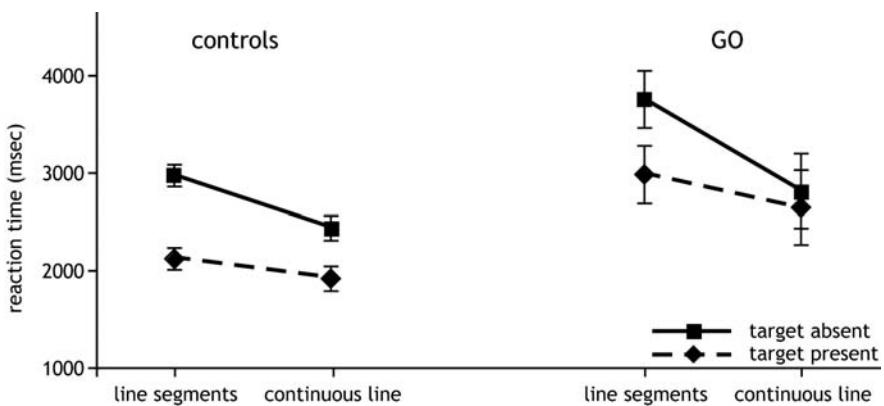


Figure 3: Results of experiment I for the healthy control subjects and GO. The mean and standard errors for the two different conditions for target present (diamond symbol and dotted line) and for target absent (square symbols and solid line).

Most importantly, GO's search time (RT) exhibited a similar response pattern to the control group. Comparing GO's performance in the line segment and the continuous line condition with the age-matched control group did not show any significant differences in reaction time behaviour (line segments: GO vs control: $t(14) < 1$ continuous line: GO vs control: $t(14) = 1.169$). Indeed, when further exploring GO's facilitation effect by testing the line segment condition against the continuous line condition (pooled over target conditions) by means of an independent samples t-test, a trend was found toward significance ($t(55) = 1.45$, $p = 0.076$).

With respect to performance accuracy, GO showed a larger proportion of errors (25%) as compared to the control group of which the performance was close to perfect. GO had on average 75% correct (for line segments: 78% correct, 14% false positives, no false negatives, and 8% wrong finger; and for the continuous line: 71% correct, 11% false positives, 4% false negatives and 14% wrong finger). The percentage of errors is considerably higher than in healthy controls (13.5% and 14.5%, respectively). Errors were always at either the middle or the ring finger of the right hand. False positives may have been caused by reduced tactile sensitivity of GO on the right hand. Chi-square calculations on the proportion of false positives revealed that these values did not differ significantly between the line segments (22%) and the continuous line condition (39%; $\chi^2 < 3.84$). Similar results were found for the proportion "wrong finger" (line segments = 35% and continuous line = 48%; $\chi^2 < 3.84$).

Experiment II

The second experiment was similar to the experiment reported earlier by Benedetti et al. (1985, 1988) which was described in the introduction. By testing GO with this relative spatial judgement experiment we investigated her ability to keep separate and compare the position of the tactile information perceived over two adjacent fingers.

Experimental set up

Participants were seated at a table opposite the experimenter (see Figure 4A). During testing either the left or right hand was positioned on top of the table with the palm of the hand downward. To prevent participants from relying on visual feedback, a wooden board was positioned over the participant's hand. The other hand was on top of the board to perform the responses. To enable the fingers to be crossed and manipulated in various orientations we used a similar device as was used in the Benedetti studies (Benedetti, 1985, 1988; see Figure 4B). The index finger was inserted in a tube and the middle finger was rotated around the index finger. The position of the middle finger was obtained by the experimenter moving this finger and confirmed with a calibrated clinical goniometer or protractor (Medizintechnik KaWe) and subsequently recorded. As a result, the exact position of the middle finger varied somewhat around the intended target orientations used in the experiment (0° , 45° , 90° and 135°). In tactile trials stimuli consisted of two simultaneously applied simple tactile stimulations, a small 0.5 mm diameter pin, and a 5 mm diameter blunt pin, further referred to as "ball". The perceived position of either the finger relative to the reference finger, or the tactile stimulus ("ball") relative to the pin was indicated on a calibrated disk (see Figure 4B).

The disk itself was positioned on top of the wooden board and this board covered the stimulated fingers. The rotating bar which was positioned on the calibrated disk could be aligned by means of turning the bar so that the target point correlated with the perceived target position. 2 symbols were drawn on this bar indicating the reference stimulus (index finger or 0.5 mm small pin) and the target stimulus (middle finger or 5 mm blunt pin ("ball")). The experimenter recorded set angle of the bars horizontal being considered to be 0° .

Design and Procedure

A 2 (Task: Perceived relative position of ball, Perceived relative position of finger) x 4 (Position: 0° , 45° , 90° and 135°) repeated measures design was used in this experiment. Each Position x Task condition was presented 4 times, except the 135° condi-

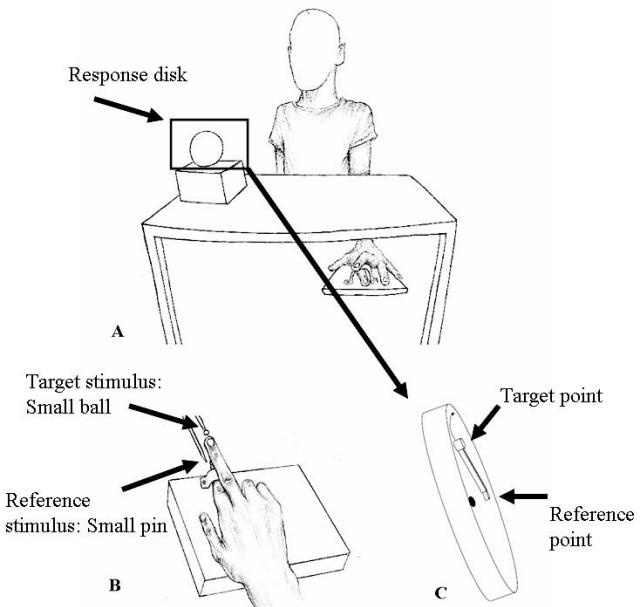


Figure 4 (A): A schematic drawing of the setup of experiment II. (B) A close up of the hand in experiment II. The middle finger is stimulated by the "ball" and the index finger by a pin simultaneously. (C) The response disc. Note: the bar could be rotated either to the left or right.

tion that was tested 8 times. Together this resulted in 40 trials in total. All orientation x task combinations were presented in a random order.

A trial started when the experimenter placed the middle finger in one of four possible target positions (0° , 45° , 90° and 135°). The exact final target position of the middle finger was verified by the experimenter using a goniometer (protractor). Next, in a finger trial the experimenter asked the participant to judge the orientation of the middle finger with respect to the reference (index finger). In the ball trials, two simultaneous tactile stimulations (5mm blunt pin and 0.05 mm sharp pin) were presented for 1500 ms and participants were required to judge the position of the ball with respect to the pin. In both cases the responses were made by rotating a bar on a disk (see Figure 4A). In order to prevent participants from using other reference information, only the 0° position was indicated on the disc. After the response was recorded by the experimenter, the middle finger was returned to the start position about -4° and the response bar was preset to about 0° . Finger trials and ball trials were randomly interleaved. Prior to testing, participants practiced the task without the stimuli being applied to the fingers, in order to ascertain correct handling of the response device.

Data analyses

A 2×4 (task: Perceived relative position of ball, Perceived relative position of finger; Position: 0° , 45° , 90° and 135°) repeated measures design was used. Deviations from the target position were calculated by subtracting the target position for each trial (in angular degrees) from the orientation provided by the participant. A 2×4 (task x position) repeated measures ANOVA was performed on the averages for each task x position combination.

Crawford and Garthwaite's test for abnormality scores in single case studies (Crawford & Garthwaite, 2002) was used in order to test GO's performance against that of healthy controls. Testing each condition per task accumulates to 8 t-tests in total. When means are noted in the text, standard errors are also given (mean (\pm SEM)).

Results

Age matched controls

The averaged responses for the different position conditions (0° , 45° , 90° and 135°) for both GO and the controls are plotted in Figure 5. Visual inspection of the data suggests that in a fingers crossed position (135°) healthy controls judge the ball to be at an uncrossed position ($76^\circ(2)$) whereas they judge the fingers correctly as being crossed ($121^\circ(6)$). The analysis of variance (ANOVA) of the deviations revealed a significant main effect of task ($F(1,4) = 12.60$, $p < 0.05$) and of Position ($F(1,4) = 27.69$, $p < 0.05$) as well as a significant Task x Position interaction effect ($F(3,12) = 10.53$, $p < 0.05$). The significant interaction was further explored using one sample t-tests (test value 0) on the difference between ball and finger judgments for each condition. In the 135° condition there was a significant difference between the ball and finger judgments (mean difference = -45° (5) $t = -9.391$, $p < 0.0125$), whereas this was not so for the other posi-

tions (0° position = 11° (9); 45° position = 2° (8); 90° position = -8° (5)).

GO

Visual inspection of the data (see Figure 5) reveals that most aspects of GO's performance on the finger judgement task are within normal ranges. Indeed, for the 45° and 90° conditions we failed to observe significant differences between performance of GO and that of the healthy controls (45° : GO finger = -2.3° (± 14) versus control finger = 9.6° (± 5) $p = 0.432$; 90° : GO finger = -8.75° (± 10) versus control finger = -11.6° (± 10), $p = 0.913$. However, when judging the relative position of the finger when the fingers were in a horizontal position, GO's performance deviated from that of the healthy controls (GO = 62° (± 8), control = 16° (± 4); $t(4)$

= 4.516 , $p < 0.05$). Furthermore, with respect to her performance in the ball judgment task, again visual observation of the data suggests that she is able to perform the task, except for the horizontal position. Comparison of her performance in this horizontal position to that of the healthy controls however, failed to confirm a significant difference (GO = 57° (± 3), control = 26° (± 6); $t(4)$ = 1.982 , $p = 0.118$). Also, her performance in the 45° and 90° conditions were similar as compared to the healthy control participants (45° : GO = 25° (± 15) versus control ball = 12° (± 4); $t(4)$ = 1.359 $p = 0.246$; 90° : GO = -6.8° (± 8) versus control ball = -20° (± 10); $t(4)$ = 0.916 , $p = 0.411$. Most strikingly, her performance in the 135° condition appears to be even better as compared to the healthy controls. That is, the healthy control subjects judged the ball to be at a 76° position instead of 135° (error of $-59(2)$), whereas GO was able to perform more accurately in this condition. Her lower amount of error was further confirmed by a significant difference between her performance and that of the healthy controls (-11° (± 10)); ($t(4)$ = 11.393 , $p < 0.001$).

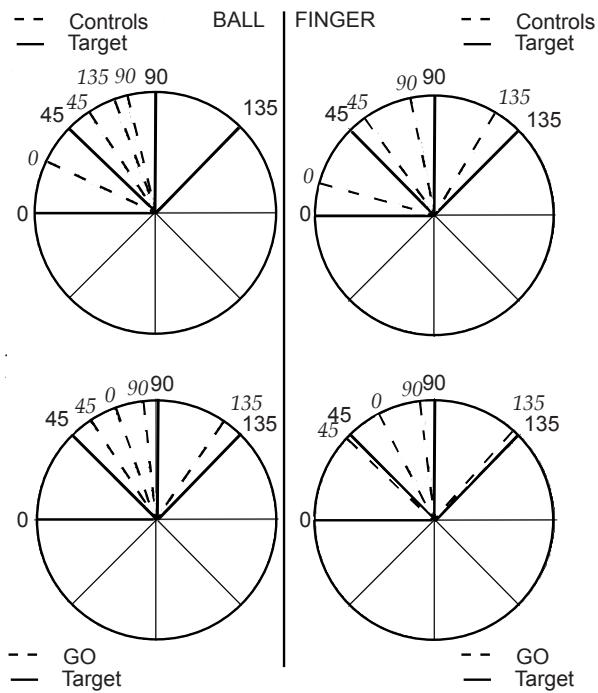


Figure 5: The average responses in experiment II for both the controls (upper left and right panel) and GO (lower left and right panel). The two left panels are the responses to the tactile stimuli and the right two panels are responses to the finger configuration. The dotted lines represent the answers of the controls and GO and the solid lines the orientation of the stimulus.

Discussion

In two experiments we aimed to identify the capability to integrate somatosensory information over several fingers of a patient with finger agnosia. In experiment I we investigated the implicit integration of somatosensory information over several fingers into one percept by manipulating the relative positions of the fingers. In experiment II we investigated the ability to judge the relative positions of tactile stimuli delivered to different fingers. Neither task required explicit identification of the fingers, but in order to perform these tasks, the proprioceptive and tactile information from each finger have to be combined. The fact that our finger agnosia patient was able to perform these tasks, albeit with some additional difficulties in the horizontal condition, shows that she could make these individual combinations. As she was impaired when asked to explicitly identify the touched finger, we conclude that GO is able to keep separate somatosensory information over several fingers, but only when the use of information in terms of a particular finger is implicit.

As such, the suggested fusion of the fingers (Kinsbourne and Warrington, 1962) might only be applicable when a finger has to be explicitly individuated from its neighbours. The fusion of the fingers probably arises at a higher processing level, perhaps at the level of higher order body representations such as the body image (Paillard, 1999). This representation is important for constructing a conscious perceptual experience of the body and stores knowledge about bodily features such as size, and the normal configuration of the body parts (Paillard, 1999; Gallagher, 2005).

Some studies have identified the posterior part of the parietal lobe as an area involved in higher-order body awareness and perception of, for example, the size and the configuration of body parts (Berlucchi & Aglioti, 1997; Melzack, 1990; Ehrson, 2005; Dijkerman & de Haan, 2007). Finger agnosia patients most commonly suffer from lesions in a specific part of the posterior parietal cortex, i.e. the angular gyrus (e.g. Roux et al., 2003; Mayer et al., 1999). Some investigators have emphasized the role of impaired spatial imagery in the inability to identify ones own fingers in patients with finger agnosia (Mayer et al., 1999; Carota et al., 2004). This role however, is derived from investigations aimed to identify the common nominator of the full tetrad of impairments as is observed in Gerstmann's syndrome (left/right disorientation, acalculia, agraphia, finger agnosia). Although of possible importance in the explanation of this syndrome in a whole (but see Benton, 1959), GO has preserved visuospatial abilities when tested at a spatial line orientation task, implying that the suggested spatial impairments cannot entirely explain the unique aspects of finger agnosia.

It could therefore be suggested that specific finger related knowledge about the configuration of the hand cannot be accessed, hence the identification problems. A possible explanation for the isolated finger recognition problems, as opposed to an identification impairment of other body parts, might be provided by the suggestion that fingers are represented in a separate finger schema (Benton, 1959; Haggard, et al., 2006).

The above suggestion might be in line with our observation that in experiment II GO was not

hampered by the crossed finger condition when judging the spatial position of a tactile stimulus (small ball). In line with Benedetti's observations (1985, 1988) our age matched controls perceived the location of the small ball during a fingers crossed position, as if the fingers were uncrossed. Benedetti explained this illusion by suggesting that the perceptual system is limited and unable to detect the veridical information when the fingers are crossed beyond the borders of functionality. Based on these findings, it strikes us that GO was clearly able to use proprioceptive information to locate a tactile stimulus in external space when the fingers were beyond such a functional range.

Further elaboration on Benedetti's conclusion leads us to introduce another phenomenon of the perceptual system. As is commonly accepted, perception is influenced by common prior knowledge stored in our long term memory. More specific, top down influence of prior knowledge about normal body part configuration normally affects perceptual behaviour in healthy control subjects (Kim and Cruse, 2001; Yamamoto and Kitazawa, 2001; Zampini et al., 2005). Taking this line of reasoning further, it could be that perception with crossed fingers is hampered since we have built up prior knowledge about common tactile-proprioceptive co-activation leading to a default uncrossed finger position. Perhaps Benedetti's functional limitations should be interpreted by limitations based on experience rather than limitations of functionality per se. Possibly GO's stored knowledge about common somatosensory co-activation with respect to the fingers has become inaccessible, resulting in a more accurate performance when the fingers were crossed. However, such reasoning needs further investigation.

Our experiments showed that with respect to tactile/proprioceptive integration specific for each finger GO appeared to be able to perform the tasks as she did not deviate greatly from age-matched controls. However, some aspects of her performance were clearly different. In experiment I she made almost twice as many errors as the controls. Most errors were targeted at the middle or right finger, which might be due to the slightly raised pressure sensitivity thresholds of her right hand as the stimuli were not very protruded. In experiment II GO clearly misjudged the positions of both the ball and the finger in the horizontal condition (0°) as being almost above the reference, instead of next to the reference. Surprisingly, performance of the age matched controls reveals a similar, though smaller, overestimation of the angle required to reach the position of the ball stimulus. GO's performance has a bias in the same direction, but with increased magnitude.

Together, our results suggest that GO's ability to accurately use proprioceptive input from the different fingers for integration with tactile input has remained intact at least at an implicit level despite her impairment in the explicit identification. In addition her performance with crossed fingers in experiment 2 suggests that GO's finger agnosic deficit, perhaps due to lost stored knowledge about the prototypical finger configuration, actually resulted in improved performance in one configuration. However, more finger agnosia patients have to be tested in order to provide converging evidence for the existence of a separate finger representation and its loss in patients with finger agnosia.

CHAPTER VII

Thinking touch: Investigating the mechanisms underlying tactile imagery

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Manuscript under review

Abstract

Most understanding about imagery processes is derived from studies investigating visual imagery. Tactile imagery, however, has been scarcely studied and so far studies have been solely aimed at specifying its neural correlates. The current study was set up in order to determine behavioural effects of tactile imagery. Participants were asked to imagine the touch or sound of a visually presented scene (e.g. dry leaves, pebbles) and were subsequently asked to perform a two-alternative forced choice (left/right) spatial discrimination task, of tactile and auditory stimuli. The results revealed that tactile imagery, relatively to auditory imagery, speeded up left-right discrimination of tactile taps to the finger. In contrast, the reverse effect was observed for auditory imagery that is, faster left-right discrimination of auditory beeps in auditory imagery conditions as compared to tactile imagery. These findings are the first that show specific effects of tactile imagery on a touch discrimination task and are in line with previously found unimodal effects of imagery on the processing of sensory information.

Introduction

For many of us, reading a book or listening to a story will generate mental pictures filled with colourful characters, music or perhaps smell from a damp woodland. Remarkably, few of these commonly imaged sensations are tactile. And perhaps this is why most studies on mental imagery haven been investigating visual and auditory imagery. Nevertheless, it is not difficult to imagine how a creepy spider crawls down on your back or to imagine the somatosensory qualities of a hug by a good friend or partner. These self evoked “mental” sensations are originating from stored representations, developed by recurrent tactile experience throughout the lifespan. Representations can be either automatically activated by bottom-up stimuli or voluntarily by means of imagery processes. An important debate in the imagery literature is whether imagery and real perceptual processes have partially overlapping neural substrates, and/or shared representations. Currently, a similarity between mental imagery and real perceptual processes is the most commonly accepted view in this topic (e.g. Farah, 1983; Kosslyn, 2001). In contrast to visual and auditory imagery processes, only few studies have been set up investigating that of tactile imagery processes. Those dedicated to the tactile modality are studies investigating the neural substrates of tactile imagery (Davids & Schwarz, 1977; Uhl, 1994; Fallgatter, 1997 and Yoo; 2003). However, to our knowledge, behavioural effects of tactile imagery (Note: not shape) on the processing of “real” physical stimuli have never been reported so far. More recently, a clear and elegant study by Davidson and Schwarz (1977), investigated the neural basis of tactile imagery compared to visual imagery using Electro Encephalo Graphy (EEG). Here, tactile imagery was induced by having participants imagine the sensation of a vibration stimulus on the forearm which was presented 30 seconds prior to they started to generate the image. Similarly, visual imagery was induced by imagining a previously presented flashlight. Recordings of EEG alpha rhythm simultaneously over the occipital and the parietal cortex,

revealed relatively larger occipital activation during visual imagery as compared to tactile imagery and relatively larger sensorimotor activation during tactile imagery as compared to visual imagery. These results provided converging evidence for overlapping brain areas involved in the processing of a real stimulus and during imagery of that stimulus, an idea which was increasingly accepted by that time (see for review Farah, 1988 and more recently: Kosslyn & Thompson, 2003). Other studies explored the neural basis of tactile imagery using Event Related Potentials (ERP's; Uhl, Kretschmer, Lindinger, Goldenberg, Lang, Oder Y Deecke, 1994; Fallgatter, Mueller, & Strik, 1997). Uhl et al. (1994) investigated tactile imagery processes in blind and healthy participants. Tactile imagery was induced by having participants imagine the sensation of textures they had felt prior to the experiment. A number, indicative of which texture was subject of imagery in a trial was acoustically presented. Analyses were performed on the signal 4 to 6 seconds after imagery onset since this interval was thought to represent the interval in which the image is generated. The results of the sighted participants showed parietal cortex activation during tactile imagery, contralateral to the hand which was subject of imagery. Also, occipital cortex activation was observed during visual imagery. Similar findings were reported by Fallgatter et al., (1997). In their ERP study tactile imagery, among visual and auditory imagery, was evoked by words presented on a computer screen indicating a tactile, visual or auditory sensation. On basis of the observed imagery modality specific differences in P300-fields it was suggested that modality-specific cortical areas contribute to mental imagery results, inline with the hypothesis. Yoo, Freeman, McCarthy, & Jolesz, (2003) investigated the neural substrates of tactile imagery using Magnetic Resonance Imaging (fMRI). In their study participants were required to imagine a previously applied tactile stimulus consisting of a gentle stroke of a Von Frey Hair (2Hz). Both real tactile stimulation and tactile imagery were used as experimental conditions. Their results revealed that the neural substrates of tactile imagery partially overlapped with that of the neural substrates of tactile stimulation and included primary and secondary somatosensory cortices. Together these observations are in line with the idea of shared representations and neural substrates between mental imagery and perception. Thus, tactile imagery is a process closely resembling that of real tactile perception.

From a large body of literature it is known that tactile perceptual events can influence each other by spatial or modality cueing mechanisms in which attention processes are modified (see for review, Spence & Gallace, 2007). Similarly, it is likely to expect that the activation of higher order knowledge by means of imagery will influence the perception of real physical stimuli. Indeed, many studies have reported effects of mental imagery processes on the perception of a real stimulus (Segal & Fusella, 1970; Craver-Lemley & Arterberry, 2001; Pearson, Clifford and Tong, 2008). Pearson et al. (2008) investigated whether mental imagery alters the balance of competitive visual interactions, such as observed in binocular rivalry, in favour of the imagery content. The results revealed that imagery biased subsequent perception in favour of the imagined pattern. Also, both interfering effects of imagery on perception is observed (i.e. Segal & Fusella, 1970; Craver-Lemley & Arterberry, 2001) whereas other studies report facilitory ef-

fects (see below). For example, Segal and Fusella (1970) investigated how detection of a visual (blue arrow) or auditory signal (harmonica chord) was affected by visual and auditory imagery when the stimulus was presented for 2s exactly at the time participants had a clear image. The results revealed that detection of the signal was poorer for the imaging condition than the no-imagery condition and detection of the signal was even poorer when signal and imagery came from the same modality. These interfering effects were attributed to a confusion of the imagined and the real stimulus when these stimuli were presented during imagery processes.

Facilitating effects of imagery on the perception of physical stimuli are for example reported by Ishai & Sagi, (1997) and Farah & Smith (1983). According to these studies, it depends on various stimulation and task variables whether imagery facilitates the processing of a perceptual stimulus. Farah and Smith (1983) for instance, revealed that the time between the start of the imagery and the onset of the physical stimulus determines whether imagery causes facilitation or interference of the perceptual process. Imagining an auditory stimulus before the presentation of a physical auditory stimulus (tone) produced lower detection thresholds as compared to imaging during the presentation of the tone. Moreover, this effect was stronger for the condition in which frequencies of imagery and stimulus were similar as compared to imagining a different frequency. Finke (1986) suggested that whether imagery facilitates or interferes with performance depends on the match between the image and the stimulus features, and in addition on the type of task. Together these studies suggest that certain factors play an important role in the size and direction of the effect imagery has on the processing of real stimuli. These factors should be taken into account when investigating the effect of imagery processes.

The current study sought to demonstrate that tactile imagery effects can be measured not only on a neuroanatomical/ physiological level, but additionally at a behavioural level. To this extent we used a spatial left/ right discrimination task of tactile and auditory stimuli. These stimuli were presented after participants started to either imagine tactile or auditory sensations. Specific imagery content was determined by complex visual stimuli informative of both tactile and auditory sensations (e.g. dry leaves, pebbles). To increase the likelihood of observing facilitory effects of unimodal imagery and discrimination, imagery was always generated prior to the presentation of the real stimulus. Also, three different time intervals between imagery onset and the presentation of real tactile and auditory stimuli were used to determine when facilitory effects of imagery would occur. Also we expected that the time between the imagery onset and the onset of the peripheral stimulus would influence the expected facilitory effect of unimodal imagery.

Method

Participants

Fifteen participants of Utrecht University (7 male, 8 female, mean age 24.8 ± 3 years) without a medical or neurological condition, participated in this study. Two of them stated to be left-handed. All participants were naive as to the purpose of the experiment and received either a

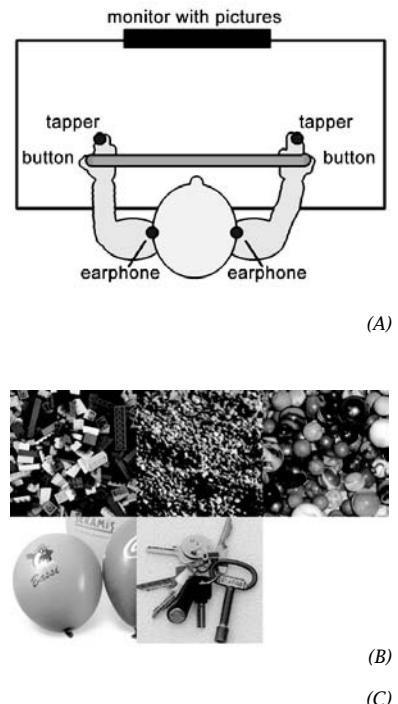
small payment or course credits required as part of their studies.

Experimental set up

Participants were seated at a table in front of a monitor with their hands in parallel (+/-30cm apart) on top of the table. The palms of the hands (palm up) were placed underneath a response device, which was mounted onto the table, so that the thumbs of each hand could press a button (see Figure 1A).

Tactile stimuli were presented by computer controlled miniature solenoid tappers (MSTC3 M&E Solve, Rochester, UK: <http://www.me-solve.co.uk>) which were attached distally at the dorsal part of the left and right little, ring, middle and index finger. After each block of trials (see procedure) we changed the active tapper to another finger in order to prevent the skin from becoming increasingly sensitive after several stimulations. The tactile stimuli (further referred to as Tap) consisted of metallic pins with a diameter of 2mm and were presented for 5ms. Together this skin indentation produced a well above detection threshold stimulus.

Auditory stimuli consisted of 20 ms pink noise (further referred to as Beep) and were presented directly into the left or right ear using E-A-RTONE 3A insert earphones (Earlink Inc). The stimuli used to generate tactile and auditory imagery consisted of visual scenes informative of tactile as well as auditory sensations (e.g. a bunch of dry leaves of a tree or a key ring with several keys, see Figure 1B). So, each picture could evoke an auditory as well as a tactile image. The pictures used in the experiment were collected from a total of 131. These pictures were rated for their association with: taste, smell, touch, or sound in a pilot study by 48 participants. For the main imagery experiment, 5 pictures were chosen that participants rated as either



*Figure 1 (A): Experimental Set up. (B):
Stimuli used to generate imagery (C):
Experimental conditions.*

associated with touch or sound, and only with few associations with other modalities.

Procedure & Design

General procedure

In the main reaction time experiment, tactile stimuli were randomly presented to the fingers or auditory stimuli to the ears. Before this experiment started, participants were presented with a beeps-and-taps comparison task and were instructed to adjust the intensity of the beep and the tap to a point of subjective simultaneity. That way we were able to control for differences in perceived saliency between the two sensations.

Next, the main reaction time experiment started. In the first block of trials participants were required to discriminate beeps and taps to obtain a baseline measurement. At that time the participants were not aware of the imagery conditions further on in the experiment. Immediately after the baseline block, participants were asked to practise the imagery procedure in an imagery practice task. Finally, the two imagery blocks were performed (see for overall procedure Figure 1C).

Baseline experimental condition

In the baseline block, a trial started with the presentation of one of the visual scenes (5 pictures, 6 trials per picture and beep or tap; 60 trials in total (30 beeps, 30 taps; 15 left hand and ear, 15 right hand and ear; 10 practice trials). Participants were instructed to view this scene attentively. After 2500ms, a 3000ms time interval started in which either a left or right beep or tap was presented to the left or right ear or to a left or right finger. Participants had to determine as fast as possible whether the stimulus was presented at their left or right side. Responses were given by means of pressing with the left thumb on the left button for left sided stimuli and with the right thumb on the right button for right sided stimuli. Trials were presented randomly.

Imagery practice task

During the imagery practice task participants were acquainted with the imagery procedure (see Figure 1C). Practising was necessary since a pilot study revealed that participants ($N=7$) needed 6 rehearsals of each imagery picture before the time to generate a clear and vivid image of either the tactile or the auditory sensation image stabilized to 1491ms ($SD = 252ms$). During the imagery practice task, participants were presented with the visual scenes and were instructed to imagine the touch sensation (sensation to the hands and fingers) or the sound provoked by these scenes. As soon as they had achieved a vivid experience of the requested sensation, participants had to press a button. After the button press the visual scene remained on the computer screen for another 5000ms, after which the trial ended and the next scene would be presented. During this period, participants were instructed to maintain the imagined sensation as long as possible. When the imaged sensation disappeared within the 5000ms time

interval they had to press the button again. If the sensation could not be generated at all, the visual scene would disappear after 10000ms after which the next trial started. Type of imagery (auditory or tactile) was blocked and each scene was randomly presented 6 times in each imagery block, adding up to 30 trials in total. Participants finished the imagery practice by rating each visual scene on the amount of effort it took to generate the required sensation using a 10-point Likert scale (0 = no imagery at all, 10 = extremely easy to generate image).

Imagery experimental conditions

After the imagery practice task was finished, the imagery experimental blocks were presented. The entire procedure was equal to that of the baseline block of trials except for the imagery instructions and the amount of trials presented in a block. Here, participants were asked to generate either an auditory or a tactile image when presented with the visual scene and to determine as fast as possible whether a presented beep or tap was left or right. Type of imagery was blocked and subjects were informed about the type of imagery by the presentation of a picture of an ear or a hand before a block started. An imagery block consisted of 20 trials in which an equal amount of the 5 visual scenes and the beeps and taps were randomly presented (2 beep trials per picture and 2 tap trials per picture; 50% left and 50% right). Auditory and tactile imagery blocks were repeated three times and order of presentation was counterbalanced across subjects. Together, each imagery x stimulus condition was presented 30 times (6 per visual scene) and trials were presented in a random order within each block.

Timing parameters of the presentation of the visual scenes and taps and beeps were not randomly determined. The visual scene was presented for 2500ms since a pilot study (see for procedure imagery practice task) revealed that participants were able to obtain a vivid imaged sensation after about 1419ms (SD = 252ms) and 95% (SD 1%) of the participants were able to maintain the image for at least 5 seconds. After the presentation of the visual scene and the generation of the image, the beeps and taps were randomly presented in a 3000ms time interval. The time interval was introduced both to reduce the predictability of the taps and beeps and to test whether the hypothesized effect of unimodal facilitation would change according to the amount of time between imagery onset (in imagery blocks) and the arrival of the taps and beeps. However, given a fixed time interval in which the stimulus is presented, the participant's anticipation will be higher at the end of the interval as compared to early in the interval. After waiting for 2500ms for the stimulus to be presented, one knows that it must be presented within the next 500s. Presumably this will draw attention away from the to be maintained image. Therefore we will focus mainly on the first two time intervals when interpreting the data.

Together, the effect of imagery on the discrimination of left and right beeps and taps was measured using a 3 (Task: Baseline, Auditory imagery (Aud), Tactile imagery (Tact)) x 2 (Stimulus Type: Beep, Tap) x 3 (Time of stimulus arrival: (T1) 0-1000ms, (T2) 1000-2000ms, (T3) 2000-3000ms) factorial within-subjects design with Reaction Time as independent variable. All Fac-

tors and their subsequent levels were counterbalanced.

General imagery ability measurements

To obtain a measure of the subjects overall imagery ability, we collected additional data. We asked participants to complete the Dutch version of the Interpersonal reactivity Index (IRI; Davis, 1983; Dutch version: Bogaerts & De Doncker, 1994). This is a 28-item self-report survey of empathy, and includes a fantasy scale which focuses on the ability to generate visual images for example when watching movies or reading a book. To our opinion the fantasy scale might give an indication of the ability to generate images in general. For the same purpose the VVIQ (Marks, 1973) was administered as well. This is a 16-item questionnaire which measures the self-reported vividness of imagery in several assignments such as "Think of some relative or friend whom you frequently see (but who is not with you at present) and consider carefully the picture (such as contour of face, head etc) that comes before your mind's eye". Participants were required to rate the vividness when imaging the requested picture both with eyes open and closed on a 5-point Likert scale (1 = no image at all, 5 = perfectly clear and vivid as normal vision). Finally, participants were asked to rate, for tactile and auditory imagery separately, on a 10-point Likert scale how good they were able to obtain a clear image of the visual scenes that were used to generate imagery.

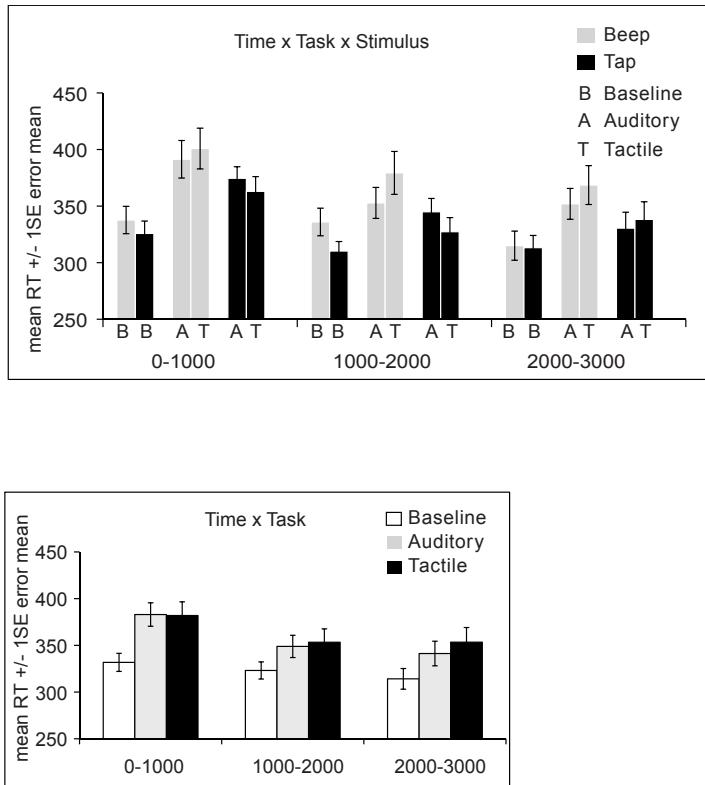
Data analyses

First, for the Imagery stabilisation task, the average time needed to generate an image was calculated for each visual scene. Only on average in 1% ($SD = 0.04\%$) of the trials participants were unable to generate an image and only on average 5% of the trials they were unable to maintain the imaged sensation. Data of these trials were discarded. Outliers were calculated using Grubbs's test and one subject (mean = 676ms, $SD = 733$) was excluded from the main analyses on basis of an overall low reaction time in the stabilisation experiment (group mean = 1837ms, $SD = 647$ ms).

Next, the average time a participant needed to accurately determine whether a tap or beep was presented at the left or right sight was calculated for each Task (Base, Aud, Tact) and Time interval (T1, T2, T3) separately. Note, participants performed almost perfect, on average only 0.9% ($SE = 0.2\%$) of the trials were incorrect. Also, presentation of beeps and taps were equally distributed over the 3 different time intervals. Reaction time was determined as the time between the onset of the beep or tap and the moment the response was registered by the response device. In order to test our hypothesis about faster unimodal imagery-stimuli combinations, averaged resultant reaction times were subsequently submitted to a $3 \times 2 \times 3$ omnibus repeated measures ANOVA with resultant reaction time as independent variable. Also in case of a significant main effect, we calculated planned Helmert contrasts for the factors Task, and repeated contrasts for Stimulus Type and Time. Particularly we expected differences in reaction time between the first two and the last time interval. Significant interactions were further explored

Figure 2 (A): Mean Reaction Time results of all experimental conditions separately. For each time interval separately; the first two bars are the taps and beeps in the baseline condition. The second two bars are the beeps in the auditory and tactile imagery condition. The third two bars are the taps in the auditory and tactile imagery condition.

Note: error bars are between subjects standard errors around the mean. (B): Reaction Time results for Task x Time conditions, collapsed over Stimulus Type.



using separate ANOVA's and paired samples t-tests.

Results

The mean reaction times for each Time, Stimulus Type and Task condition combination are depicted in Figure 2A. An omnibus ANOVA revealed a significant main effect of Task ($F(2,26) = 8.976, p < 0.01$), indicating that reaction times were faster in the Baseline condition (323ms), as compared to the Auditory Imagery block (357ms) and the Tactile Imagery block (362ms) (Helmert contrasts: Base vs Aud and Tact together: $F(1,13)=10.74, p < 0.01$; Aud vs Tact $F(1,13) < 1$). We also found a main effect of Stimulus ($F(1,13)=8.976, p < 0.01$) as Taps were responded to faster than beeps. A third main effect was found for Time interval ($F(1,13) = 33.28, p < 0.01$). Planned repeated contrasts between T1 (0-1000; 366ms) and T2 (1000-2000ms; 342ms) and between T2 (1000-2000ms; 342ms) and T3 (2000-3000ms; 336ms) revealed a significant difference between T1 and T2 ($F(1,13) = 33.40, p < 0.01$) but not between T2 and T3.

Most relevant for our hypothesis, Task interacted significantly with the Type of Stimulus ($F(1,13) = 7.503, p < 0.01$). Irrespective of the amount of time between the imagery onset and the arrival of the stimulus, beeps were responded to fastest in the baseline condition (330ms) when compared to the auditory imagery condition (365ms; $t(13) = -2.865, p < 0.05$). Also, reaction

times were lower for beeps in the auditory imagery condition as compared to the tactile imagery condition (382ms; $t(13) = -2.353$, $p < 0.05$). Similarly, reaction times to taps in the baseline condition (316) were lower as compared to taps in the tactile imagery condition (342ms; $t(13) = 2.228$, $p < 0.05$). And again, taps in the tactile imagery condition were responded to faster as compared to the taps in the auditory imagery condition (350ms), however, this difference did not reach significance ($t(13) = 1.308$, $p = 0.214$). Together, these results indicate relatively faster responses to unimodal imagery and stimuli as compared to cross-modal imagery and stimuli. An important factor in our design is the amount of time present between the onset of the imagery processes and the arrival of the beep or tap. Indeed we found an interaction of Time and Task ($F(4,52) = 5.480$, $p < 0.01$). Figure 2B revealed that beeps and taps under auditory and beeps and taps under tactile imagery presented in the first time interval, were responded to slower as compared to beeps and taps arriving in the second interval which is confirmed by t-test pair-wise comparisons (Aud1 = 383 vs Aud2 = 349, $t(13) = 7.016$, $p < 0.0$; Tact1 = 382 vs Tact2 = 353, $t(13) = 4.152$, $p < 0.01$). However, no significant differences were observed between the second and the third interval (Aud2 vs Aud3, $p = 0.14$; Tact2 vs Tact3, $p = 0.99$). Similarly response times for beeps and taps presented in the baseline condition were longest in the first time interval (Base1 (332ms) vs Base2 (232ms); $t(13) = 1.912$, $p = 0.078$ and shortest in the third time interval (Base3 (314) vs Base2; $t(13) = 2.553$, $p < 0.05$).

As expected, Time interacted in a three-way interaction with the Task and the Type of Stimulus ($F(4,52) = 1.637$, $p = 0.06$), albeit only marginally significant. Figure 2A indeed reveals that the Task x Type of Stimulus interaction, and most importantly our hypothesized Imagery Task (Aud, Tact) x Stimulus interaction, varies over time: the interaction is not significant at T1 $F(2,26) = 1.983$, $p = 0.08$; one-tailed) but is at T2 $F(2,26) = 5.884$, $p < 0.01$, and in T3 $F(2,26) = 4.433$, $p < 0.05$. Paired samples t-tests on the data of T2 reveal similar reaction times for Baseline beeps (336ms) and beeps during Auditory imagery (353ms; $t(13) = -1.166$, $p = 2.265$) and faster responses to beeps during Auditory as compared to Tactile imagery (379ms; $t(13) = -2.087$, $p < 0.05$). Also, Baseline taps (310ms) and taps during Tactile imagery (327) are responded to equally rapidly ($t(13) = -1.372$, $p = 0.139$) whereas responses to taps during Tactile imagery are faster as compared to responses to taps during Auditory imagery (344ms; $t(13) = 3.654$, $p < 0.01$). Together, these results further confirm the above described decrease in dual task costs for the unimodal imagery conditions or, to describe it differently, a relative facilitation in the left/right discrimination of beeps and taps under unimodal imagery. In T3, however, the relatively facilitation effect of unimodal Tactile imagery and taps had subsided. Baseline taps (331ms), Tactile taps (338ms) and Auditory taps (330ms) were responded to equally fast (all $p > 0.156$). However, for the Baseline (315ms), the Auditory (351ms) and the Tactile beeps (369ms) the relative unimodal facilitory effect remained significant (Auditory beep vs Tactile beep; $t(13) = -2.163$, $p < 0.05$; one-tailed; Auditory beep vs Baseline beep; $t(13) = -3.382$, $p < 0.01$).

With respect to the imagery ability measurements, none of the scores correlated significantly with the facilitation of beeps and taps after unimodal imagery (see table 1). However, the rela-

tive facilitation of tactile taps under tactile imagery correlated negatively with the scores on the Fantasy Scale of the IRI, albeit only marginally significant (Pearson's R = -0.55, p = 0.06; Note: Bonferroni uncorrected).

	FS	IRI	Auditory Vividness	Tactile Vividness
Diff-beep/ T2	0.13	0.17	0.41	-0.26
Diff-tap/T2	-0.55*	-0.23	-0.42	0.31
FS	-	0.56	0.39	-.03
IRI	0.56	-	-0.02	-0.2
Auditory Imagery	0.39	-0.02	-	0.15
Tactile Imagery	-0.03	-0.20	0.15	-

Table 1: The correlations between RT measures and scores on the questionnaires. * = marginally significant

Discussion

The current study investigated the effect of tactile and auditory imagery on the left/ right discriminations of tactile and auditory stimuli. Overall, taps were always discriminated faster as compared to beeps, probably due to the spatial and somatotopic proximity of the fingers receiving the taps and the thumbs performing the response (button-press). Also, we observed slower responses in the imagery condition possibly indicating a dual task cost. Within these overall slower imagery conditions, we observed that tactile imagery speeded up response times for tactile stimuli relatively to auditory imagery, in line with our hypothesis. A similar unimodal facilitation was found for auditory imagery and auditory peripheral stimuli. Moreover, these effects were most pronounced when the taps and beeps were presented between 3500 and 4500ms after the onset of imagery generation. This is in line with the hypothesized influence of the time between the generation of the image and the presentation of the peripheral stimulus on the effect imagery has on perceiving a real stimulus. Together, these results are in line with previously found relative facilitory effects of imagery on the processing of "real" stimuli in other sensory modalities (Ishai & Sagi, 1997; Farah & Smith, 1983) and provide the first evidence of a behavioural effect of tactile imagery on the perception of tactile stimuli.

Furthermore we observed overall slower response times for stimuli presented in the first time interval (2500-3500ms after imagery onset), as compared to the stimuli presented 3500ms to 5500ms after imagery onset. Two factors could account for the observed results. First, generating an image requires considerable effort. Discriminating a tap or a beep during this process will increase the task-load and therefore reaction times will increase. However, reaction times for stimuli in the baseline condition were also slower when presented 2500-3500ms after onset

of the imagery picture, albeit only marginally. A second possible explanation for the observed slower reaction times in the first time-interval therefore, is the amount of anticipation which develops over time. In this view, the reaction times are not slower in the beginning of the total time interval but the reaction times are increasingly faster for stimuli presented in the second and the last time-interval. In our experiment, each trial consisted of a beep or tap, somewhere presented in the 3000ms time interval (starting from 2500ms after imagery or picture onset). Therefore, participants became increasingly anticipated when no stimulus had been presented in the first interval, or in the second time interval, leading to increasingly faster response times for stimuli in the second and third time interval. However, this is primarily the case for the reaction times in the baseline condition. With respect to the imagery conditions, reaction times did not decrease further in the third interval which was possibly caused by the ongoing or previously active imagery related processes.

Time between onset of imagery generation and the presentation of the real stimulus was also of influence on the observed effect of relative facilitation effects of unimodal imagery and the processing of real stimuli. For sensory stimuli arriving in the first time interval, between 2500 and 3500ms after imagery onset, the relative facilitation of stimuli after unimodal imagery was not statistically significant. It could be suggested that the impact of type of imagery was smaller than the amount of noise generated when performing two tasks at the same time. However, on basis of the amount of time allowed to generate the image, effects of unimodal imagery would likely be observed. Even more, as was indicated by our pilot study we expected that imagery would have been generated after 2000ms. In this pilot experiment we observed that participants on average spent 1419 ms ($SD = 252$) to obtain a clear image. Perhaps matters are different when participants are also attending to a different task, as in the pilot study no beeps and taps had to be discriminated. Although the participants were able to learn that stimuli would not be presented immediately after imagery onset, there was no sign indicating that the time interval started in which the taps and beeps could arrive. Therefore it could be that participants were both attending to possible stimuli during the generation of the image which could have caused overall longer imagery generation times. As such to much attentional processes are allocated to the activation of the mental image, hence the lack of unimodal imagery effects for beeps and taps presented in the first time interval.

Another factor which could have contributed to the lack of unimodal imagery effects observed for these early stimuli is the influence of the requested imagery content. For example, Farah and Smith (1983) and Ishai and Sagi, (1997) observed relative facilitation effects even when stimuli were presented exactly at the same time participants were required to imagine the requested sensation. The requested imagery content and the way participants were informed what sensation they were required to image are two important differences between those studies and ours. In our study the content was dictated by visual scenes indicative of both auditory and tactile information. That is, the to-be-imaged sensation was provided by visual information from which the participants were required to extract the auditory and tactile sensation.

Also, the content of imagery was a-specific and possibly influenced by participant specific interpretations whereas the imagery content studied by Farah and Smith (1983) and Ishai and Sagi (1997) was rather specific (a specific frequency of a tone or a Gabor pattern) and participants were previously exposed to this specific stimulus. As such, the visual scenes we used to evoke imagery can be regarded as higher order and complex as opposed to the more simple content of imagery used in most imagery experiments (such as blue arrow, triangle for visual imagery, tactile vibration for tactile imagery etc). Indeed, a study by Craver-Lemly and Arterberry (2001) revealed that imagery induced interference might be reduced with more complex visual displays. As a result, it could be suggested that it requires more effort to generate the requested image from our stimuli as compared to more simple stimuli and perhaps it is this effort which acquires too much attention in order to observe the unimodal imagery effects in the first time interval.

Two possible explanations might account for the observed unimodal effects for stimuli presented 3500-4500ms after imagery onset. Since we cannot state anything about the time participants were able to maintain that image in the experimental conditions, it could be suggested that participants stopped building the image before the end of the first time interval. Next, by the time the second interval started, two different situations might have been at hand. First, the image could have been faded somewhat and thinking about touch activated similar neural substrates such as primary and secondary somatosensory cortex, albeit to a lesser extend as compared to real stimuli. Subsequently presented stimuli would than be re-activating the somatosensory cortex faster. Secondly, participants were able to maintain that image for another few seconds and subsequently presented tactile stimuli activated the somatosensory cortex even further, leading to better processing of the stimulus. Since we did not measure neural correlates we can only speculate about the exact underlying mechanism.

Reconsidering the theory that imagery and perception share neural substrates, one could argue that at the time our participants generated the requested image, for instance the tactile sensation of dry leaves, somatosensory areas are activated but only to a subliminal level. Under these circumstances thresholds will be reached faster when a tactile stimulus is presented as opposed to when an auditory stimulus is presented. In the latter case participants have to reallocate their attention away from the imagined tactile sensation in order to attentively process the auditory stimulus. Important evidence for such costs of expecting events in the wrong sensory modality is demonstrated nicely by Spence, Nicholls and Driver (2001). Although their study was about effects of the presentation of real stimuli on the processing of subsequently presented stimuli, the suggested mechanism may be the same. In their study, expectancy was manipulated by informing participants about the modality they had to attend to and by adjusting the percentage of trials in the attended modality. For example when participants were asked to attend to the visual stimuli, visual stimuli were presented in 75% of the trials whereas auditory and tactile stimuli were only presented in 12.5% of the trials. The results showed that reaction times for targets in the unexpected modality were slower than when that modality was

expected or when no expectancy was applied (divided attention and equal percentages of trials). Therefore it was suggested that the cost of shifting to another modality raised processing times. It could be that our imagery assignment served as the “modality expectancy cue” and as a result, same modality stimuli were responded to faster as compared to different modality stimuli. Whether effortful imagery is necessary for the same modality effects we observed in our study, is a question we cannot answer using our data. Merely presenting participants with the word “touch” or “sound” might be sufficient. In this view, “seeing touch”, or seeing body parts or even objects touching each other activates somatosensory cortex also (see Keyser et al., 2004). As such, it can be suggested that activation of the somatosensory area’s, either subliminal or above threshold, draws attention to the tactile modality, irrespective of how this activation is generated. Therefore, we believe that the origin of the relationship between imagery and attention is in need of further investigation, as was earlier emphasized by Farah and Smith (1983).

Finally, certain aspects of our data require some discussion. First of all we did not observe the unimodal facilitation effect for tactile imagery and tactile stimuli presented in the last time interval, 4500-5500ms after imagery onset and the effect for auditory stimuli also subsided. As described earlier, taps and beeps are responded to fastest when presented in this final time interval, possibly due to the increasing anticipation this may result in a ceiling effect, with little scope for reduced RT’s due to imagery. Furthermore, the differences between tactile and auditory imagery may be related to processes, having the latter more easily maintained. Secondly, none of our additional questionnaires and scales correlated with the unimodal imagery effects. The investigation of individual differences in for example visual imagery has a long history in psychology (see for review McAvinue & Robertson, 2006-2007). However, using measures for visual imagery only (VVIQ) would not necessarily be of help when studying tactile imagery. Also, the fantasy scale of the Interpersonal Reactivity Index might measure the spontaneous generation of imagery, and not so much how well a person performs in voluntarily generated imagery. Indeed, according to these authors, correlational and factor analytic studies often fail to reveal any kind of relation between imagery ability and the scores on such objective and subjective tests.

In all, we observed that tactile imagery speeded up response times for peripheral tactile stimuli relatively to auditory imagery. Also, a similar unimodal facilitation was found for auditory imagery and auditory peripheral stimuli and this effect was restricted for stimuli presented between 3500-4500ms for tactile imagery and stimuli, and between 3500 and 5500ms for auditory imagery and auditory stimuli.

CHAPTER VIII

Grasping Weber's illusion: The effect of receptor density differences on grasping and matching

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Abstract

Weber found that distances between tactile stimuli on a high receptor density area are perceived as being larger as compared to an identical distance on a low receptor density area (Weber's illusion). Previous studies of visual illusions suggest that illusion effects vary with the type of response given. Here we tested a modified version of Weber's illusion in which a solid object was placed on the forearm or hand. Blindfolded participants were required either to give a size estimation or grasp the object. The results showed that size estimation of solid objects was consistent with Weber's illusion, whereas grasping responses showed an opposite pattern (e.g. larger hand opening for objects on the forearm). A second experiment showed that this pattern is not due to biomechanical differences induced by the difference in spatial position of the target objects on the hand and arm. We suggest that the larger grip aperture when grasping objects on the arm were due to an increase in safety margin as a response to greater uncertainty about the object dimensions due to reduced receptor density.

Introduction

Somatosensory information is essential for many aspects of behaviour, such as recognizing objects which are concealed from our vision, or scratching an itch on our back. It plays an important role in the perception of our own body and provides us with the ability to interact with the external world, although in many cases vision is the more dominant sense. Within vision research, perceptual illusions have been used to investigate differential effects on implicit motor responses and conscious perceptual judgements in healthy participants (Aglioti, DeSouza, & Goodale, 1995; Haffenden & Goodale, 1998; e.g. Carey, 2001, Franz, 2001, for reviews). These studies have found that perceptual judgements of size are influenced more by a size illusion than maximum grip aperture during a grasping task. This differential sensitivity to the illusion has been considered to be consistent with the idea that visually guided grasping and perceptual judgements are based on separate representations of the same stimulus (Milner & Goodale, 1995). However, this interpretation of these findings remains controversial and several authors have suggested alternative explanations for the observed differences in illusion sensitivity (e. g. Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999; Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Franz, 2001; Franz, 2003; Smeets & Brenner, 1999). For example, grasping responses are not only affected by object size, but also by other variables such as uncertainty about the perceived information. Furthermore, Franz (2003) suggested that a confounding factor of these visual illusion studies lies in the type of response selected for testing motor responses and perceptual judgements. He argued that a manual size estimation response is highly sensitive to a change in object size, illusory or real, whereas traditional perceptual measures are less sensitive. Correcting for this aspect leads in some cases to equal sensitivity for perceptual judgements and grasping responses. Also, it might be possible that the difference in illusion sensitivity depends on whether different aspects of sensory information are relevant for the task. Indeed, Smeets & Brenner (1999) showed that illusion effects found in

several tasks performed on the same stimuli can be explained by the use of different spatial attributes. Furthermore, Bruno (2001) suggested that it depends on the reference frame used when responding to a stimulus whether the response is sensitive to an illusion or not. For example, grasping a stimulus requires viewer-related coding of the stimulus whereas estimating its size requires an object-related coding. Changing perspective rather than changing the type of response determines whether effects of the illusion are observed.

With respect to other sensory modalities, Dijkerman and de Haan, (2007) recently presented a model which specifies different somatosensory processes and their underlying neural substrates. In line with the two visual streams model of the visual system (Milner & Goodale, 1995), the authors suggested that neural processing of somatosensory input does not only depend on the type of stimulus, but also on how this information is used. Evidence for task dependent somatosensory processing comes among others from dissociations in neuropsychological patients (Paillard, 1999 ; Rossetti, Rode, & Boisson, 1995, Rossetti, Rode, & Boisson, 2001, Reed, Caselli, & Farah, 1996, Valenza et al., 2001) and from studies with healthy participants (see Dijkerman & de Haan, 2007, for a review).

Few studies have used haptic illusions to study task dependent differences in healthy participants. Kammers, van der Ham, and Dijkerman (2006) used a vibrotactile illusion to explore differences between matching and reaching involving the position of a body part. This illusion was induced by vibration of a muscle tendon (here the biceps muscle), resulting in an illusory displacement of the stimulated arm. The effect of the illusion was larger when participants were asked to perceptually match the position of the vibrated arm with the non-vibrated arm as compared to a reaching response with the non-stimulated arm towards the felt position of the vibrated arm (see also Marcel, 2003 for similar findings). This suggests that body representations underlying perception and action may be differentially sensitive to the illusion. Task dependent effects have been observed not only regarding somatosensory input pertaining to the body, but also with respect to haptic exploration of external objects. Westwood and Goodale (2003) investigated how grasping and matching responses were affected by a size-contrast illusion. Participants were instructed to manually explore with the left hand two objects, a target and a flanker object. After touching the objects, they either had to grasp the target object or estimate its size (right hand). The size of the flanker object was identical, smaller or larger compared to the target object. Consistent with several previous visual illusion studies (Aglioti et al., 1995; Haffenden & Goodale, 1998; Otto-de Haart, Carey, & Milne, 1999), size estimation was affected by the illusion (albeit, for the larger flanker object only) whereas grasping was not. A limitation of the Westwood and Goodale study is that the size contrast illusion is likely to induce visual imagery processes, which means that the observed differences between matching and grasping might be related to differences in visual rather than somatosensory processes. A tactile illusion which originates in the difference of tactile receptor densities in various skin areas was reported originally by Weber (1834, translated by Ross and Murray, 1978). It refers to the impression that a tactile distance contracts when moved from a region of high to low

receptor density (e.g., from hand to forearm). In 1982, Green further explored this effect on various body parts such as the palm, forearm, thigh etc, and found that the effect of the illusion was dependent on the stimulus orientation and that the misperceptions are based upon errors in perceived location of the stimuli. More specifically, he suggested that “perceived location of a stimulus depends on the relationship of a tactile stimulus both to the body frame and to nearby stimuli”. As a consequence, a certain distance perceived by a skin area with high receptor densities is perceived to be larger as compared to this same distance perceived by a skin area with a lower receptor density which was later confirmed by Taylor-Clarke, Jacobsen, & Haggard (2004). These authors argued that the illusion cannot be entirely explained by the differences in receptor density and instead suggested that when judging tactile distances presented to various skin areas, neural signals from these varying receptor densities are rescaled to an object-centred space. However, this rescaling process is imperfect and thus Weber’s illusion emerges.

In the current study we sought converging evidence for the idea that processing of tactile input about an external target is influenced by the type of response that is required by using Weber’s illusion. To this purpose, we performed two experiments. In the first experiment, participants either grasped an object or provided a size estimate by varying the thumb-index finger separation. We hypothesized that the size estimation response would be consistent with Weber’s illusion (e.g. larger length estimates for objects on the hand), whereas the implicit motor grasping response would not. In the second experiment a control grasping task was studied in order to rule out biomechanical differences between grasping conditions as a possible cause for the observed differences. Prior to the main two experiments, three independent pilot studies were performed to assess the feasibility of using a size matching response for measuring Weber’s illusion and to assess possible differences in sensory attributes.

Methods

Participants were students from Utrecht University or its surrounding area and received either a small payment or course credits required as part of their studies. Written informed consent was obtained before the start of the study. This study was approved by the local ethical medical board and has been conducted in accordance with the declaration of Helsinki.

Pilot I

This pilot experiment was set up in order to investigate whether the method of varying thumb-index finger separation is a reliable measure of quantifying Weber’s illusion. The illusion was evoked by applying tactile distances either to the palm of the hand or the forearm, in line with the paradigm used in the studies by Green (1982) and Taylor-Clarke et al., (2004).

Participants

Four healthy participants without history of psychiatric or neurological illness experiment

(3 male, 1 female; mean age 25.5; ranging from 22 to 29 years of age) and who were naïve as to the purpose of the experiment participated in the first pilot.

Procedure

Blindfolded participants were seated in front of a table with both arms in parallel (250 mm apart) and in supine position (see Figure 1). The experimenter manually applied the appropriate distance (either, 50 mm, 60 mm or 70 mm) by using a caliper which produces two simple tactile stimulations. Stimuli were applied on either of two areas, the palm of the hand or the ventral side of the forearm, 30 mm proximally of the wrist joint. Both areas of stimulation were delineated prior to the experiment. During stimulation participants were required to indicate the perceived distance between the two points by adjusting the right thumb-index finger distance. The two fingers were always pinched together in between trials. Participants verbally reported whenever they were finished adjusting their fingers. The position of the index finger and thumb was recorded subsequently using the Mini-bird magnetic movement recording device (Ascension Technologies). This system samples the 3D position of electro-magnetic markers with a frequency of 86.1 Hz. As indicated in Figure 1, markers were attached to the nails of the right index finger and thumb. Each size-area combination was tested five times and trials were presented in a random order.

Data analysis and statistics

The 3D position data of the markers were analyzed off-line using a Matlab (Mathworks Inc.) programming environment. The dependent variable of interest was mean aperture (mGA; or, mean thumb-index finger separation) which was calculated by averaging the 3D difference of both markers for all 86 samples recorded during one second.

First, we calculated the total percentage of overestimations across size conditions. Thus, per subject, for each distance, mean grip apertures for all arm conditions were subtracted from the mean grip apertures for hand conditions (first 50 mm object on hand minus first 50 mm object on arm, second 50 mm object on hand minus second 50 mm object on arm, etc.). This

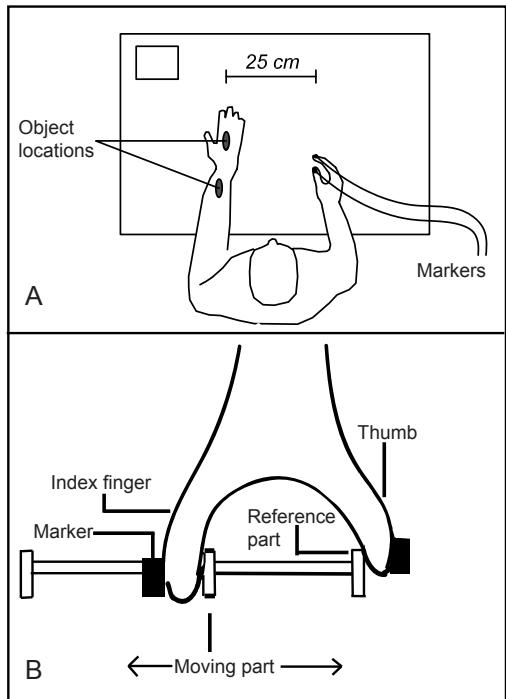


Figure 1. Experimental set up pilot experiments and experiment I (figure A). Adjustment method pilot experiment II (figure B).

difference was then defined as either over-estimation, or under-estimation. The number of over-estimation trials was summed and subsequently this total was calculated as a percentage of the total amount of trials. Second, mean grip apertures were analyzed using a 2(Area) x 3(Object size) repeated measures ANOVA with a significance level of $p = 0.05$. Significant main effects with more than two levels were disentangled using post hoc helmert contrasts. Significant interactions were further explored by computing simple main effects for each interacting factor. Only significant effects are reported.

Results and Discussion

As was expected (see Figure 2A), tactile distances perceived on the palm of the hand are estimated larger as compared to the same distances perceived on the forearm albeit only for the larger objects. Also, this overestimation occurred in 78% of the trials ($SD = 19$). Submitting the aperture data to a 2(Area) x 3(Object size) repeated measures ANOVA revealed an significant main effect of Area ($F(1, 3) = 12.92, p = 0.05$) and of Object size ($F(2,6) = 20.23 p <0.01$). Further exploration of the factor Object size main effect revealed a significant increase in grip aperture from the 50 mm to the 60 mm object ($F(1,3) = 22.16, p < 0.05$) and from the 60 mm object to the 70 mm object ($F(1,3) = 17.73, p < 0.05$). In addition, Area interacted significantly with Object size ($F(1,3) = 20.92, p < 0.01$) and disentangling this effect reveals significant differences between hand and arm apertures for the 60 mm ($F(1,3) = 18.36, p < 0.05$) and the 70 mm object ($F(1,3) = 15.98, p < 0.05$) only.

In sum, Weber's illusion reliably affected the manual estimation of tactile distances. Tactile distances on the hand were overestimated as compared to identical distances on the arm, which occurred in 78% of the trials ($SD = 19$). This percentage is in line with what might be expected from the percentages found in the study by Taylor-Clarke et al. (2004), using similar skin regions but a different direct comparison task. In their study, comparison of distances applied on the index finger and the forearm resulted in an overestimation in 77% of the trials. However, overestimations did not occur for the smallest distance, which was also observed by Green (1982). In that study, significant differences were found in perceived distances between palm of the hand and forearm but not for the smallest distance (here 20 mm, compared to 40 mm and 60 mm). Also, the increase in distance estimates was larger for the hand perceived distances as compared to the arm perceived distances, similar to our results. The differences in slope have also been reported for visual stimuli (Newsome, 1972). Green (1982) related this finding to the differences in peripheral receptor density and suggested that certain receptor areas (fovea or hand) are specialized in extracting veridical information about features such as size and distance. Other areas only detect coarser differences and when closer analysis is desired, detection can be enhanced by moving the stimulus to an area of higher receptor density.

Despite the observed similarities between our findings and that of others, the use of a manual size estimation (adjusting thumb-index separation) is highly debated (see Franz, 2003). There-

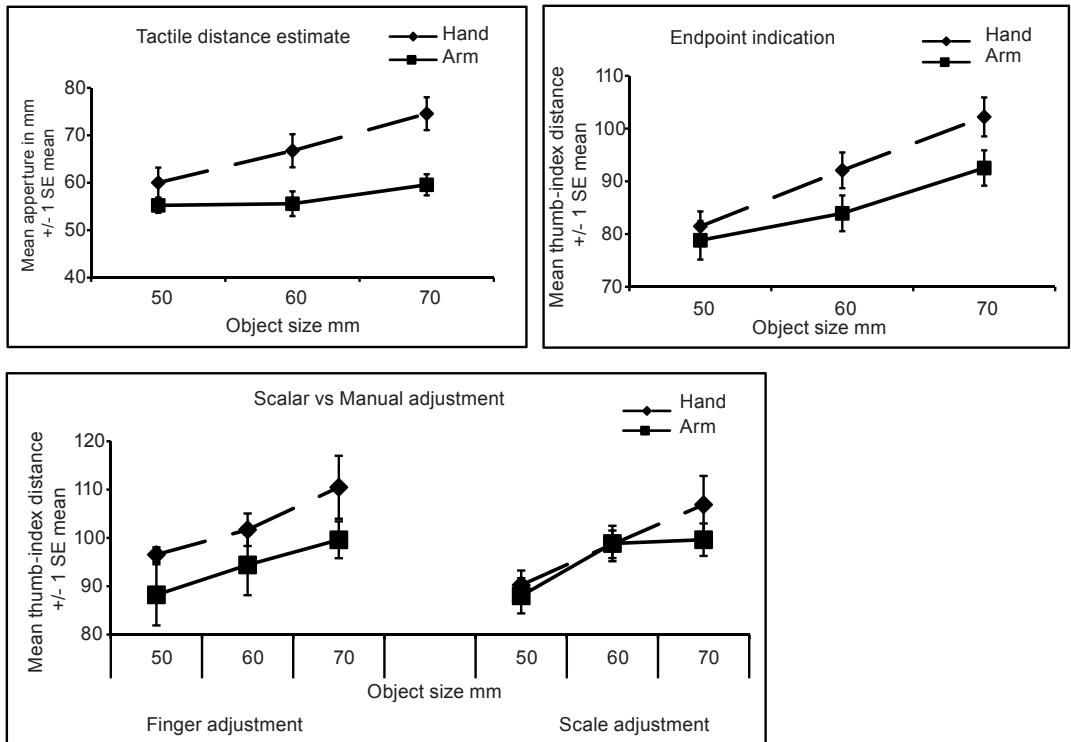


Figure 2. Mean thumb-index separation for estimation response in mm as a function of Object size, in pilot experiment I (figure A) and pilot experiment III (figure C) and of Object size and Response, in pilot experiment II (figure B): Error bars = between participants error of the means.

fore a second pilot experiment was set up in order to test for differences in effects of the illusion between a manual size estimation task and a more traditional perceptual measure, the method of adjustment. Also, this experiment will test for similarities of the illusion effect evoked with two simple tactile stimuli (by using the caliper) and effects induced by solid objects.

Pilot II

Participants

Five participants (1 male, 4 female; mean age 22; ranging from 19 to 25 years of age) and who were naïve as to the purpose of the experiment, participated in the second pilot experiment.

Procedure and data analyses

The procedure resembled that of pilot experiment I except for the tactile stimuli and the response given. In this experiment the participants were stimulated with rectangular aluminium objects (height 25 mm; width 20 mm) which varied in size, 50 mm (68 g), 60 mm (86 g) and 70 mm (92 g). Since aluminium conducts heat quickly and is perceived as being cold, objects were

preheated in order to prevent participants from using perceived coldness as a cue. Objects placed on the arm were always located 30mm from the wrist joint, and objects on the palm of the hand were always positioned centrally. Both objects were positioned in a longitudinal [or proximal to distal] orientation. By varying the location of the stimulus somewhat (a few mm) in lateral and medial direction between trials, adaptation of the skin receptors to the stimulus was prevented. In two separate blocks blindfolded participants were required either to estimate the size of the object by adjusting thumb and index finger separation or to adjust a linear scale (see Figure 1B). This wooden scale was equipped with a fixed part which was used as a reference point, and an adjustable part. Participants were required to adjust the moving part so that the distance between the reference point and the adjustable part resembled the perceived distance of the object. Participants verbally reported whenever they were finished adjusting the scale and prior to the data recording participants placed the thumb on the reference part and the index finger on the adjustable part. Subsequently, the position of the index finger and thumb was recorded by the Minibird. Each Object size x Area combination was tested five times which resulted in thirty trials per block condition. Within each block trials were presented in a randomized order.

The data analyses resembled that of pilot experiment I.

Results and Discussion

As was observed in pilot experiment I, we found a pattern of overestimations of hand responses as compared to arm responses for both types of responses (see Figure 2B). Overestimations occurred in 81% ($SD = 0.09$) of the trials for the manual size estimates and in 53% ($SD = 20$) of the trials for the method of adjustment. A 2(Response) x 2(Area) x 3(Object size) ANOVA shows a main effect of the factor Object size indicating that responses increased reliably with size ($F(1,4) = 12.23$, $p < 0.01$). Also, Weber's illusion reliably affected the size estimation of solid objects (overall main effect of Area $F(1,4) = 36.22$ $p < 0.01$). Further exploration of this effect revealed significant increases between the 50 mm and the 60 mm object $F(1,4) = 11.54$, $p < 0.05$) and between the 60 mm and the 70 mm object ($F(1,4) = 16.60$, $p < 0.05$). With respect to the method used to indicate the size of the objects, no significant difference was found between the adjustment method and the manual size estimation (overall main effect of Response $F(1,4) < 1$) and consequently the effect of Area did not significantly differ between both responses, interaction $F(1,4) < 1$.

The results of this pilot study suggest that it is possible to induce Weber's illusion by stimulating the palm of the hand and the ventral side of the forearm with solid objects. Second, an overall effect of Weber's illusion was found and no difference between methods used was observed. Visual inspection of the results (see Figure 2B) suggests that Weber's illusion was more pronounced for the manual estimation method as compared to the method of adjustment, although this difference did not reach significance (possibly due to the small number of participants in this pilot). This difference in effect of the illusion between manual size estimation and

method of adjustment has been reported previously by Franz (2003) for a visual size illusion. In the current study, it might be explained additionally by the influence of external reference information provided by the fixed part of the device, which subsequently led to recalibration of the position of the thumb and index finger with respect to the manipulated device. This type of feedback information is not available during the grasping response in the main experiment. Because of this potentially confounding factor and we aimed to induce a robust Weber's illusion, we decided that index-finger-thumb separation may be the most suitable response to use as a size estimation measure in the main experiment.

As mentioned earlier in the introduction, a manual size estimation response is aimed at object rather than spatial features, while the latter may be more important for the grasping responses (Smeets & Brenner, 1999). Therefore, we conducted a third pilot experiment in which we changed the manual size estimation response so that it is aimed explicitly at the endpoints of the object.

Pilot III

Participants

Nine healthy female participants without history of psychiatric or neurological illness (mean age 21.5; ranging from 19 to 24 years of age) and who were naïve as to the purpose of the experiment, participated in the second pilot experiment.

Procedure and data analyses

The procedure resembled that of pilot experiment II except for the type of response. After stimulus placement, participants were required to align their thumb and index finger as precise as possible with the perceived object's endpoints. To keep all other factors equal, it was decided to keep the position of the response hand similar to that in the first pilot experiment (see Figure 1). Each size-area combination was tested eight times and trials were presented in random order. Data analyses and statistics were similar to that of pilot experiment I.

Results and Discussion

As is shown by Figure 2C, Area of stimulation showed a significant main effect ($F_{1,8} = 16.19$, $p < 0.01$). In addition, the factor Object size was significant as well ($F_{1,8} = 99.11$, $p < 0.01$) and post hoc contrasts revealed increases from the 50 mm to the 60 mm object as well as from the 60 mm to the 70 mm object to be significant ($F(1,8) = 286.5$, $p < 0.01$; $F(1,8) = 25.12$, $p < 0.01$). Summing up, modifying the size estimation response into a response aimed at spatial rather than object attributes, did not interfere with the effect of Weber's illusion. Also, the percentage of overestimated trials appeared to be similar to that was found in pilot experiment I (74.5%, $SD = 15.4$). Overall, these findings suggest that Weber's illusion affected judgments of the object endpoints similar to distance judgments. One possibility which we cannot exclude entirely is that participants might have used object size information to solve the task. However, this was

never reported by any of the participants.

The data from these three pilot experiments suggest that the effect of Weber's illusion on manual size estimation responses appears to be quite robust and the results are very similar to earlier findings (Green, 1982; Taylor-Clarke et al., 2004). As there are possible confounds with alternative measures of perceptual estimates, we decided to adopt it as our perceptual measure of size in our main experiment.

Experiment I

Participants

Eighteen right-handed undergraduate students (3 male, 15 female; mean age 22 years; ranging from 19 to 26 years of age) with no history of psychiatric or neurological illness and who were naïve as to the purpose of the experiment, participated in experiment 1.

Experimental set up and procedure

The experimental setup was similar to that of the second pilot study with two differences. First, in this experiment we added an extra object of 80 mm (95g). Second, besides a size matching response (similar to pilot II), participants were additionally asked to reach out and grasp the object. Both responses were tested in separate blocks.

A grasping trial started when the object was positioned on the participant's forearm or hand after which participants were instructed to grasp the object immediately by its long axis (see Figure 1), without actually lifting it. The stimulus remained on the skin during the response and was removed after the response arm was back in starting position. Data recording during grasping trials started just before the stimulus was placed and ended after 4 seconds. Prior to the experiment, all participants practiced both tasks with novel stimuli, and were blind to the number and shape of the objects used in the experiment.

Design

The experiment had a 2 (Area; palm of the hand or forearm) x 2 (Response; grasping or estimating) x 4 (Object size; 50, 60, 70 or 80 mm.) within-subjects design. A total of 128 grasping (A) and matching (B) trials were tested in ABBA order and within each block of 32 trials the order of stimulus Area and Object size were randomized.

Data analysis and statistics

The 3D position data of the markers were analyzed off-line using a Matlab (Mathworks Inc.) programming environment as was done in the pilot experiments. Here the dependent variables of interest were mean grip aperture (mGA) responses for the size matching and peak grip aperture (PGA) for grasping movements. Also, the average standard deviation of these values was calculated per subject within a condition in order to determine variability in grip aperture. The analyses of the estimation trials were similar to that of pilot experiment I whereas the analyses

of grasping trials differed to a certain extent. For grasping trials, raw data were filtered with a polynomial filter (Press, Teukolsky, Vetterling & Flannery, 1994). Secondly, movement onset was defined as the first sample after velocity exceeded 50 mm/s whereas movement offset was defined as the first sample after velocity dropped below 50 mm/s. In order to define maximum grip aperture, 3D differences in x, y and z values between marker 1 and 2 were calculated. Other kinematic parameters such as: peak velocity (PV), time to peak velocity (TPV) in %, time to peak grip aperture (TPGA) in % and movement time (MT), were calculated from the data within the same temporal boundaries.

Mean and peak grip aperture values as well as average standard deviation values (variability in grip aperture within a condition for each participant) were analyzed using a 2(Area) x 2(Response) x 4(Object size) repeated measures ANOVA with a significance level of $p = 0.05$ for experiment I. Significant main effects with more than two levels were disentangled using post hoc helmert contrasts. Significant interactions were further explored by computing simple main effects for each interacting factor. A second set of analyses was conducted in order to explore the above mentioned kinematic variables of grasping movements. These values were analyzed with separate 2(Area) x 4(Object size) repeated measures ANOVA's (experiment I) and. Again, significant interactions were further analyzed by calculating simple main effects for each interacting factor. Only significant effects are reported.

Results

Factor		F GA	F SD	F TPGA%	F MT	F PV	F TPV%
Response		26.80**	8.584**	-	-	-	-
Area		NS	14.04**	4.516*	NS	42.63**	8.780*
Object size		251.9**	NS	11.38**	NS	NS	NS
Area x Response		55.95**	NS	-	NS	NS	NS
Area x Size		53.88**	NS	NS	-	-	-
Response x Size		11.03**	NS	-	-	-	-
Area x Response x Size		NS	NS	-	-	-	-
Contrast	Level						
Object size	50 vs 60mm	31.12**	-	19.33**	-	-	-
	60 vs 70mm	22.84**	-	7.285*	-	-	-
	70 vs 80mm	13.62**	-	NS	-	-	-
Interaction effects	Level	Factor					
Response x Area	Estimate	Area	15.71**	-	-	-	-
	Grasp	Area	29.16**	-	-	-	-
Area x Size	Hand	Size	24.78**	-	-	-	-
	Arm	Size	44.35**	-	-	-	-
Response x Size	Grasp	Size	83.52**	-	-	-	-
	Estimate	Size	17.27**	-	-	-	-

Table 1. The results of repeated measures ANOVA performed on the data of experiment 1. GA = grip aperture. SD = Standard deviation of the grip aperture. TPGA% = Time to peak grip aperture as a percentage of total movement time. MT = movement time. PV = peak velocity. TPV% = Time to peak velocity as a percentage of total movement time. * $p < 0.05$; ** p

Grip aperture values

As can be observed from Figure 3 and Table 1, a main effect of Response was found, reflecting the overall larger grip aperture in grasp responses ($112.2 \text{ mm} / \text{SEM} = 2.5$) compared to estimation responses ($92.8 \text{ mm} / \text{SEM} = 3.1$). In addition, there was a main effect of Object size, implying that the smallest object generated the smallest grip aperture and the largest object generated the largest grip aperture ($50 = 93.2 \text{ mm} / \text{SEM} = 1.8$; $60 = 99.9 \text{ SEM} = 2.1$; $70 = 105.2 \text{ mm SEM} = 2.3$; $80 = 111.5 \text{ mm SEM} = 2.3$) irrespective of the area of stimulation or which response was required.

Most relevant for our hypotheses, Area interacted significantly with Response (see Table 1). Further exploration of this effect revealed that mean grip aperture during estimation responses was consistent with Weber's illusion (Hand = $97.6 \text{ mm} / \text{SEM} = 3.2$; Arm = $88.0 \text{ mm} / \text{SEM} = 3.4$). In contrast, when grasping the stimulus, the subject responded with larger grip aperture values for stimuli located on the arm ($115.3 \text{ mm} / \text{SEM} = 2.8$) as compared to stimuli located on the hand ($108.9 \text{ mm} / \text{SEM} = 2.4$). A significant interaction between Object size and Response (see Table 1) suggested that scaling was more evident in the manual estimation condition, ($50 = 82.2 \text{ mm} / \text{SEM} = 2.9$, $60 = 89.0 \text{ mm SEM} = 3.1$, $70 = 96.2 \text{ mm} / \text{SEM} = 3.1$, $80 = 103.9 \text{ mm} / \text{SEM} = 3.2$), than in the grasping condition, ($50 = 104.3 \text{ mm} / \text{SEM} = 2.3$, $60 = 110.8 \text{ mm} / \text{SEM} = 2.7$, $70 = 114.3 \text{ mm} / \text{SEM} = 2.6$, $80 = 119.1 \text{ mm} / \text{SEM} = 2.7$). Also, this Object size effect is present both for objects located on the arm as well as for objects located on the hand, although the significant interaction between Object size and Area (see Table 1) indicated that this scaling effect is more pronounced on the hand, ($50 = 90.1 \text{ mm} / \text{SEM} = 1.9$, $60 = 99.5 \text{ SEM} = 2.1$, $70 = 107.2 \text{ mm SEM} = 2.4$, $= 80 = 116.5 \text{ SEM} = 2.3$) compared to the arm, ($50 = 96.4 \text{ mm} / \text{SEM} = 2.0$, $60 = 100.3 \text{ mm} / \text{SEM} = 2.7$, $70 = 103.3 \text{ mm} / \text{SEM} = 2.3$, $80 = 106.5 \text{ mm} / \text{SEM} = 2.5$).

Analysis of performance variability (average SD within a condition for each participant) revealed a main effect of Response. Grasping responses (8.5 mm) are less variable compared to estimation responses (10.2 mm). Also, a main effect of area was found, which shows that hand directed responses (8.53 mm) are less variable as compared to arm directed responses (10.25 mm).

Other kinematic variables

No significant effects of Area of stimulation, Object size or an interaction of both were found concerning movement time (see Table 1). Peak velocity appeared to be significantly higher when

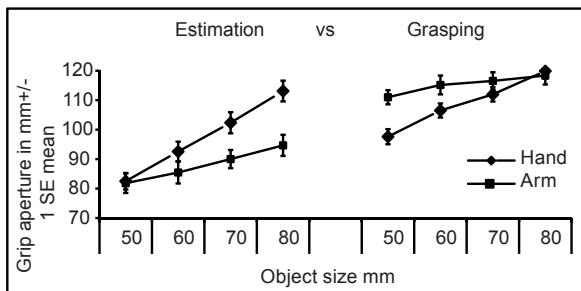


Figure 3. Mean grip aperture for estimation responses and peak grip aperture for grasping responses, in experiment I. Aperture in mm, Error bars = between participants error of the means.

grasping movements were directed to the forearm (Hand = 644 mm/sec; Arm = 756 mm/sec). Also, it emerged significantly later in time for the arm compared to hand directed responses (Hand = 28%; Arm = 31%). PGA was reached approximately at two third of the movement. In this study PGA was reached significantly later in grasping movements directed to objects located on the hand (67%), compared to the arm (66%; see Table 1).

In sum, the results showed that the manual size estimations of solid objects were consistent with Weber's illusion. In contrast, the grasping responses appeared to show the opposite pattern of that observed for estimation responses; larger PGA towards objects located on the arm, compared to objects on the hand.

An important confounding factor which could have caused the observed opposite pattern of results is the influence of tactile feedback which participants received when grasping the objects. Participants received haptic feedback during the grasping blocks whereas during the estimation blocks this was not the case. As such, the right hand received size information which is not available to the right hand in the matching condition. Therefore, participants may have been affected initially by Weber's illusion but then, following feedback, learned that the somatosensory information from the arm leads to size underestimation. As a consequence, participants might have corrected for this by purposely increasing their grip apertures for objects on the arm as compare to objects on the hand. This might have resulted in an opposite effect of the illusion as is found in the matching task. To test this hypothesis, peak grip aperture data of the original experiment's first trial per object size were submitted to the same repeated measures ANOVA as in the main analysis. This will be described in the following section.

First trial analyses

Again, a 2(Area) x 2(Response) x 4(Object size) repeated measures ANOVA revealed significant main effects of Response (Grasping = 110 mm/ SEM = 2.9 , Estimating = 92mm/ SEM = 3.4; F(1,17) = 17.61 p < 0.01) and Object size (50 = 92 mm/ SEM = 2.4, 60 = 99 mm/ SEM = 2.1, 70 = 103 mm/ SEM = 2.9 and 80 = 111mm/ SEM = 3.0; F(1,17) = 28.90 p < 0.01). When exploring differences in Object size we found significant increases in PGA between 50 mm and 60 mm (F(1,17) = 26.39, p < 0.01), 60 mm and 70 mm (F(1,17) = 26.41, p < 0.01) and 60,

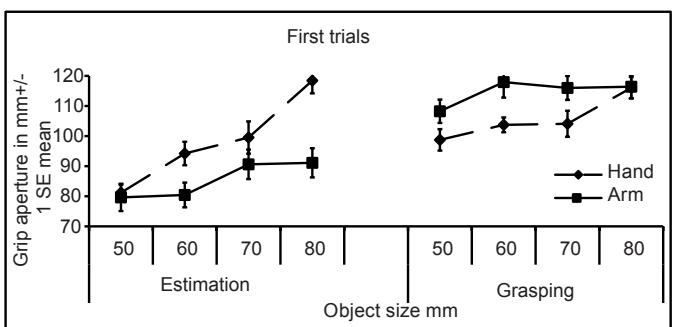


Figure 4. Mean grip aperture for estimation responses and peak grip aperture for grasping responses of all first trials for each Response x Area x Object size condition , in experiment I. Aperture in mm, Error bars = between participants error of the means.

70 mm ($F(1,17) = 51.65$ $p < 0.01$). Most interesting, Area interacted significantly with Response ($F(1,17) = 21.863$ $p < 0.01$), as was found when analyzing all the trials (see Figure 4). Also, this interaction effect yielded a similar effect of Weber's illusion for estimation responses $F(1,17) = 15.77$, $p < 0.01$) versus an opposite pattern of results for grasping responses $F(1,17) = 9.175$, $p < 0.01$).

Discussion

Experiment I assessed the effect of Weber's illusion on a manual size estimation response and a tactually guided grasping response. As was observed in our pilot experiments, the pattern of responses revealed an effect of Weber's illusion on the manual size estimations of solid objects; larger mGA for objects located on the hand, compared to objects on the arm.

In contrast, the grasping responses appeared to show the opposite pattern of that observed for estimation responses, a finding which was not predicted prior to running this experiment.

However, this opposite pattern of results for grasping movements existed only for the smaller objects. The increase in peak grip aperture was only significant between the smaller (50 mm and 60 mm), but not between the larger objects (70 and 80 mm). A straightforward explanation for this lack in increase in thumb and index separation may be that participants had reached their maximal grip opening (the biomechanical constraint in the joints) when grasping the 70 mm wide object. A further increase in PGA for the 80 mm wide object could therefore not be achieved.

Furthermore, differences in tactile feedback between the matching and grasping conditions may have caused the opposite patterns to occur. However, additional analysis of each first trial per condition suggests that the presence of tactile feedback in the grasping condition is unlikely to be the sole reason for the difference in the observed results.

Another important potentially confounding factor causing the observed larger peak grip apertures for arm directed grasping responses is the difference in biomechanics in arm versus hand directed movements. Hand directed grasping movements were always aimed at a more distal location whereas arm directed movements were aimed more proximally. Also, peak velocity co-varied significantly with location, which in itself could have caused the larger arm directed peak grip aperture data. Therefore we ran a second experiment in which we tested whether the difference in spatial location could have caused the observed larger peak grip aperture values for grasping responses directed towards the arm. This was assessed by keeping the grasping movements aimed at one location in external space, but towards different positions on the body (forearm vs. hand). It was expected that peak velocity would not differ between arm and hand directed movements, but that the difference in peak grip aperture remained.

Experiment II

Participants

Thirteen right-handed participants (4 male, 9 female; mean age 27 years; ranging from 20 to 34

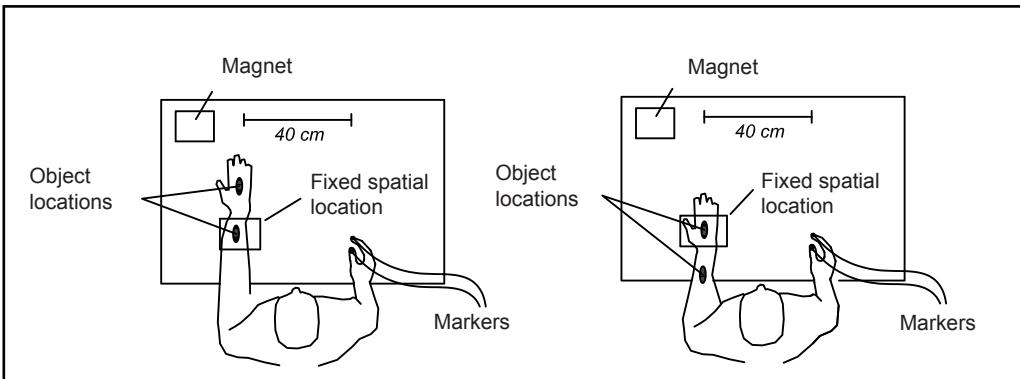


Figure 5. Experimental set up experiment II; note: objects are now located in the same spatial location

years of age) with no history of psychiatric or neurological illness and who were naïve as to the purpose of the experiment, participated in experiment II.

Procedure and design

In this experiment only grasping responses were performed by the participants. Keeping grasping responses aimed at the same location in external space (see Figure 5) was achieved by varying the position of the arm on the table in between trials (prior to the placement of the object). The object of 80 mm length was removed from the experiment since the results of experiment I suggested influences of biomechanical constraints when grasping objects of 80 mm. The rest of the procedure as well as the experimental set up were identical to that of the grasping condition of experiment I.

The experiment had a 2 (Area; palm of the hand or forearm) x 3 (Object size; 50, or 60, 70mm) within-subjects design. A total of 48 grasping trials were tested in randomized order.

Results

All pre-processing procedures and statistics were similar to that of Experiment I. In this experiment PGA data was submitted to a 2 (Area: palm of the hand or forearm) x 3 (Object size; 50, or 60, 70mm.) repeated measures ANOVA.

As expected, the analyses of the peak grip aperture data revealed similar main effects of Area (hand= 103 mm/ SEM = 2.2, arm= 110 mm/ SEM = 2.2) and of Size (50 = 103 mm/ SEM = 2.1, 60 = 107 mm/ SEM =

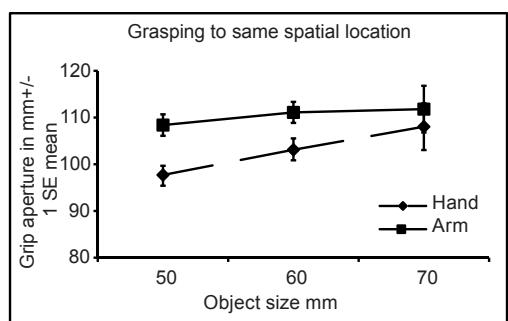


Figure 6. Peak grip aperture for grasping responses, in experiment II. Aperture in mm Error bars = between participants error of the means.

2.2, 70 = 110 mm/ SEM = 2.2; see Table 2). Both 50 mm and 60 mm objects differed significantly in grip aperture as well 60 mm and 70 mm objects.

Finally, Area interacted significantly with Object size (see Figure 6). Further analysis of this effect revealed significant effects of Object size, both in the hand condition as well as the arm condition, however, the increase in PGA in the latter condition was less pronounced, similar to the observed Area x Object size interaction in experiment I.

Factor		F GA	F TPGA%	F MT	F PV	F TPV%
Area		35.69**	NS	NS	NS	NS
Object size		25.09**	5.864*	NS	5.927*	NS
Area x Size		17.96**	NS	NS	NS	4.160*
Contrast		Level				
Object size	50 vs 60 mm	35.80**	NS	-	23.60**	-
	60 vs 70 mm	10.05**	14.41**	-	NS	-
Interaction effects		Level	Factor			
Area x Size	Hand	Size	42.85**	-	-	NS
	Arm	Size	8.130**	-	-	NS

*Table 2. The results of repeated measures ANOVA performed on the data of experiment II. GA = grip aperture. SD = Standard deviation of the grip aperture. TPGA% = Time to peak grip aperture as a percentage of total movement time. MT = movement time. PV = peak velocity. TPV% = Time to peak velocity as a percentage of total movement time. * p < 0.05; ** p < 0.01*

Other kinematic variables

A significant main effect emerges for Object size (see Table 2 for F and p values) when analysing the relative time to PGA (TPGA%). The smallest and middle object causes the TPGA% to occur significantly earlier in time as compared to the larger object size (50 mm = 67.0%, 60 mm = 67.7%, 70 mm = 69.9%). Also, a significant main effect of Object Size was found for peak velocity (50 = 722 mm/sec/ SEM = 52, 60 = 749 mm/sec/ SEM = 54, 70 = 744 mm/sec/ SEM = 54; see Table 2). This implies that grasping movements towards the smallest object resulted in significantly slower movements as compared to the larger objects. Most importantly, the difference in peak velocity values between arm and hand directed grasping responses observed in experiment I disappeared ($F(1,12) < 1$). However, with respect to the relative time to peak velocity (TPV%), an interaction effect of Area and Object size was found. Further exploration of this effect revealed only a trend towards significance for Object size on the hand ($F(1,12) = 3.345$, $p = 0.052$). This implies that the larger the object, the earlier the peak in velocity emerges (50 mm = 33%, 60 mm = 32 % and 70 mm = 30%), although post hoc contrasts did not reveal any significant differences. No significant effects were found when analyzing movement time.

First trial analyses

To test the hypothesis of tactile feedback causing the observed grasping pattern which is opposite to that of Weber's illusion, an additional analysis of the aperture data of the first trial per object size were submitted to the same repeated measures ANOVA as in the main analysis. Again, a 2 (Area: palm of the hand or forearm) x 3 (Object size; 50, or 60, 70mm.) repeated measures ANOVA revealed a significant main effect of Area (Hand = 103 mm/ SEM = 2.8, Arm = 112 mm/ SEM = 2.7; $F(1,12) = 22.26$ $p < 0.01$). No significant effects were found for Object size ($F(1,12) = 1.710$) or Area x Size ($F(1,12) = 1.056$).

Discussion

The results of experiment II suggest that biomechanical differences between grasping responses directed to different spatial locations cannot account for the observed larger peak grip aperture, but did produce the higher peak velocity values for arm directed responses in experiment I. However, some new significant effects of other kinematic variables which did not occur in the first experiment require some discussion.

First, the time at which PGA occurred was related to object size. Similarly, peak velocity was related to object size as well. Both findings are consistent with the idea of more time for online adjustment for the smaller object. This effect might be consistent with higher spatial accuracy demands (a more precise grip) for grasping smaller objects, as also observed in visuomotor grasping (Gentilucci et al., 1991). But, why was this effect not observed in our first experiment in which grasping movements to the arm were uncertain as well? A simple reason may be that in experiment II the position of the arm was changed in between trials and this new position had to be recurrently updated in order to accurately perceive the spatial location of the object to grasp. It could be that these updates generate noise leading to uncertainty about location of the arm and therefore uncertainty about the location of the object. Together with the higher spatial demands of the smaller objects, this might have caused the need for more online adjustments.

General Discussion

The current study aimed to investigate whether Weber's illusion differed depending on the type of response given. Experiment I assessed differences in grasping and manual size matching of objects placed on the hand and the arm. The results of the size matching responses were consistent with Weber's illusion. In contrast, PGA during grasping of the objects showed an opposite pattern with larger hand openings for objects placed on the arm. Experiment 2 showed that the observed pattern was not caused by biomechanical differences. Overall, these findings are consistent with the idea that the somatosensory system deals differently with tactile information depending on whether the information will be used to provide a conscious perceptual size judgment response, or an implicitly driven motor action. With respect to the size esti-

mation responses, the current findings are consistent with previous studies showing differences in distance judgements between areas with low and high receptor density. As described above, this pattern has been attributed to incomplete size constancy judgements for which visual input about the size of the body part is used (Taylor-Clarke et al., 2004). In contrast, the current results suggest that differences in receptor density (and incomplete size constancy mechanisms) are not the most dominant when determining the pattern of grip aperture during tactually guided grasping. Instead, other mechanisms must have caused a pattern which is opposite to that expected based on Weber's illusion. One possibility might be that differences in tactile feedback between the matching and grasping conditions may have caused the opposite patterns to occur. However, additional analysis of each first trial per condition suggests that the presence of tactile feedback in the grasping condition is unlikely to be the sole reason for the difference in the observed results. Thus, although tactile feedback may have influenced performance in later trials, the pattern of larger hand opening for objects placed on the arm was already present during the very first trials. Another possible explanation could be that the manual size estimation used in this experiment is not a feasible perceptual measure. Indeed, Franz (2003) suggested that a manual size estimation response such as the adjustment of the thumb-index separation is highly sensitive to a change in object size, illusionary or real, whereas a more "classical" measure of size such as the method of adjustment shows less sensitivity to an illusion. The author showed that when using a more traditional measure of size, a frequently found difference between grasping and matching responses in effect of the Tichener illusion disappeared. Results from our second pilot experiment indeed showed that the traditional measure was less sensitive to Weber's illusion however this difference was not significant. Furthermore, this response still showed an overestimation of hand versus arm perceived objects and a reversal of this pattern as observed for the grasping response found in experiment I did not occur. Therefore, other factors might have caused the observed differences between matching and grasping in our experiment.

Interestingly a similar response pattern for grasping movements was found in a visuomotor experiment (Brown, Halpert, & Goodale, 2005). They compared grasping towards foveally and peripherally presented objects and found larger grip apertures in the peripheral condition. This similarity in response patterns suggests that when grasping is directed towards areas with reduced receptor density such as the skin of the forearm, or peripheral vision, the hand is opened wider. A possible explanation for this is that when sensory input about the target is non-optimal, the motor system responds by increasing its safety margin (Schlicht & Schrater, 2003); when grasping an object, the participants must be aware of the possibility to collide with the object. The more uncertain they are about the size or location of the object, the wider they would open their grip in order to avoid collision (Jakobson & Goodale, 1991). In addition to a larger grip aperture, one would perhaps also expect increased variability when sensory input is reduced. Although Brown et al. (2005) could not find evidence for increased variability in their peripheral grasp condition, in our experiment both grasping and matching responses

revealed a larger variability for arm placed objects. Hence one could argue that size information for objects placed on the arm is processed with less certainty compared to the objects located on the hand. This uncertainty forced participants to open their thumb and index finger wider when grasping objects located on the arm, in order to avoid collision. When estimating the size of an object, however, collision avoidance is not necessary as there is no direct contact with the object. Therefore, a possible underlying mechanism responsible for the observed differences between grasping and matching responses may be that in principle all incoming tactile information is affected by the (imperfect) size constancy mechanisms resulting in an underestimation of tactile size for areas with reduced receptor density. However, uncertainty about tactile input causes an extra safety margin between thumb and index finger when grasping the object. Consequently this could mask Weber's illusion for the grasping trials. Based on the current data, we cannot rule out this possibility, but the extra safety margin must be of a considerable magnitude for this pattern to emerge.

A second possible mechanism could be that differences in effects of an illusion depend on which reference frame is used to solve the task (Bruno, 2001). Size judgment responses are more likely to be based on an object based frame of reference and therefore are influenced by imperfect size-constancy mechanisms as suggested by Taylor-Clarke (2004). In contrast, for grasping responses object features (e.g. size or object endpoints) are coded with respect to the actor's grasping hand, in a 'hand-centred reference frame'. These are not necessarily influenced by size constancy mechanisms.

However the current data do not allow us to distinguish between the discussed mechanisms and therefore future studies should further investigate causes of the observed pattern, for example by manipulating sensory input about the target object in a different way. One way to achieve this is by increasing certainty about tactile input provided by non informative visual input of the arm, as was done by Kennett, Taylor-Clarke, & Haggard (2001) and Taylor-Clarke et al. (2004). Finally, exposure to a visually magnified version of ones own arm might be a way of assessing whether size constancy mechanisms also affect grasping responses.

CHAPTER IX

Summary & conclusions

Higher order effects and task dependent processing

The research reported in this thesis aimed to study the relationship between lower-level and higher-order somatosensory processes and whether this relationship can be modulated by the required response. Using various experimental paradigms in healthy participants and stroke patients we were able to ascertain that higher order stored somatosensory knowledge influences bottom up perception in several ways. We observed that these influences were most salient when bottom-up information was processed in order to consciously identify or recognize the somatosensory information (**Chapter 6, 7 & 8**). On the contrary, the processing of information for the computation of a goal directed motor response was less affected by higher order processes (**Chapter 8**). An important test that can account for such conclusion was provided by comparing the performances of two stroke patients, revealing a classical double dissociation (**Chapter 4**). That is, one patient performed relatively well when programming a motor response directed towards a touched location on his hand, but was impaired when indicating this location on a drawing of a hand of which it is suggested to involve stored knowledge about general body characteristics. In contrast, a second patient showed the reverse pattern of results indicates the relative independence of the two tasks. Further support for the assumption that higher order somatosensory information influences are most pronounced in perceptual tasks is provided by **Chapter 5**. In this chapter, we tested three patients without low-level tactile processing disturbances, but who suffered from finger recognition problems. The pointing to localise results revealed preserved pointing localisation responses directed to the touched fingers as compared to pointing aimed at a drawing of the fingers. Finally, although not part of the main question, we further confirmed that fingers are not just some body parts, but are

possibly represented separately as compared to the rest of the body (**Chapter 2, 3**).

Results from localisation studies

In **Chapter 2** we investigated the localisation performance towards low-level, simple, tactile pressure stimuli using a reaching to point paradigm in blindfolded healthy participants. Although many studies have been carried out to investigate this function, until now, the focus has been aimed at perceptual identification of a location, instead of its contribution to goal directed action towards identified body parts. Moreover, this method allowed us to investigate how tactile location information is initially processed, and how tactile feedback influences the final localisation response. As was hypothesized, tactile localisation performance improved for stimuli presented to areas with better tactile acuity, however, we failed to find support for the idea that recurrent proprioceptive input about the location of the limb would improve localisation accuracy in general. Unexpectedly, we did not observe more accurate localisations for finger as compared to hand stimuli. This might be explained by a ceiling effect in the pointing performance. That is, localisations cannot be more accurate as the localisations on the hand simply because motor parameters induce too much noise to allow more accurate localisations. This lack of accuracy difference was evident before tactile feedback about the location of the tip of the pointing finger on the skin was used to correct the initial pointing movement. After the first landing on the skin, participants corrected their response, leading to an overall better performance for stimulation on the finger as compared to stimulation on the hand. Such corrections were largest in the lateral-medial direction as compared to the distal-proximal direction. Despite the influence of uncertainty when pointing towards a small landing area such as a finger, this observation triggers a different question. Perhaps participants were uncertain about the origin of the tactile stimulus in terms of which finger has been touched? It has been previously suggested by Schweizer et al., (2001) that fingers may have overlapping receptive fields. When a tactile stimulus activates skin on one finger, overlapping receptive fields allow for an activation of cells involved in the processing of information originating from a neighbouring finger. However, the influence of overlapping receptive fields described in the study by Schweizer et al., (2000) was observed when near-threshold stimuli were applied, in contrast to our above-threshold stimuli. Nevertheless, we think that this finding may be supportive of the notion that fingers are represented differently as compared to the rest of the body.

In **Chapter 3**, we further explored the influence of digit overlapping receptive fields using a more perceptual response. An important characteristic of areas involved in higher order somatosensory processing is that these areas contain multimodal cells. These cells become activated by visual as well as tactile and proprioceptive information and have some remarkable spatial properties as they play a crucial role in the incorporation of tools in our body schema (Maravita and Iriki, 2004). Moreover, these cells respond to somatosensory information from a given body region as well as to visual input informative of the space surrounding the body part. The authors suggest that this system may be crucial for coding action in space. As fin-

gers almost always perceive information when actions are performed, implying that (spatial) visual and proprioceptive input is tightly connected, it could be suggested that the receptive fields as mentioned by Schweizer et al., (2000) might be constructed by these multimodal cells. Therefore we reasoned that overlapping receptive fields might be spatially defined instead of somatotopically. To test this, we asked participants to localize (unseen) tactile stimuli applied to their fingertips by verbally naming the number corresponding to the perceived location in three different posture conditions: fingers together, fingers spread and fingers interwoven. When fingers are interwoven, the hands are positioned on top of each other and the fingers are interleaved, the spatial distance between the fingers would be the same as in fingers spread, although the space would be occupied by a finger of the other hand. If there are spatially defined tactile receptive fields that normally span more than one finger, localisation will improve when the fingers are spread as compared to fingers together. Moreover, fewer errors will be made to the neighbouring fingers, a result which was earlier observed by Schweizer et al., (2001). Here we observed that fewer errors were made when the fingers were spread, indicative of spatially defined overlapping receptive fields. However, the reduction of errors was not specific to the neighbouring fingers since the number of errors decreased in general. This suggests that spreading the fingers leads to more distinct information about the position of the fingers, which in turn can improve tactile localization. Together, these findings are more supportive for somatotopically as opposed to spatially defined receptive fields. In addition, it might be suggested that these somatotopic receptive fields are constructed by cortical cells in earlier processing areas as compared to previously mentioned multimodal areas.

In **Chapter 4 and 5** we combined perceptual and motor localisation responses in one study. We investigated direct localisation responses towards simple tactile stimuli on the body and an indirect response (on a line drawing of a hand) indicative of the perceptual recognition of the location of the stimulus. Two stroke patients with preserved basic somatosensory processing were tested with these two tasks. The results suggest that the processes of perceptual identification and sensorimotor body-directed movements are mutually independent. We demonstrated a double dissociation that was suggested by earlier observations of Paillard, (1983), Halligan et al. (1996) and Rosetti et al (2001). However these previous studies were based on patients suffering from impaired tactile detection, whereas our patients had preserved low-level tactile detection abilities. As such the data reported in the present thesis complement to the already described dissociation as it supports the notion that the action perception dissociation is a more general mechanism, and not just merely valid in cases of low level perception (detection) impairments as was earlier observed in the studies of Paillard, (1983), Halligan et al. (1996) and Rosetti et al., (2001).

Given the apparent relationship between the processing of somatosensory information and the representation of the body, we further discussed the observed pattern of behaviour in terms of this representation. Cognitive neuroscience suggests that there are two distinct body representations (e.g. Paillard, 1999; Gallagher, 2005). Body image and body schema are, respectively,

thought to be involved in conscious perceptual judgments about body size and configurations etc. and unconscious sensorimotor guidance directed to one's own body. Therefore, our results provide further support for separate processing for body image and body schema. Additional evidence for such a suggestion is provided by the study described in Chapter 5 as three patients with finger agnosia were impaired in localising a (unseen) touched finger on a drawing but performed relatively well when localising the touched finger when localisation responses were directed to the own body. An important difference as compared to the findings in the previous chapter is that the localisation responses were aimed to entire body parts, and not to a specific tactile location. As such, we demonstrate that the suggested task dependent difference in somatosensory processing is also valid when higher order information about an entire body part is processed. Finger agnosia has been described as an inability to explicitly individuate between the fingers, possibly caused by the loss of specific knowledge about finger configuration. This condition can be seen as separate from a general body recognition deficit such as seen in patients with autotopagnosia. Therefore, these findings are additionally supportive of separate, or different, representations for the fingers and the rest of the body.

Results from illusions and imagery tasks

In **Chapter 6** we investigated the integration of tactile information over fingers when fingers cannot be explicitly individuated (finger agnosia). Many studies on finger agnosia report cases that only have been tested on their explicit knowledge about finger identity, however, implicit processing of such knowledge has yet received little attention. Also, it has been suggested that finger agnosia arises from fused neural representations of the fingers (Kinsbourne & Warrington, 1962; Haggard and Wolpert, 2004) and as a result, the fingers are merged into a solid lump. As a consequence, tactile information can no longer be attributed, or coupled, to the finger to which the tactile stimulus belongs. This might imply that tactile information perceived by the fingers cannot be accurately integrated over the fingers, as some separation between the fingers must be maintained when for example haptically exploring objects. To that purpose we tested a finger agnosia patient (GO) on two tasks that measured the ability to integrate somatosensory information perceived by the individual fingers when the explicit finger identity is not important. Our results showed that GO's ability to implicitly use information about the relative positions of the fingers for the interpretation of tactile information at the fingertips, was comparable to that of age-matched controls, despite her difficulties in explicitly identifying the fingers.

In a second task, we investigated the attribution of tactile information to a corresponding finger on a more explicit level. Again we observed that GO was able to couple tactile information to the accurate finger, as she accurately used this information to judge the position of the stimulus, relatively to a second, simultaneously applied stimulus on a neighbouring finger. Interestingly, we observed that when the fingers were crossed, performance was even better as compared to healthy controls. In three different studies testing healthy participants, Benedetti

(1985, 1988; Benedetti et al., 1991) revealed that tactile information presented to two neighbouring, crossed, fingers leads to a erroneously perceiving the tactile stimuli as if the fingers were uncrossed. It was suggested that humans do not have functional experience in such range of joint position, since crossing the fingers is a very uncommon situation. In the 1991 study, Benedetti and co-workers asked participants to spend their days with their fingers crossed and taped together. That way participants were able to gain more tactile experience in a finger crossed condition. Only after several months participants were able to accurately judge the position of the tactile information when the fingers were crossed. Our findings suggest however, that it is not just the lack of tactile experience in a crossed fingers situation which is responsible for the observed illusion. In fact, GO's accurate performance in a fingers crossed condition suggests that the lack of finger related knowledge might be of importance. Elaborating further on this, we suggest that if finger specific information is lost, then GO's paradoxical improvement might be caused by a lack of interfering finger related knowledge. Fingers are almost always presented horizontally aligned, and visual as well as tactile and proprioceptive information about these uncrossed fingers has been acquired throughout the lifespan and stored as long-term knowledge. As a consequence bottom-up information is always interpreted in this default "fingers are never crossed" situation. However, such reasoning is in need for further investigation, as GO was not entirely "normal" in all aspects of the task. Nevertheless, our findings do suggest that the inability to individuate between the fingers does not arise from a "fusion" of the fingers at an early level of integrating tactile proprioceptive information over the fingers.

Influences of stored knowledge on bottom-up processes are commonly seen in everyday behaviour. For instance stored representations of objects and the body play a crucial role in constructing a haptic perceptual experience and are essential for the ability to evoke an internal experience without external stimulation (imagery). Most understanding about imagery processes is derived from studies investigating visual or auditory imagery. Tactile imagery, however, has not been studied. In **Chapter 7** we investigated behavioural effects of tactile imagery, using a 2AFC spatial discrimination task. For the first time we show that tactile imagery, relatively to auditory imagery, speeds up left right discrimination of tactile stimuli. On the contrary, the reverse was true for auditory imagery, which speeded up left right discrimination of auditory stimuli more than tactile imagery. These findings are in line with previously found unimodal effects of imagery on a simple auditory and visual detection task.

Finally, **Chapter 8**, we investigated the effects of a higher order perceptual illusion on a perceptual and a motor response. Weber found that distances between tactile stimuli on a high receptor density area are perceived as being larger as compared to an identical distance on a low receptor density area (Weber's illusion). Previous studies of visual illusions suggest that illusion effects vary with the type of response given. Here we tested a modified version of Weber's illusion in which a solid object was placed on the forearm or hand. Blindfolded participants were required either to give a size estimation or grasp the object. The results showed

that size estimation of solid objects was consistent with Weber's illusion, whereas grasping responses showed an opposite pattern (e.g. larger hand opening for objects on the forearm). A second experiment showed that this pattern is not due to biomechanical differences induced by the difference in spatial position of the target objects on the hand and arm. We suggest that the larger grip aperture when grasping objects on the arm were due to an increase in safety margin as a response to greater uncertainty about the object dimensions due to reduced receptor density.

Concluding remarks and general discussion

The studies reported in this thesis dealt with interactions between higher order and lower somatosensory processing level in the context of task dependent processing. They suggest that somatosensory information is processed differently when used for the guiding of immediate goal directed "action" responses as compared to when used for conscious "perceptual" recognition. However, this does not entail that these systems operate without communication. In the following sections I will further integrate our findings and where possible, discuss alternative views concerning the action perception dissociation in terms of these responses and the results they bring about.

Discussion of alternative explanations

In the pointing tasks we investigated in **Chapter 2, 3, and 4**, pointing responses were programmed on basis of tactile input and were either aimed at a line drawing of the hand or the participant's own hand. It has been suggested that in order to perform body directed movements in reaction to tactile stimuli, tactile information needs to be integrated with proprioceptive information (Haggard Wolpert, 2005; Bonda, 1995). The way the brain solves this integration is to code somatotopic location information in an egocentric reference frame. On the other hand, when pointing towards a drawing of the hand, tactile information which is initially coded in somatotopic coordinates, needs to be transferred to a different, visually based reference frame, informative of how our body looks from the outside. In order to overcome this problem, tactile location information needs to be processed in terms of its relative position within the body part rather than its egocentric position relative to the pointing hand. Therefore, the brain has to compute how far the perceived location was from the wrist joint, of from the lateral border of the forearm etc. Doing so, tactile location information is integrated on a higher level with stored long term knowledge about the configuration and the visual characteristics of ones own hand and subsequently scaled according to a 2D drawing of some other hand. It seems that the additional scaling to other body features, necessary when indicating the position on a drawing of a hand, is the most salient difference between the action and perception response. In order to generate a body directed movement, merely integration of tactile and proprioceptive information needs to occur. The integration of somatosensory information

with higher order knowledge seems to be an important factor when consciously recognizing perceptual qualities of the information. In contrast, body-directed action responses do not involve this type of integration.

When re-interpreting our double dissociation results (**Chapter 4**), one could argue that KE is impaired when coupling tactile to proprioceptive information (necessary to guide the pointing arm to the touched location). On the other hand, his performance seems relatively preserved when coupling tactile information to stored higher order visually defined information about the body (such as joint features, boundaries etc), which is necessary to guide the pointing arm to the location on the drawing of the hand JO, however, is impaired when integrating tactile information to stored knowledge about body features, whereas she is intact when coupling tactile to proprioceptive information. Interestingly, when specific information about the common configuration of the fingers is lost, a similar dissociation is observed (**Chapter 5**); intact localisation responses when targeting the fingers of ones own body, but impaired localisation responses when integrating tactile information with higher order visual knowledge about the common configuration of our fingers. But why should it be important to use visual information when individuating between the fingers? As yet, no study has been investigated this question directly nevertheless, I take the opportunity to further elaborate on this matter. Fingers are to some extent different as compared to other body parts since there are five different parts positioned in close proximity. The thumb and little finger are the easiest to differentiate as they are not accompanied by a second neighbouring finger whereas the three middle fingers are the most difficult to identify. Moreover, several authors have suggested that finger overlapping receptive fields exist (Iwamura, Tanaka, Sakamoto, & Hikosaka, 1983a, 1983b; McKenna, Whitsel, & Dreyer, 1982) which implies that a tactile stimulus applied to one finger might activate cortical cells "belonging" to the neighbouring finger, albeit to a lesser extent. Perhaps, in order to individuate between one's own fingers additional sources of information are required. A plausible source of information is provided by knowledge about common finger configuration. Such knowledge is acquired by recurrent co-activation of tactile and visual input throughout the lifespan and subsequently stored as long-term knowledge. Future research may focus on the importance of such contribution in the identification of ones own fingers.

Regarding the matching and grasping responses used in **Chapter 8** to test task related effects of Weber's illusion an alternative interpretation may be formulated. We observed an effect of a tactile illusion (Weber's illusion) in a perceptual size matching response, but failed to observe this effect in a grasping response. When grasping the object located on the hand, one alternative explanation may be as follows: the initially somatotopically defined input about the endpoints of the object is spatially coded and subsequently coupled to proprioceptive information of the grasping arm to program the grasping response. Indeed, Smeets and Brenner (e.g. 1999) stated that grasping movement consists of two pointing movements of the thumb and, for example, the index finger, each aiming to land on the endpoint surface of the object. These two surfaces are defined in space and can be viewed as unrelated, at least with respect to the grasp-

ing response. Generally, grasping is considered a response consisting of two components; the transport of the hand to the object and the opening of the hand according to the object's size (Jeannerod, 1986). However, Smeets and Brenner argued that grasping is merely a matter of controlling the digits. Therefore, size is not essential for a grasping response, whereas the exact location of the object's endpoints is in fact important. In contrast, when estimating its size, the goal is to adjust the separation between thumb and index finger so that it corresponds with the size of the object. However, this alternative explanation was tested in a pilot experiment described in **Chapter 8** and we still observed a similar effect of the perceptual illusion when we asked participants to match their fingers precisely at the perceived endpoints of the object, thereby forcing them to process the spatially coded endpoints of the object.

So far, the dissociation between action and perception seems to be also one of dissociating tactile- proprioceptive lower-level integration on the one hand, and the integration of tactile information with higher-order knowledge on the other. However, many authors have questioned the fundamental idea of dissociating bodily related processing into two (or more) representations (e.g. Brozolli et al., 2007; de Vingemont et al., 2007). Although an important goal in science is to be parsimonious, dividing a complex mechanisms into two separate entities does not inevitably lead to better understanding. In a further attempt to discuss the existence of separate pathways for action and perception, I would like to consider the following approach.

An alternative view

When studying the integration of information across or within modalities, many authors have been taking a more general Bayesian approach (e.g. Ernst and Bulthoff, 2004; Rowland, Stanford and Stein, 2007). This approach can be regarded as a general framework which specifies the information in representations that allows someone to perceive the world. Importantly, it defines the information in terms of inferences, not in how the information is used. An important implication of such a framework is that it states that the brain needs to make inferences about the world, using knowledge acquired through experience. Such approach is able to reveal common behavioural mechanisms when minimizing the use of strong concepts, subdivisions or all or nothing statements.

For example Ernst and Bulthoff (2004) investigated how a robust percept is created in an ever changing environment, sometimes full of conflicting information. A common solution of our brain to overcome such conflict is to gather more and more information about the perceptual event until the ambiguity will be resolved. However, in order to prevent an extensive delay in behaviour, the brain decides on one source of information and uses it to calculate the required response. These decisions are facilitated by prior knowledge about the perceptual event and will affect sensory input in a top-down fashion. In the natural world, correlations exist between perceptual events from different modalities. Implicit knowledge about these correlations is build up by experience acquired throughout the life span and is an important source of information when sensing the world. So, the most common situation for that particular perceptual

event will guide the decision of the brain in picking the signal. For example, the best side to view an object is that corresponding most to the view in which we initially learned the object (usually the front). In the tactile modality, the best orientation to recognize the object is that most common to the fingers to explore (Newell et al., 2001). Such prior knowledge is nourished by sensory experience and builds up from early childhood. For instance, the ability to use visually guided grasping movements and more differentiated finger movements (+/- 6 months of age) provides the fundamental tool to the development of exploratory procedures that correspond to a specific object property (Piaget, 1952; Bushnell and Boudreau, 1993). Also, an important consequence of tactile experience is that it continues to shape the perceptual configuration of our hands and fingers, even in adult life. An interesting example which might indicate the importance of using prior information when perceiving tactile information is given by our finger agnosia patient. GO did not suffer from a perceptual illusion after an impairment in the individuation of finger related information. As described in the introduction, the position of fingers influence the way the haptic world is perceived. A good example of this is provided by "Aristotle's illusion". When two fingers of the same hand are crossed, and a pencil is placed between these crossed fingers, a sensation of two pencils rather than one is experienced (see for overview of the literature Tastevin, 1937; Jackson et al., 1953). In normal, everyday life, our fingers are never crossed, nor are they crossed when perceiving tactile input from an object. Keeping in mind that the brain makes inferences about the world, the prior knowledge used to perceive the tactile information will most definitely be that of "uncrossed" fingers. Tastevin describes the illusion as perceiving two rather than one object which might be the only possible interpretation the brain can come up with. In fact, Benedetti (1985, 1988) observed that participants, when judging the position of a stimulus perceived by one finger relatively to that of a reference stimulus applied to a neighbouring finger, perceived the tactile information as if the fingers were uncrossed. However, in Tastevin's example, knowing that a pen is a single object does not prevent someone from the perception of two rather than one object. Interestingly, changing the content of prior knowledge from "fingers never crossed" to "fingers can be crossed" allows participants to accurately perceive the position of tactile stimuli when applied to crossed fingers. However, in order to accomplish such change Benedetti (1991) had participants tape their fingers together in a crossed position for over at least a month². Besides influencing bottom-up information, stored conceptual knowledge can also be activated by voluntary processes, or, mental imagery, and this can be regarded as fundamental to all our reasoning, remembering, dreaming etc. Most studies have been dedicated to disentangle visual imagery processes and those few studies using tactile imagery have been investigating its neural correlates.

² Note: some participants started to perform accurately in the crossed position only after 6 months.

A commonly accepted view of mental imagery is that the neural areas involved when imagining a certain sensation, overlap largely with those areas normally involved in the perception of that sensation, even though the activation is less as compared to real perception (see for review Farah, 1983; Kosslyn, 2001). In that view it is plausible to suggest that imagery can interfere with real perception, similar to what is normally observed when a perceptual event is affected by a previously processed perceptual event. Indeed we observed such mechanism for tactile imagery; thinking about touch relatively facilitated processing times as compared to thinking about a sound.

Together, task dependent processing of somatosensory input may be better explained in terms of complex interactions between various bottom-up processes and top-down knowledge and experience. These interactions need to be specified in more detail and future studies should be aimed at exploring them.

Final remarks

The reported results, derived from the investigation of healthy participants and patients suffering from a stroke, are supportive of the theory of task dependent processing within the somatosensory. This theory holds that the brain organizes incoming input according to the response it has to perform on it. However, the fact that we found results supportive of an action-perception dissociation in situations that strictly investigate either an action or perception response, does not rule out the possibility that in other, perhaps more natural, cases the dissociation is less clear-cut.

When reading a book by Hella Haasse (Sterrenjacht, 1950, 2007) I came across a nice example of such a situation in which action and perception are in close harmony.

"Keeping an eye on the woman sleeping in the bed, I put my hand in her bag and searched for her wallet among all the other stuff I encountered. One by one, my finger tips explored a key ring, a bottle of perfume, a small container with pills, a handkerchief, an ink pen..... and.... (at that point I almost cried out) a I couldn't even dear to think of the word anymore. With trembling fingers I took the object from the bag. It was the garnet star.

This example strikingly emphasizes how perception and action can interact. Perhaps investigating interactions between perception and action offers an exciting direction in the study of the somatosensory system. Moreover, such perspective might be of additional help in finding effective rehabilitation strategies in sensorimotor impairment as often observed in stroke patients. All in all, gaining more insight in the world of touch might accelerate the accumulation of knowledge about brain function in its widest scope. I hope by now you have been touched by the importance of the investigation of touch, just as I have been while working on my thesis.

CHAPTER X

Samenvatting in het Nederlands

De weersvoorspellingen op internet, een glossy magazine, muziek die door de woonkamer schalt; ons leven wordt voortdurend gevuld met visuele- en geluids informatie. Informatie waarop we continu onze beslissingen baseren: wel of niet deze film kijken, wel of niet even een rondje wielrennen, etc. We zouden bijna vergeten dat er nog andere zintuiglijke informatie is die ons gedrag in het dagelijks leven vormgeeft. Pas als je verstoken bent van informatie van een bepaald zintuig, na het doormaken van bijvoorbeeld een beroerte (herseninfarct of bloeding), dringt het tot je door hoe belangrijk de betreffende bron van informatie kan zijn. Een passage uit "the disembodied woman", geschreven door Oliver Sacks, beschrijft het reelaas van een jonge vrouw die na een hersenbeschadiging te hebben opgelopen, niet in staat was informatie uit haar gewrichten, spieren en huid waar te nemen. Ze had geen enkel gevoel meer in haar lijf, was "zichzelf kwijt". Ze was zelfs niet meer in staat zichzelf te identificeren met de foto's van de vrouw die ze ooit was. Alleen wanneer ze in een cabriolet rondreed en de wind haar huid zachtjes beroerde, had ze het idee dat ze zichzelf weer kon ervaren. Naast het belang van tast voor het ervaren van jezelf en je eigen lichaamsbeeld, speelt de tast een doorslaggevende rol bij allerlei handelingen met voorwerpen in de buitenwereld. Stel je eens voor om zonder gevoel in je handen en vingers door een tijdschrift te bladeren. Het wordt dan wel erg ingewikkeld om een pagina om te slaan, of met onderkoelde vingers een knoop uit een touw te halen. Ook al kunnen we veel compenseren door te kijken naar wat we doen, we krijgen geen informatie over hoe glibberig en glad materiaal is, of hoe zwaar. Dit soort informatie is van doorslaggevend belang om onze grip aan te passen. Wanneer onze vingers en handen niet worden voorzien van de juiste informatie dan knijpen de vingers te hard dicht of juist niet hard genoeg. Tastinformatie over de vorm,

structuur van het materiaal en het gewicht verzameld door de handen en vingers, sturen ook weer de volgende reeks van vinger en handbewegingen aan om zo een voorwerp te kunnen manipuleren. Veel van dit soort veel voorkomende en relatief eenvoudige handelingen zijn in grote mate automatisch. We doen het vaak zonder dat we er erg in hebben. Onze ogen zijn gericht op de tv, onze handen zoeken feilloos het knopje om de zenders door te lopen. In de wetenschappelijke literatuur (o.a. Dijkerman & de Haan, 2007) zijn er aanwijzingen dat de verwerkingsroute van de tastinformatie door de hersenen afhankelijk is van wat je met de informatie doet. Als er een vlieg op je hand landt kun je precies aangeven waar deze vlieg zich op je hand bevindt, maar je kan hem ook wegslaan. In het kort betekent dit dat er onderscheid gemaakt kan worden tussen: (1) het verwerken van tastinformatie om er een actie of handeling mee uit te kunnen voeren (actie), of, (2) of het verwerken van tastinformatie om tot een herkenning van de informatie te kunnen komen (perceptie). Met andere woorden, sensorische informatie wordt verwerkt naar gelang het doel waarvoor deze informatie gebruikt wordt. Hierbij wordt uitgegaan van een theorie uit de visuele waarneming die stelt dat visuele informatie gebruikt voor bewuste herkenning op een andere manier en via een andere route in de hersenen wordt verwerkt dan visuele informatie gebruikt voor het programmeren van een actie (Milner & Goodale, 1995, 2008). Bewijs voor de hierboven beschreven theorie over het onderscheid tussen de verwerking van visuele informatie voor een handeling of voor een herkenning, komt onder andere uit onderzoek naar patiënten met visuele agnosie en optische ataxie. Patiënten met visuele agnosie³ hebben ondanks normaal zicht specifieke stoornissen in de verwerking van visuele informatie, variërend van stoornissen in het herkennen van vormen oriëntatie en kleur, tot objecten en gezichten. Dit kan tot grote beperkingen in het dagelijks leven leiden. Dit wordt geïllustreerd door de volgende gevalsstudie van een dame die het verschil tussen een horizontale en verticale lijn niet meer kon zien (perceptie). Desondanks was zij nog wel in staat moeite-loos een brief in een opening van een brievenbus te stoppen (actie). Om dit goed te kunnen doen is het noodzakelijk de specifieke oriëntatie van de opening verwerkt wordt. De perceptieroute is bij deze patiënt blijkbaar beschadigd, terwijl de actieroute nog intact is. Het omgekeerde van dit verhaal blijkt uit de beschrijving van een patiënt die geen problemen heeft met de perceptie van objecten, maar moeite heeft om op basis van visuele informatie een actie uit te voeren. Dit wordt ook wel optische ataxie genoemd. Voor het tatsysteem lijkt zo'n zelfde tweedeling te bestaan, wat onderbouwd wordt door het literatuuroverzicht van Dijkerman & de Haan (2007). Dit proefschrift beschrijft een zoektocht gericht op het beantwoorden van de vraag of tastprocessen inderdaad ingedeeld kunnen worden naar "tastvooractie" en "tastvoerherkenning" en of deze functionele tweedeling ook terug te vinden is in de hersenen gebieden die betrokken zijn bij deze processen.

³ Visuele agnosie: het niet meer kunnen herkennen van objecten bij intacte visuele waarneming en specifieke object kennis. De objecten worden wel waargenomen, in sommige gevallen kunnen kleur en vorm etc. nog benoemd worden, maar de objecten worden niet meer als zodanig herkend.

Hierbij worden studies beschreven met patiënten die een hersenbeschadiging hebben opgelopen als gevolg van een beroerte, en studies met gezonde deelnemers. En we beginnen met het onderzoeken van de meest belangrijke "verzamelaars" van de tast, de vingers.

Tastlokalisatie

In **hoofdstuk 2** hebben we onderzocht hoe gezonde mensen (verder aangeduid als "proefpersonen") aangeraakte plekken op de huid konden lokaliseren, zonder dat ze daarbij konden zien waar ze aangeraakt werden. Een belangrijke bevinding uit de literatuur is dat de huid van de vingers meer gevoelig is voor tastinformatie, dan de hand en de arm. Het lokaliseren van tastprikkels is op meerdere manieren onderzocht maar tot nu toe heeft niemand nauwkeurig gekkeken naar hoe we met de wijsvinger van de andere hand naar de aangeraakte plek kunnen wijzen. Op deze manier kan worden onderzocht hoe mensen tastinformatie gebruiken in interactie met hun eigen lichaam. Ook geeft deze methode de mogelijkheid om te kijken waar mensen wijzen vlak voor ze op de huid landen, en hoe mensen tastinformatie gebruiken om correcties te maken. Zoals verwacht vonden we dat er minder wijsfouten gemaakt werden naar tastprikkels op de gevoelige gebieden (vinger) in vergelijking met de minder gevoelige gebieden (arm). Echter, tegen onze verwachtingen in vonden we geen meetbaar verschil in wijsfouten tussen de vinger en de hand. Dit gebrek aan verschil in wijsfout tussen hand en vinger was alleen aantoonbaar vlak voordat de wijzende vinger op de huid was geland, dus nog voordat er correcties plaatsgevonden hadden. Nadat proefpersonen konden corrigeren en dachten de juiste plek gevonden te hebben was dit verschil er wel. Blijkbaar waren ze in eerste instantie niet helemaal in staat dicht in de buurt van de juiste plek terecht te komen. Voor de hand en de arm waren de correcties veel kleiner dan die voor de vingers. Wij denken dat dit komt omdat de gevoeligheid van de vingers het toelaat om nog correcties te maken, terwijl dat voor de hand en arm in mindere mate geldt. Blijft over de vraag waarom proefpersonen dan niet in eerste instantie direct dicht in de buurt van de juiste plek terecht komen. Een mogelijkheid is dat de vinger een dergelijk smal oppervlak is, dat men onzeker is of het doel (de vinger) wel wordt geraakt. Nadat men "bewijs" heeft dat de vinger is geraakt kan het zoeken naar de juiste plek beginnen. Wat opvalt, is dat de fouten op de vinger vooral in de links/rechts (horizontale) richting werden gemaakt waarbij fouten soms zo groot waren dat de landing eigenlijk bijna op de buurvinger was. Dit kan suggereren dat de proefpersonen onzeker waren over welke vinger aangeraakt werd. Het is eerder gesuggereerd dat vingers overlappende receptieve velden hebben (Schweizer et al., 2000). Een receptief veld kan gezien worden als een deel van de ruimte (hier bepaald door een deel van de huid/ segment) wat waargenomen wordt door één zenuwcel (neuron). Wanneer een neuron gevoelig is voor informatie uit een segment dat op twee naburige vingers ligt, wordt de cel geactiveerd zowel bij een tastprikkel op de ene, als op de andere vinger. Dit kan ervoor zorgen dat het

moeilijk wordt voor de proefpersoon om te voelen van welke vinger de prikkel vandaan komt. Zoals verwacht laten de bovenstaande resultaten zien dat de aangeraakte plekken op de vingers beter gelokaliseerd worden dan die op de arm. Echter, we hadden ook verwacht een duidelijk verschil te meten in de hoeveelheid fouten tussen de aanwijzingen op de vingers en die van de hand wat we niet hebben kunnen aantonen. Daarbij vinden we dat er meer correcties worden gemaakt in horizontale richting voor locaties op de vinger dan op de hand en arm. Wellicht is de betere gevoeligheid van de vingers ten opzichte van de hand niet afdoende om de tastinformatie beter te lokaliseren en spelen er mogelijk andere factoren, zoals het voorkomen van vingeroverlappende receptieve velden, een rol. In **hoofdstuk 3** hebben we specifieker gekeken naar de lokalisatie van tastinformatie voor de vingers wanneer er gebruik gemaakt zou worden van een perceptierespons (in tegenstelling tot een, wijsrespons (actie) zoals hierboven). Eerder onderzoek toont aan dat de verwerking van tastinformatie door de vingers beïnvloed wordt door de onderlinge positie van de vingers. Om die reden hebben we het lokalisatievermogen onder verschillende condities gemeten, namelijk met de vingers helemaal gespreid, met de vingers dicht naast elkaar, en met de vingers van de linker en rechterhand door elkaar. Voor die laatste positie moesten de handen op elkaar gelegd worden (zie H3 Figuur 1C). Daarbij waren we vooral geïnteresseerd in de vraag of vinger overlappende receptieve velden echt verbonden zijn met de locatie op de huid (het huidsegment), of ook met de ruimte direct rondom de vingers. Hiervoor werden proefpersonen zonder dat ze hun handen zagen, aangeraakt op 1 van 30 posities op de vingers (3 per vingertop). Op een kaart waarop 2 handen en 10 vingers en alle stimulatiepunten (genummerd) getekend waren, kon er door het noemen van het betreffende nummer aangegeven worden waar de tastprikkels gevoeld werd (zie Figuur H3D). Uit de oorspronkelijke studie bleek dat als er fouten gemaakt werden, deze fouten vaker in de buurt lagen van de vinger waarop de stimulatie had plaatsgevonden dan ergens anders. Dus, als er een puntje op de middelvinger werd gestimuleerd, dan werd er in het geval van een fout antwoord vaker een nummer van een punt op de ring of de wijsvinger van dezelfde hand genoemd, dan een ander punt. Dit resultaat werd uitgelegd aan de hand van vingeroverlappende receptieve velden. Doordat de tastprikkels hersencellen van niet 1 maar 2 of misschien wel 3 naastliggende vingers activeerde, was de kans dus groot dat een fout antwoord terecht op 1 van die “mede geactiveerde” vingers terecht kwam. Om uit te zoeken of die vingeroverlappende receptieve velden bepaald worden door een bepaalde ruimte tussen de vingers, hebben we dezelfde taak herhaald. Hierbij varieerde we de ruimte tussen de vingers, namelijk 1) vingers gespreid, 2) vingers tegen elkaar aan en 3) 2 handen op elkaar en vingers “gemengd” (vingers van de ene hand afwisselend met vingers van de andere hand). Als die variatie in ruimte invloed zou hebben op het foutenpatroon, dan zou het erop wijzen dat de receptieve velden ook, of misschien zelfs alleen maar ruimtelijk bepaald zijn. Uit de resultaten blijkt dat wanneer de vingers gespreid zijn er minder fouten worden gemaakt in vergelijking met de vingers bij elkaar en de vingers gemengd. Echter, de vermindering van fouten was niet specifiek voor de naburige vingers. In het oorspronkelijke experi-

ment van Schweizer et al., (2000) waren er meer fouten gemaakt naar de buurvingers dan naar andere vingers. Als je die buurvingers nou ver van de gestimuleerde vingers houdt, dan zou je dus ook verwachten dat er minder foute antwoorden op die buurvingers terecht zouden komen. Dit was alleen niet het geval daar er over het algemeen minder fouten werden gemaakt. Dus er vond ook een vermindering plaats van het aantal foute antwoorden die terecht kwamen op de vingers die ver weg lagen van de gestimuleerde vinger. Het lijkt er dus op dat het spreiden van de vingers er voor zorgt dat de tastprikkel beter wordt verwerkt. Een verklaring hiervoor zou kunnen liggen in het feit dat iedere vinger meer geïsoleerd is wanneer alle vingers gespreid zijn. Daarnaast is er meer huidcontact wanneer je de vingers tegen elkaar, of gemengd hebt. Dit huidcontact geeft zelf ook tastinformatie en kan een storende invloed gehad hebben. Dus, niet het vergroten van de ruimte tussen de vingers zorgt dat de informatie beter verwerkt wordt, maar het minimaliseren van huidcontact van de eventuele buurvingers. In **hoofdstuk 4** en **5** hebben we explicet gekeken naar het verschil tussen het lokaliseren van tactiele prikkels door er direct op de eigen hand naar te wijzen en indirect door aan te geven op een tekening van de hand waar de gestimuleerde locatie zich bevindt⁴. Zoals aangegeven in de introductie lijkt het erop dat het verwerkingsproces van tastinformatie voor het programmeren van een directe handeling anders is dan het verwerkingsproces van tastinformatie voor het herkennen. Ook bestaat het idee dat deze processen redelijk onafhankelijk zijn en dat er twee verschillende routes in de hersenen bij deze processen betrokken zijn. Hieruit volgt dat de gebieden in de hersenen die betrokken zijn bij de verwerking van tast voor actie nog steeds (deels) hun functie uit kunnen oefenen ook als de delen voor de "herkenningsstaak" beschadigd zijn. De resultaten van twee patiënten met hersenbeschadiging ondersteunen deze redenering. Eén patiënt had problemen om een bewust waargenomen tastprikkel te lokaliseren door er direct met zijn andere wijsvinger naar te wijzen. Daarbij was hij wel goed in staat om aan te geven waar hij was aangeraakt wanneer hij dit op een tekening van de hand mocht aangeven. Een ander patiënt daarentegen had geen problemen met het aanwijzen van een bewust waargenomen tastprikkel op haar eigen hand, maar presteerde slechter dan verwacht wanneer ze de locatie op een tekening van de hand moest aangeven. Beide patiënten waren dus in staat tactiele informatie te verwerken, maar alleen niet meer voor perceptie en actie tegelijkertijd. In **hoofdstuk 5** hebben we nogmaals drie patiënten onderzocht die problemen hadden met het herkennen van hun eigen vingers (vingeragnosie). Dat betekent dat wanneer de proefleider een vinger aanwees de patiënt niet kon vertellen welke vinger het was, ook al konden de namen van alle vingers probleemloos worden opgenoemd en de rest van de lichaamsdelen probleemloos worden herkend.

⁴ Wijzen naar een locatie op een tekening van de hand betekent hier een herkenning, de locatie van de prikkel moet namelijk geschaald worden van eigen hand-coördinaten naar visuele coördinaten zoals gedefinieerd door de tekening van de hand.

De vraag is nu, “kunnen deze patiënten nog wel de juiste vinger aangeven door er naar te wijzen?”. Net als in hoofdstuk 4 werd er gevraagd direct naar de aangeraakte vinger te wijzen, en naar de vinger op een tekening van de hand. De resultaten van drie patiënten toonden aan dat het aanwijzen van de aangeraakte vinger nauwelijks problemen gaf indien de wijsbeweging gericht was naar de eigen hand. Echter, wanneer de wijsbeweging werd gemaakt om op een kaart aan te geven welke vinger er aangeraakt werd, ging dit stukken slechter. Hierbij ging het er niet om dat de patiënt de exacte locatie van de aanraking kon aangeven, maar ging het er alleen om de vinger uit de set van 10 te selecteren. Dit onderzoek toont aan dat het onderscheid tussen de verwerking van tast voor een handeling en tast voor herkenning niet alleen geldt voor een locatie op de huid, maar ook voor een geheel lichaamsdeel zoals de vinger.

Illusies en mentale voorstelling van tast

In **hoofdstuk 6** hebben we een patiënt met vingeragnosie specifieker getest op een aantal tast-taken. Hoe komt het nu dat patiënten het vermogen verliezen om hun eigen vingers te herkennen terwijl de herkenning van de andere lichaamsdelen niet gestoord is. Onderzoek heeft aangetoond dat een mogelijke verklaring ligt in het vervagen van de grenzen tussen representaties van de vingers in de hersenen. Dit als gevolg van de hersenbeschadiging. Alleen, waar en hoe vindt deze vervaging dan plaats? Als er echt een samensmelting tussen de vingers zou zijn, dan zou je verwachten dat we een tastprikkel niet meer kunnen koppelen aan de vinger die de tastprikkel ontving. In dit hoofdstuk hebben we middels twee tastexperimenten onderzocht of een patiënt met vingeragnosie nog in staat was om een tastprikkel te koppelen aan de vinger die deze prikkel ontving. In het ene experiment werd er explicet gekeken of de patiënt in staat was de tast-informatie, verzameld door 6 vingers, te integreren tot de waarneming van 1 voorwerp (een lijn). In het andere experiment werden er tegelijkertijd 2 tastprikkels (een scherpe punt en een speldenknop) gegeven op 2 naburige vingertoppen. De hand lag hierbij te rusten op een tafel met de handpalm naar beneden, en de vingers gericht naar de proefleider (zie H6 Figuur 4). De onderlinge posities van de twee vingers die de tastprikkel kregen werden gevarieerd tot ze zelfs volledig over elkaar heen gekruist werden (bv vingers naast elkaar, vingers boven elkaar, vingers gekruist). De patiënt had de taak om de positie van de scherpe punt te beoordelen relatief ten opzichte van de speldenknop. Om dit foutloos te kunnen is het noodzakelijk de positie van de vinger en de tastprikkel aan elkaar te koppelen. De resultaten lieten zien dat de patiënt in de eerste taak in staat was om tastinformatie te koppelen aan de juiste vingers en deze informatie te integreren tot een object. Hetzelfde werd gevonden in het tweede experiment; de patiënt was in staat om de twee tactiele prikkels op de twee naburige vingers uit elkaar te houden en de positie ervan weer te geven. Dit suggereert dat de vingers bij deze patiënt niet “samengesmolten” zijn op het niveau van het verzamelen van tastinformatie. Echter, in tegenstelling tot gezonde controle proefpersonen maakte de patient juist minder fouten wanneer de positie van de scherpe punt beoordeeld moest worden in een vingers gekruiste positie. Dit is een normale

fout die optreed bij ons allemaal. Op het moment dat we 2 vingers van 1 hand over elkaar heen kruisen dan nemen we tactiele informatie waar alsof onze vingers gewoon ongekruist naast elkaar liggen. Een mogelijke verklaring hiervoor is dat we niet gewend zijn om met gekruiste vingers tastinformatie te verzamelen. In deze voor ons onbekende situatie interpreteren we de informatie op basis van onze lichaamsrepresentatie. Deze lichaamsrepresentatie is gebaseerd op eerder opgedane ervaring waarin onze vingers zelden tot nooit gekruist zijn. Met als gevolg dat we de tastinformatie waarnemen alsof onze vingers zich gewoon naast elkaar bevinden. Wat zegt dit nu over de prestatie van onze patiënt met vingeragnosie? Onze patiënt maakt geen gebruik van de standaard lichaamsrepresentatie waarin "opgeslagen" ligt dat onze vingers normaal niet gekruist zijn. Zij beoordeelt ook in de vingers gekruiste positie de scherpe prikkel goed. Op basis hiervan suggereren we dat opgeslagen kennis en ervaring over de vingers, zoals de volgorde waarin de vingers staan, de normale posities etc., niet toegankelijk is. Dit past goed bij de locatie van de hersenbeschadiging van deze patiënt en van andere vingeragnosie patiënten. De betreffende locatie is namelijk onderdeel van een netwerk waarvan vermoeden bestaat dat deze betrokken is bij de waarneming van ons eigen lichaam. Dit netwerk zou je kunnen zien als een representatie van het lichaam en "bevat" informatie over afmetingen van lichaamsdelen, de structuur en vorm van het lichaam, maar wellicht ook functionele standaard houdingen. In **hoofdstuk 7** hebben we onderzocht of het mogelijk is om opgeslagen ervaring en kennis over hoe een tastprikkel aanvoelt ook kunnen aanboren zonder dat er daadwerkelijk een tastprikkel aanwezig is. Door middel van ons mentaal voorstellingsvermogen kunnen we ons voorstellen hoe een tastprikkel aanvoelt. Probeer maar eens voor te stellen dat we met onze handen langs een bakstenen muur wrijven, of door een hoop dorre bladeren woelen. Om aan te tonen dat dit soort voorstellingen direct betrekking heeft op ons tastsysteem, hebben we gekeken of er een relatie bestaat tussen het voorstellen van een tastprikkel en het waarnemen van een echte tastprikkel. Voor andere zintuigen zoals geluid en zicht is het aangetoond dat er een relatie bestaat tussen het voorstellen van een geluid of beeld en het waarnemen van een echt geluid of beeld. Tijdens een experiment hebben we proefpersonen de opdracht gegeven om zich een tastprikkel voor te stellen. Bijvoorbeeld het gevoel dat je aan je handen krijgt als je door een bak grind gaat. Direct daarna werd er een echte tactiele prikkel gegeven, ofwel een tik op 1 van de vingers van de linkerhand, ofwel een tik op 1 van de vingers op de rechterhand. De opdracht voor de proefpersoon was om aan te geven of deze tik links of rechts kwam. De resultaten lieten zien dat wanneer er direct voor het geven van de prikkel een tatsensatie werd voorgesteld, de reactietijden op de echte tactiele prikkel sneller waren dan wanneer er een geluidssensatie werd voorgesteld. Precies zo werd er sneller gereageerd op een geluidsprikkel wanneer er een geluidssensatie werd voorgesteld dan wanneer er een tastprikkel werd voorgesteld. De relatie tussen het voorstellen van bepaalde zintuiglijke informatie en het verwerken van echte informatie lijkt te suggereren dat de twee door dezelfde processen en wellicht ook hersendelen worden ondersteund. Voor de visuele en geluidsvoorstelling was dit gegeven al bekend, voor de tastzin daarentegen was dit effect nog niet eerder gerapporteerd.

In **hoofdstuk 8** tenslotte hebben we gekeken naar het effect van een tactiele illusie op de verwerking van tast in een perceptietak en een actietak. Hiervoor maakten we gebruik van Weber's illusie. Deze kun je zelf ervaren door twee duidelijke punten op een afstand van bijvoorbeeld 3cm op de hand te zetten, en deze vervolgens over de handpalm, de pols en de onderarm te schuiven. Je krijgt dan het gevoel alsof de afstand tussen de twee punten kleiner wordt, terwijl dat in werkelijkheid niet zo is. In het experiment kregen gezonde proefpersonen op de palm van hun hand of op hun onderarm blokjes gelegd van 2.5cm hoogte, 2cm breedte en variërende lengte (4, 5, 6, 7, 8cm). De geblinddoekte proefpersoon werd opgedragen om het blokje wat op de hand of onderarm lag met de duim en wijsvinger van de andere hand te grijpen (actie), of de grootte (lengte) van dit blokje te schatten (perceptie). Dit schatten gebeurde door de opening tussen de duim en wijsvinger van de andere hand zo aan te passen dat het correspondeerde met de waargenomen grootte van het blokje. De resultaten lieten zien dat de onderschatting die plaatsvond voor blokjes op de arm ten opzichte van zo'nzelfde maat blokje op de hand alleen te zien was in de schatrespons. Op het moment dat zo'n blokje gegrepen werd was deze onderschatting er niet, maar was de opening tussen duim en wijsvinger juist veel groter dan wanneer datzelfde blokje op de hand lag en hiernaar gegrepen moest worden. Dit suggereert dat de illusie een meetbaar groter effect had op de schat (herkenning) respons dan op de grijprespons (handeling). Net als voor de visuele informatieverwerking tonen de resultaten van dit onderzoek aan dat een tastillusie meer vat heeft op een perceptierespons dan op een actierespons. Dit was al eerder aangetoond in onderzoek waarbij een visuele illusie gebruikt werd waarvan een tastvariant was gemaakt. Hierbij is het niet uit te sluiten dat er ook visuele hersengebieden actief zijn geweest. Dit onderzoek daarentegen laat het effect zien met een pure illusie van de tastzin.

Conclusie en aanbevelingen

Het hier beschreven onderzoek ondersteunt dat perceptie en actie onafhankelijk van elkaar kunnen opereren, ook binnen de tastzin. Dit hebben we gevonden voor de verwerking van informatie vanaf het niveau van een eenvoudige tastprikkel op de hand, tot een complexere prikkel zoals een voorwerp (blokje) of een lichaamsdeel (een vinger). Dit suggereert niet dat deze twee systemen dit ook altijd in het dagelijks leven doen. Informatie wordt verwerkt door netwerken in de hersenen, en een kenmerk van dit soort netwerken is dat de verschillende hersengebieden onderling met elkaar, maar ook met andere netwerken verbonden zijn. Blijft over de vraag hoe de twee systemen met elkaar verbonden zijn. Bijvoorbeeld in wat voor situaties is het verwerken van tastinformatie voor een actie gevoelig voor een tactiele illusie, of voor perceptie juist niet. Daarbij is het ook nog de vraag of het verschil tussen een actierespons en een perceptierespons wel zo absoluut is. Wellicht kunnen we het tastsysteem beter onderzoeken aan de hand van een model wat ook nog tussenstappen toelaat. Meer inzicht in hoe tastinformatie verwerkt wordt is niet alleen van groot belang voor het vergaren van fundamentele kennis. Onderzoek is ook nodig om inzicht te krijgen in

hoe de tastzin gestoord kan raken, en wat de gevolgen daarvan kunnen zijn voor bijvoorbeeld de motoriek. Jaarlijks krijgen in Nederland 35000 mensen te kampen met tast- en motoriekstoornissen als gevolg van het doormaken van een beroerte. Het gecombineerd aanpakken van deze stoornissen zou het herstel ervan kunnen verbeteren. De laatste jaren wordt er veelvuldig onderzoek gedaan naar de effecten van het mentaal inbeelden van beweging in de sport en in de revalidatie. Wellicht biedt mentale voorstelling van tast een opening om de revalidatie van tast en motoriekstoornissen nog verder te verbeteren.

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Publications & Conference Proceedings

International publications

- Dijkerman, H.C., McIntosh. R.D., **Anema, H.A.**, de Haan, E.H., Kappelle, L.J. & Milnder, A.D. (2006) Reaching errors are linked to eye position rather than head or body position. *Neuropsychologia* 44(13), 2766-2733.
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- Anema, H.A.**, Kessels, R.P., De Haan, E.H., Kappelle, L.J. Leijten, F. S., Van Zandvoort, M.J., and Dijkerman H.C. (2008). Differences in finger localisation performance in patients with finger agnosia. *NeuroReport* 19(14), 1429-1433.
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- Anema, H.A.**, de Haan, A.M. & Dijkerman, H.C. Thinking touch: Tactile imagery influences tactile processing. (Under review).
- Anema, H.A.**, Habets, E., & Dijkerman, H.C. Localising tactile stimuli on arm hand and fingers by means of pointing movements. (Submitted).
- Anema, H.A.**, Overvliet, K.E., Smeets, J.B., Brenner, E., and Dijkerman, H.C. Integration of tactile input across fingers in a patient with finger agnosia. (Submitted)
- Overvliet, K.E., **Anema, H.A.**, Brenner, E., Dijkerman, H.C. & Smeets, J.B. Finger position influences whether you can localize tactile stimuli. (Under review).
- Smeets, M. A.M., Klugkist, I., van Rooden, S., **Anema, H.A.** & Postma, A. Disturbed mental scanning of body images in a subclinical eating disorders population. (Submitted).

National publications

- Anema, H.A.** & Dijkerman (2006) Lichaam en Perceptie. De Psycholoog(41), 418-119
Kessels, R.P.C., **Anema, H.A.**, & Dijkerman, H. C. (2006). Het Gerstmannsyndroom: Een stoornis in de mentale verbeelding of een verstoorde lichaamsrepresentatie. Tijdschrift voor Neuropsychologie: diagnostiek, behandeling en onderzoek. 1(1), 42-47

Abstracts, Oral presentations and Conference

Proceedings (selection)

- Anema, H.A.**, Wolswijk V.W.J., and Dijkerman, H.C. (2006) Task dependent effects of Weber's illusion. Poster presented at the joint EPS/NVP meeting, Birmingham, UK, 63.
- Anema, H. A.**, Kessels, R. P. & Dijkerman, H.C. (2006). Investigations of impairment in finger representation in a patient with Gerstmann's syndrome. Poster presented at the Second Meeting of the European Societies of Neuropsychology, Toulouse, France, 290.
- Anema, H. A.**, Overvliet, K. Peeters, M., Vd Ploeg, N.B., Pelleboer, F.B., Meijer E. and ^{12}H . Chris Dijkerman (2007) Tactile imagery: Effects on tactile mislocalisation? Poster presented at European Workshop on Imagery and Cognition, Utrecht, The Netherlands.
- Anema, H.A.**, Overvliet, K.E., Smeets, J.B.J., Brenner, E., and Dijkerman, H.C. (2008). Integration of tactile input across fingers in a patient with finger agnosia. Poster selected for oral presentation at the twenty-sixth European Workshop on Cognitive Neuropsychology, Bressanone, Italy.
- Anema, H.A.** Touching upon tactile processing: Independent processing of action and perception? (2008). Invited speaker at the monthly seminar of Grup de Recerca Neurociència Cognitiva, Parc Científic de Barcelona.
- Anema, H.A.**, de Haan, A.M. & Dijkerman, H.C. (2008). Thinking touch: unraveling the mechanisms behind tactile imagery. Poster presented at the First Meeting of the Federation of the European Societies of Neuropsychology, Edinburgh, UK.

Contributions in national meetings:

Helmholtz Retraite 2005 (poster), 2007 (oral presentation); NWO summer school Doorwerth 2005 (poster), 2006 (poster). NVP winter conference 2005 (poster), 2007 (poster); UMCUtrecht 2007 (oral presentation). Helmholtz PhD meeting 2007 (oral presentation).

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Lieve Jo, jij was al mijn paranimf van af het allereerste begin. Jouw bijdrage aan dit proefschrift is niet in woorden uit te drukken, onze vriendschap zegt genoeg.

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Curriculum Vitae

Helen Alexandra Anema was born in Breda, the Netherlands on December 1st 1977. In 1996 she finished the Atheneum at Onze Lieve Vrouwe Lyceum, Breda. As part of her physiotherapy study she worked as a junior physiotherapist at the orthopedics ward of Southampton General Hospital and at Victoria House for neurorehabilitation in Southampton, UK. In 2000 she received a diploma in Physiotherapy at the Fontys Hogeschool Eindhoven. During a 4 year Psychology training at Tilburg University she worked as a research assistant at the department of Psychonomics. After succeeding the first year, she followed a separate course program with extra courses in neuropsychology, neuroanatomy (Radboud University, Nijmegen) and psychonomics. Part of her Master thesis was done at the Martinos Center for Biomedical Imaging in Boston, USA and she obtained her Masters Degree in Psychology in 2004. In that same year she started her PhD research on the somatosensory system at the department of Experimental Psychology at Utrecht University and collaborated with the Neurology Department of the University Medical Center Utrecht, with the Movement Sciences department of the Free University of Amsterdam, and with the Grup de Recerca Neurociència Cognitiva, Parc Científic de Barcelona Universitat de Barcelona in Spain. Currently she is working as a researcher at the department of Experimental Psychology at Utrecht University.

Helen Alexandra Anema werd geboren in Breda op 1 December 1977. Na het behalen van haar VWO diploma aan het Onze Lieve Vrouwe Lyceum te Breda begon zij in 1996 aan haar opleiding fysiotherapie aan de Fontys Hogeschool in Eindhoven. Als onderdeel van een stage heeft ze gewerkt als junior fysiotherapeut op de afdeling Orthopedie van het Southampton General

Hospital en in het Victoria House for Neurorehabilitation, beide te Southampton, Engeland. Na het diploma fysiotherapie te hebben ontvangen, begon ze in 2000 aan haar studie Psychologie aan de Universiteit van Tilburg. Na het behalen van de propedeuse in 2001 begon ze aan een vrij doctoraal met extra vakken in de Neuropsychologie, Neur Anatomië (Radboud Universiteit Nijmegen) en Psychonomie en werkte ze als onderzoeksassistent bij het departement Psychonomie. Een deel van haar afstudeeronderzoek werd uitgevoerd op het Martinos Centre for biomedical imaging in Boston, USA waarna ze haar Masters degree kreeg in 2004. In datzelfde jaar begon Helen als aio bij het departement Psychologische Functieleer aan de Universiteit Utrecht. Daarbij werkte ze voor haar onderzoek naar de tastzin samen met de afdeling Neurologie van het Universitair Medisch Centrum Utrecht, met de faculteit Bewegingswetenschappen van de Vrije Universiteit Amsterdam, en met de Grup de Recerca Neurociència Cognitiva, Parc Cientific de Barcelona Universitat de Barcelona in Spanje. Op dit moment is ze werkzaam als onderzoeker bij het departement Psychologische Functieleer aan de Universiteit Utrecht.

